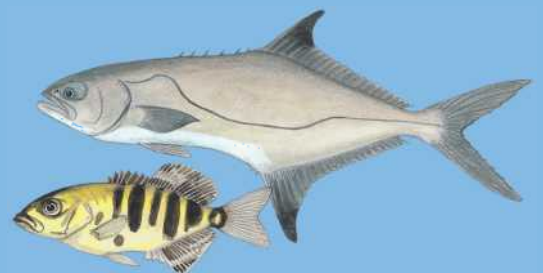
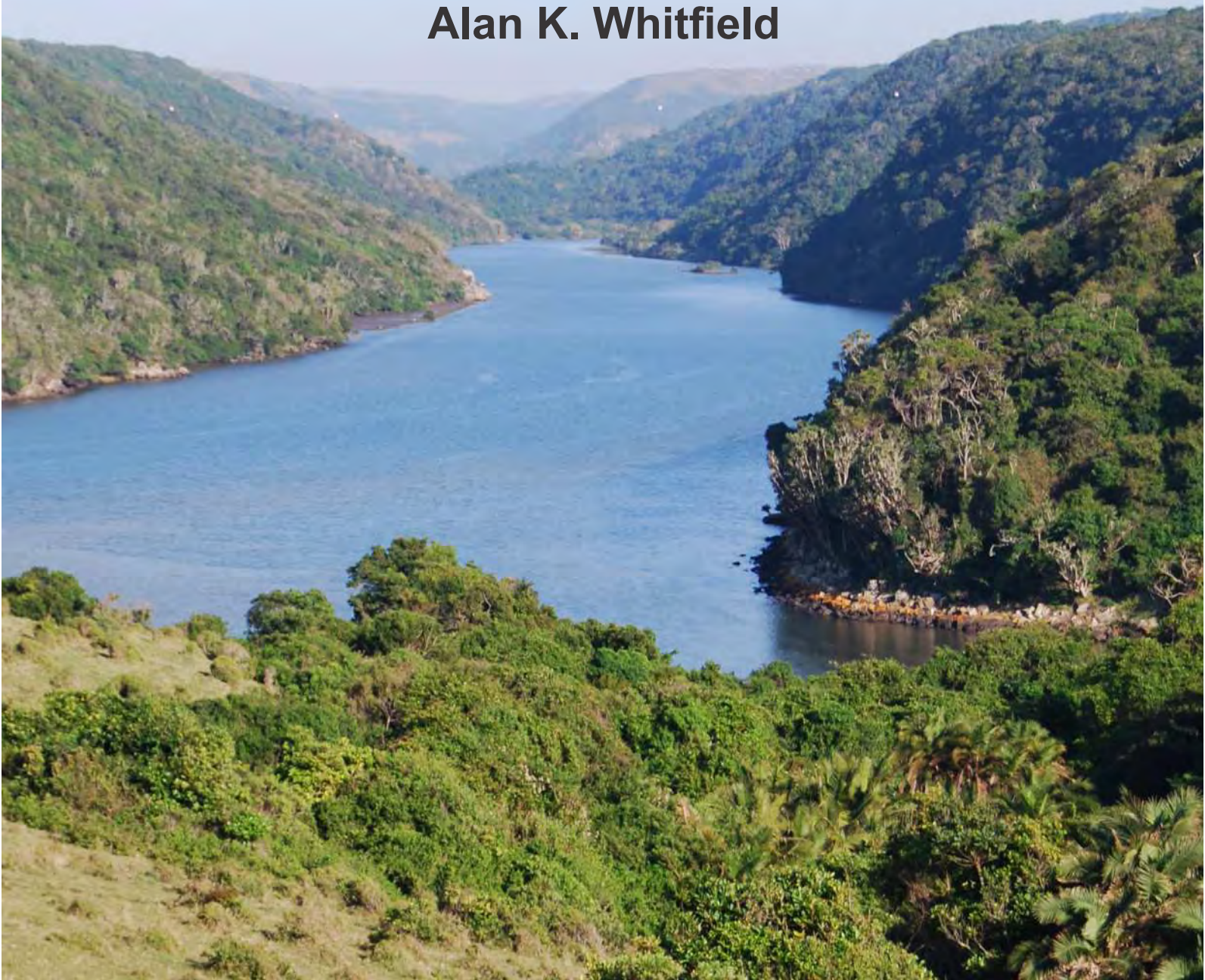


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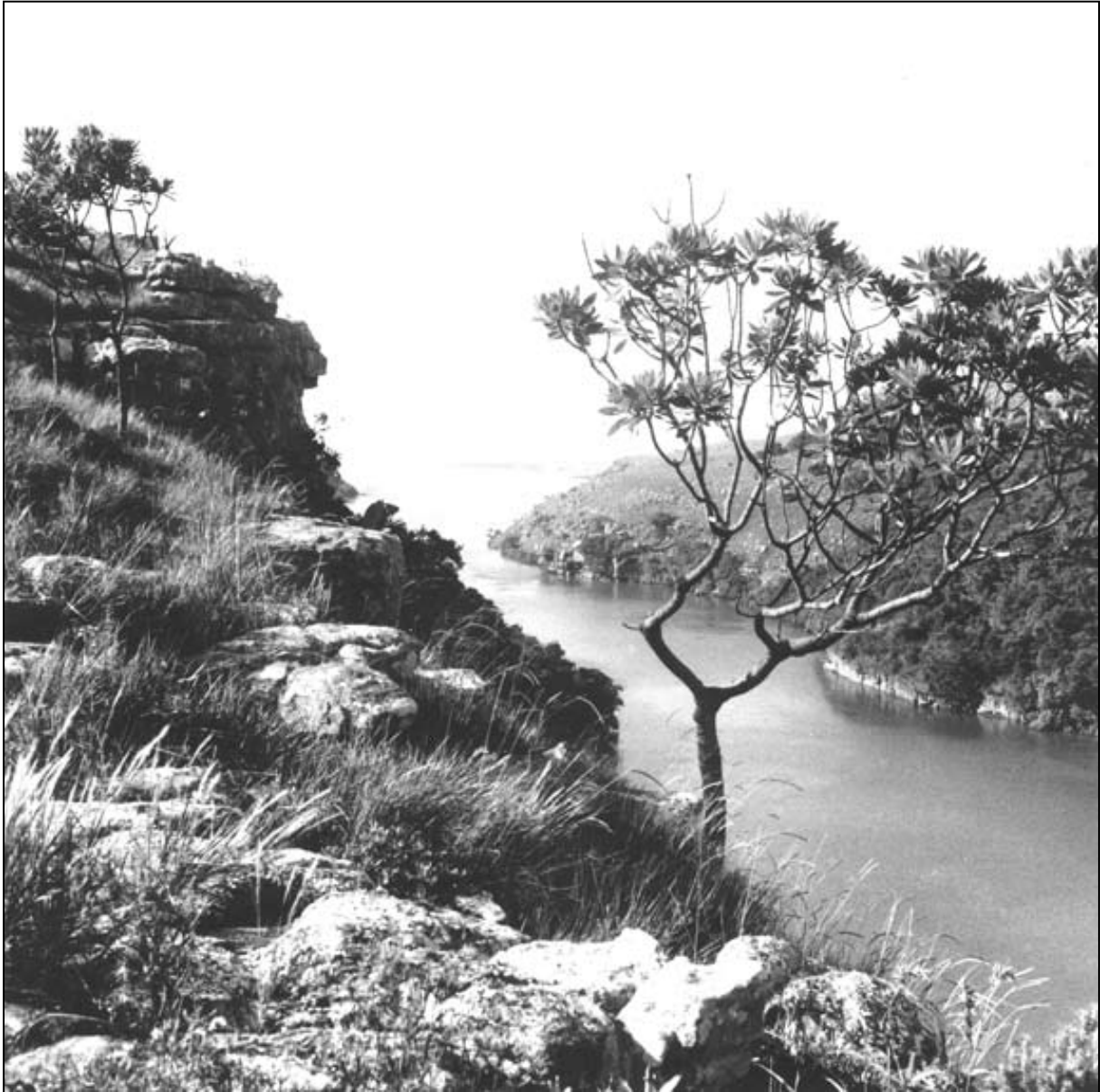
# **FISHES OF SOUTHERN AFRICAN ESTUARIES: from species to systems**

**Alan K. Whitfield**



# **Fishes of Southern African Estuaries: From Species to Systems**





In the beginning there were no estuaries  
In the end there will be no estuaries  
In between we have an opportunity to study and cherish one of  
the most fascinating aquatic environments on Earth

**Fishes of Southern African Estuaries:  
From Species to Systems**

**by**

**Alan K. Whitfield**



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Front cover: The lower Qhrorha Estuary, Eastern Cape Province (Photo: Alan Whitfield)  
and illustrations of the early juvenile and adult stages of selected southern African  
estuary-associated fish species (Artist: Elaine Heemstra)

Back cover: Underwater photographs of the estuary-dependent white steenbras *Lithognathus  
lithognathus* (Photo: Alan Whitfield) and dusky kob *Argyrosomus japonicus*  
(Photo: reeplifesurvey.com). Early juvenile and adult illustrations of selected estuary-  
associated fish species (Artist: Elaine Heemstra)

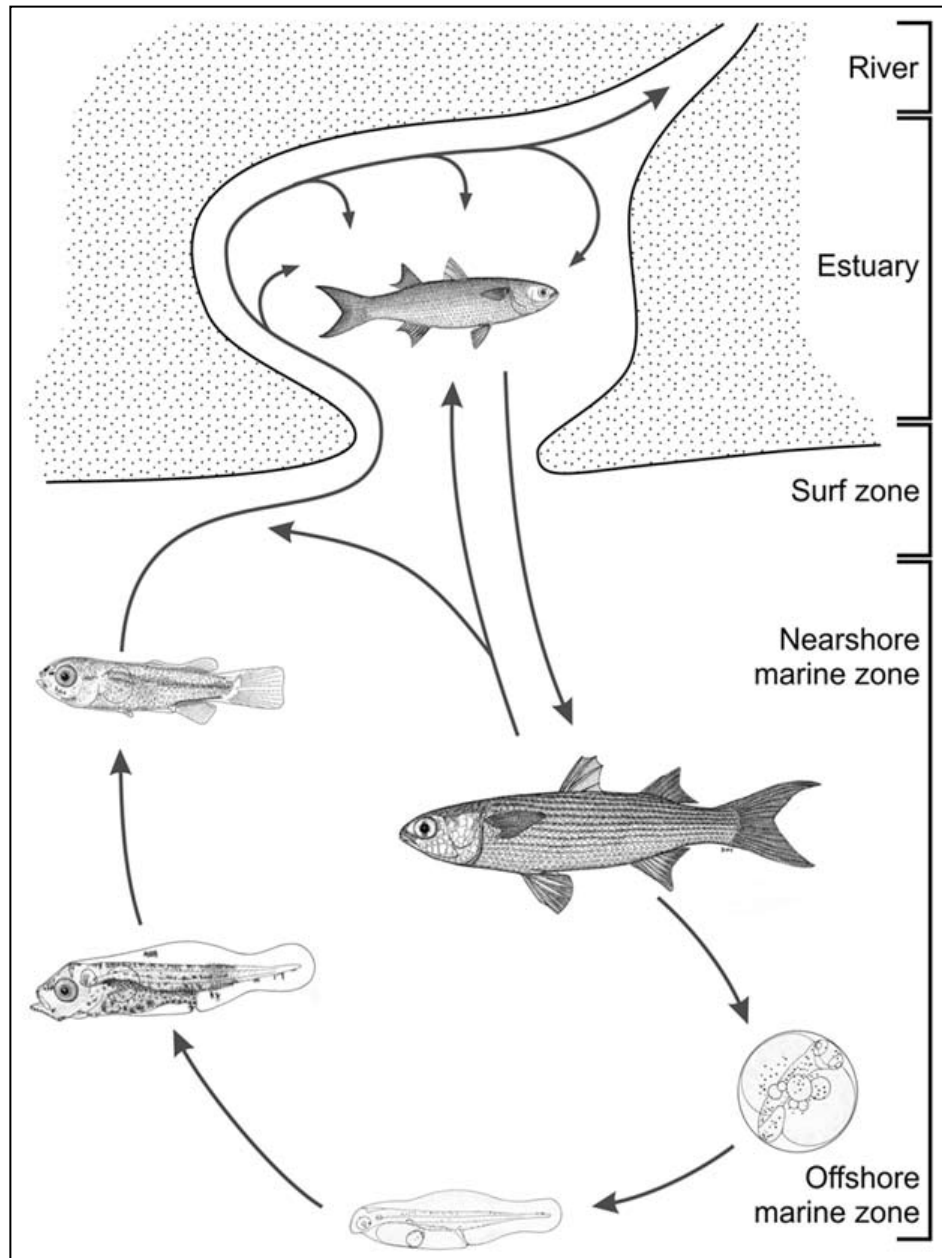
Frontispiece: Mtentu Estuary in 1952 (Photo: J.L.B. Smith)

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**This book is dedicated to:**

My family, scientific colleagues, postgraduate students and  
the fishes of southern African estuaries



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# Foreword

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This book is the culmination of forty years of dedicated research by the author in the many and varied estuaries of southern Africa. It is comprehensive in its treatment of the subject and copiously illustrated with beautiful photographs and many original diagrams. Southern Africa is blessed with a high diversity of estuaries, from small blind systems to very large coastal lakes, with a variety of physical attributes and fascinating fish faunas. Hence estuarine fish research in the region has been wide-ranging and detailed – there is little about fishes in estuaries that is not covered in this volume. The contents of the book are therefore of relevance to a worldwide readership, including scientists, fishers, conservationists and environmental planners.

The first chapter summarises the features of the many types of estuary and clearly sets out the history of estuarine fish research in southern Africa. Many of the characters who undertook or are undertaking the research are really brought to life in the text and photographs! Chapter 2 is wide ranging, including early life history of estuarine associated species, their recruitment into estuaries, influences of physical factors, zoogeography, and the guild approach to grouping fishes. It is clearly shown how the fish communities reflect the different physical nature of estuaries and that they tend to respond to these differences in a consistent way. Characteristics that make findings from the southern African situation relevant to the study of estuarine fishes throughout the world are well covered. This chapter also contains discussion of the evolution of estuarine fish communities, the influences of such phenomena as flooding and turbidity, and the ever-vexed question of estuarine dependence of fishes.

The third chapter contains species profiles of the most interesting of the fishes found in southern African estuaries. It summarizes available information on each fish and uses a guild approach to help in understanding the biology and ecology of each species. Chapter 4 highlights the key features of the various types of estuary and their relevance to the fish that utilise them. The important differences are discussed for each kind of estuary, ranging from small micro-estuaries to large coastal lakes.

The fifth chapter deals with environmental change and fish responses, using southern African case studies. As climate change is likely to have a large impact of southern African fish faunas, its effects occupy an important part of this chapter. Detailed information on the relationships between fish assemblages and the degree of coastal connectivity are discussed and the reasons for fish mortalities documented.

The final chapter looks at the conservation of estuarine fishes and their habitats. Given the various forms of degradation of most southern African estuaries (and throughout the world!), mainly from anthropogenic causes, conservation is a vital issue. The importance of the physical nature of the estuary is discussed as well as the maintenance of estuarine productivity. The vast St Lucia system is used as a case study to highlight the problems caused by declining freshwater supply, mouth manipulation and coastal development. The threats to estuarine fishes are many and increasing, including intense exploitation, both recreational and subsistence, and time is running out! The need for real conservation actions are discussed and the importance of reducing fishing pressure, promulgation of reserves and MPAs are clearly shown, together with the need for meaningful legislation, environmental planning and effective law enforcement.

Dr Stephen Blaber  
Brisbane, Australia

# Preface

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South Africa, despite its relatively small size, is often called “a world in one country”. This phrase arises mainly from the range of oceanographic and climatic features; geological and geomorphological attributes, the diversity of human cultures, languages, races and religions; the mix of developed and developing economies; the wide range in political opinion and parties; the vast array of mineral resources; and finally, what biologists find most interesting of all, the richness of the indigenous flora and fauna. Although southern African aquatic scientists cannot boast an equivalent of the Cape Floral Kingdom, the stretch of coast between northern Namibia and southern Mozambique has a particularly rich marine biota, accounting for almost 15% of all the coastal marine species known world-wide. The richness of the ichthyofauna is due to a number of factors, including the variety of habitats around the subcontinent, ranging from coral reefs, kelp beds, sheltered bays, sandy beaches, exposed rocky shores, coastal lakes to estuaries. In addition, southern Africa is the meeting place of three great oceans and is thus the recipient of species from each of these separate faunas.

In comparison to land vertebrates, the world's fish fauna is by no means well-known, either taxonomically or with regard to the biology of the component species. Apart from the very large number of fish species (estimated to be approximately 40 000), and the difficulties posed by the medium in which they live, there are other reasons for the above state of affairs. An obvious and universal reason is the shortage of funding available for taxonomic, biological and ecological studies, with increasing emphasis being placed on aquaculture, mariculture and fisheries related work. This situation is unlikely to improve and many research institutions around the world are operating on shrinking rather than expanding budgets. The onus of responsibility to disseminate information on the world's fish faunas therefore rests squarely on the shoulders of those who are fortunate enough to be employed in the fascinating field of ichthyology. This book, which is a major revision and expansion of an earlier monograph (Whitfield 1998), is an attempt to synthesize the available information on fishes associated with southern African estuaries and to highlight the importance of conserving these systems for both fishes and people of the region. Limited reference is made to international estuarine fish research due to space constraints and readers are referred to global ichthyological reviews in this regard.

The estuaries of southern Africa (defined as south of 26°S latitude for the purposes of this book) are highly diverse, both in terms of form and functioning. They range from the clear Kosi Estuary entering the coral rich subtropical Indian Ocean waters on the east coast, to the turbid Orange River flowing into the cool upwelled waters of the Atlantic Ocean on the west coast. The estuaries of the subcontinent are fed by catchments with a wide variety of climatic and geological characteristics. For example, the cool-temperate west coast is characterized by good winter rains and relatively dry summers, whereas on the subtropical east coast the opposite rainfall pattern prevails. While most south-western Cape estuaries are fed by rivers with low suspended sediment levels, those of KwaZulu-Natal normally carry high silt loads during the rainy season. Between Mossel Bay and St Francis Bay, rainfall patterns show no distinct seasonal peak and relatively acidic waters with low nutrient levels enter a variety of estuarine types along this section of the coast. The Eastern Cape is a region of transition between the subtropical and warm-temperate biogeographic provinces, and is prone to both droughts and floods occurring during any season of the year.

The southern African estuarine environment is an unpredictable and often harsh habitat to occupy, yet each year millions of larval and juvenile fishes enter and thrive in these systems. The fish species that utilize estuaries as nursery areas exhibit great diversity in size, body form, salinity tolerance, diet, habitat preference and breeding behaviour. There is also a complete gradation in terms of the dependence that each species has on the estuarine environment. These and many other issues relating to the biology and ecology of estuary-associated fish species in southern Africa are explored in the chapters to follow. It is my sincere wish that our improved knowledge of these species and their environmental requirements will contribute to the wise management and conservation of these valuable ecosystems.

Prof Alan Whitfield  
Grahamstown, South Africa

## Acknowledgements

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The contents of this book are drawn from past and present information about the fishes of southern African estuaries, some of which was published long before I embarked on a career in ichthyology. To the pioneer of estuarine ecology on the subcontinent, the late Professor John Day, and the pioneers of estuarine ichthyology, Drs Steve Blaber and John Wallace, I express my sincere gratitude for lighting the path for the rest of us to follow. I would also like to thank the late Professor Waldo Meester, Head of the Zoology Department at the University of Natal during the 1970s, for sharing his views with six young honours students. In his 1972 inaugural address to the university entitled *The Human Breakthrough* he stated “I would like to dream of a world in which our knowledge of nature is far more complete than it is now, and in which this knowledge is used for the betterment not only of mankind but of the natural world on which we depend”. Prof Meester’s dream is one that I fully endorse and, in turn, have conveyed to my students.

The bulk of this book draws on the last four decades of research, during which time numerous people have actively and unselfishly assisted me to explore the fishes of southern African estuaries. To all these friends and colleagues I express my sincere appreciation and gratitude. In particular, I should like to thank the following local ‘fishy people’ for their support, encouragement and collaboration; Lynnath Beckley, Alistair Becker, Steve Blaber, Anton Bok, Mike Bruton, Laure Carassou, Amber Childs, Allan Connell, Paul Cowley, Digby Cyrus, Trevor Harrison, Nikki James, Hennie Kok, Steve Lamberth, Mandla Magoro, Bruce Mann, Tim Martin, Angus Paterson, Deena Pillay, Ian Russell, Paul Skelton, Nadine Strydom, Leslie Ter Morshuizen, Taryn Murray, Leon Vivier, Rhett Bennett, Ryan Wasserman and Steve Weerts. A number of the above scientists are leading estuarine ichthyologists in their own right – without their contributions, this book would not have been possible. I would also like to acknowledge the hard work and valuable contributions made by numerous estuarine postgraduate students over the decades, some of whom I have had the privilege of working with in both a supervisory and co-worker capacity.

Elaine Heemstra and the late Dave Voorvelt deserve a special mention for their exceptional fish illustrations that have captured the character of the different species by virtue of meticulous attention to detail. I have enjoyed and appreciated greatly the opportunity of working closely with both these individuals but am also saddened that Dave is not able to witness the latest publication of his illustrations in this new format. Some outstanding fish illustrations (Mugilidae) by Denys Davis and Margaret Smith from the original *Sea Fishes of Southern Africa* also feature in this volume.

I would also like to acknowledge the use of some high quality photographs from a number of colleagues to illustrate the text, especially George Branch, Paul Cowley, Tatenda Dalu, Nicky Forbes and Ricky Taylor – in my opinion these pictures add considerable value to the aesthetics and possible interest by non-specialists in the book. Valuable advice in terms of ‘fine tuning’ the text were provided by my highly esteemed colleagues, Steve Blaber and Trevor Harrison – to both of you, my grateful thanks. The invaluable assistance provided by Susan Abraham with the figures, as well as page setting and indexing, is much appreciated.

To a large extent, the foundation for the current book is based on an earlier J.L.B. Smith Institute Ichthyological Monograph entitled the *Biology and Ecology of Fishes in Southern African Estuaries* (Whitfield 1998). That monograph is now two decades out of date, with numerous young and not-so-young estuarine ichthyologists having moved the discipline forward in leaps and bounds since then. It is my sincere hope that this synthesis will assist southern African estuarine scientists in obtaining processed baseline information from past work and facilitate their future research on our fascinating and dynamic estuarine ecosystems.

Funding and directorship support by Professors Brian Allanson, Mike Bruton, Paul Skelton and Dr Angus Paterson have been critical elements for all my scientific endeavours. Personal financial and infrastructural backing by Rhodes University for the period 1979-1987, the J.L.B. Smith Institute of Ichthyology from 1988-1999, and the South African Institute for Aquatic Biodiversity from 2000-2018 have been vital to the success of many of the studies reported here. The Foundation for Research Development (FRD) in the 1970s-1990s, and National Research Foundation (NRF) from the turn of the century to the present, also deserve a special mention. Finally, I would like to thank the Water Research Commission (WRC) for contributing to the funding of both fundamental and applied estuarine research over several decades. Without the support of my employers, directors and the above funding agencies, this book would not have been possible.

# Chapter I

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## Estuarine environment and ichthyological history

### 1.1 INTRODUCTION

SOUTHERN AFRICAN ESTUARIES, like the rivers that enter them, are primarily driven by the fundamental variables of water quantity, quality and movement, which in turn influence the type of substratum that prevails in different parts of each system (Reddering & Rust 1990). Fishes, like most other aquatic organisms, respond to these fundamental driving variables on spatial and temporal scales that will vary from one estuary to another (Elliott & Whitfield 2011). Central to the distribution and abundance of fishes in estuaries are the abiotic and biotic gradients that are established by the cycles of disturbance which continuously affect all estuaries (Nodo et al. 2017). Some disturbances may be small, such as the daily tidal regime, whereas others may be large, such as episodic river flooding.

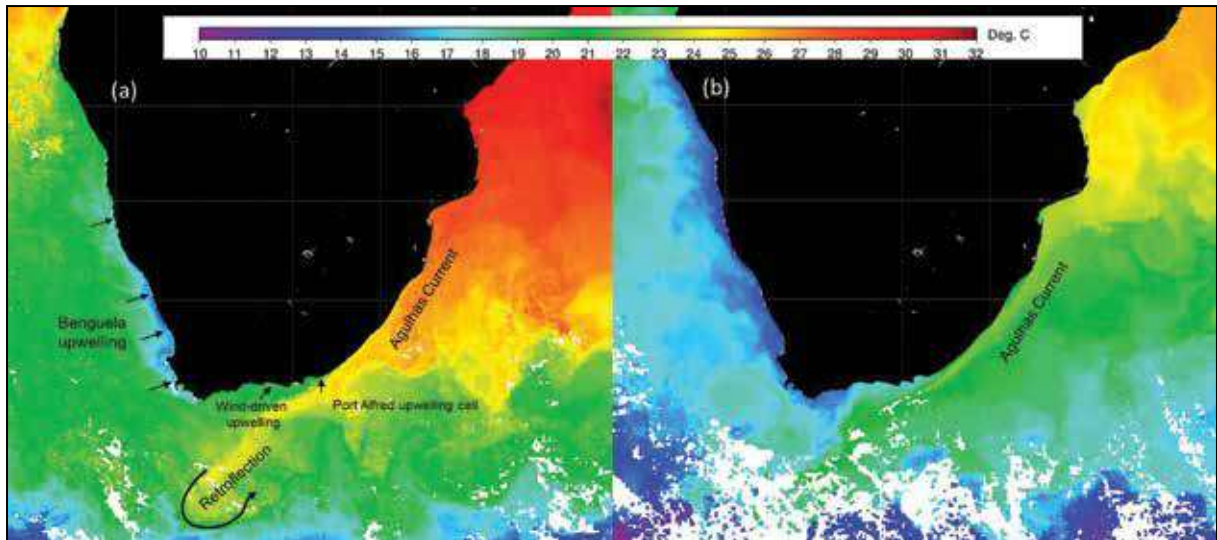
The nature of individual estuarine systems is directly related to the catchment and coastal environment characteristics in which they are located (Heydorn & Tinley 1980). This is particularly evident on the southern part of the African continent where sharply contrasting conditions occur (Heydorn & Flemming 1985). The coastal distance between the Orange River Estuary in the west and the Kosi Estuary in the east is approximately 3 000 km. To the west of Cape Agulhas the coastline borders on the South Atlantic and cool waters prevail. To the east of Cape Agulhas water temperatures increase markedly, with a transition from warm-temperate to subtropical waters occurring in the northern part of the Eastern Cape coast. These Indian Ocean waters are dominated by the warm Agulhas Current, which moves progressively further away from the coast as it flows southwards along the continental shelf margin. In contrast, the Atlantic west coast is driven by the upwelling of cool, nutrient-rich waters from the predominantly northward flowing Benguela Current regime (Figure 1).

The above oceanographic conditions also influence the coastal climate of southern Africa, with summer rainfall prevailing along the east coast, summer and winter rainfall along the south coast, winter rainfall along the southwest coast, and semi-arid conditions along the northwest coast. In general the east coast marine waters are characterized by great biotic diversity, whereas the more productive waters of the west coast have fewer species in greater profusion (Heydorn & Flemming 1985).

The geomorphology of coastal regions also has a profound influence on the type of estuarine environment (Figure 2). Because of the steep gradients, geology and heavy summer rainfall, the rivers of central and southern KwaZulu-Natal flow at a high velocity over a short distance, have greater cutting action and tend to carry a large sediment load. Rivers along the Tsitsikamma coast also tend to be short and steep, but they generally drain sandstone /quartzite formations and therefore carry relatively low silt loads. Some west coast catchments are little more than dry river beds and are only linked to the sea at times of exceptional rainfall. There are also profound differences between the vegetation surrounding the estuaries along the subtropical, warm-temperate and cool-temperate coasts (Heydorn 1989).

The number of estuaries in southern Africa varies according to which type of systems are included in the definition of an estuary. Based on information provided by Whitfield & Baliwe (2013), which deals primarily with functional South African estuarine systems from a fish perspective, their distribution along the coast is as follows; subtropical estuaries number 127, warm-temperate estuaries 127, and cool-temperate estuaries 26. Namibia has 20 river courses over a distance of about 1 000 km but these cannot be classified as functional estuaries because they





**Figure 1.** (a) A MODIS satellite sea surface temperature image in February 2009 (10 day average) illustrating the warm (red) Agulhas Current flowing down the east coast of southern Africa, the current retroflection at the southern tip of the continent, the location of the Port Alfred upwelling cell, wind-driven upwelling along the south coast and upwelling along the Benguela Current coastal region; (b) a MODIS satellite sea surface temperature image in July 2009 (10 day average) illustrating temperatures in winter (after James et al. 2013).



**Figure 2.** A typical southern African estuary, the predominantly open Mngazi system in the northern part of the Eastern Cape Province. This system is in the transition zone between the subtropical and warm-temperate biogeographic regions and is therefore most affected by changing fish composition due to global warming (Photo: Tris Wooldridge).

seldom contain any water. Langebaan Lagoon is classified as a coastal embayment type estuary for the purposes of this monograph, mainly due to freshwater input via aquifers and the presence of a predominantly estuarine biota.

From the above it is apparent that the eastern and southern coasts are better endowed with estuaries (Figure 3) than those in the western sector. Altogether, the approximately 290 functional estuaries around the South African coast make up about 70 000 ha of highly productive habitat (Turpie et al. 2002).

### **What is an estuary?**

During the first international conference on estuaries in 1964 there was wide support for the following definition: “An estuary is a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage” (Pritchard 1967). Although this definition catered for most northern hemisphere estuaries, sand bars are frequently formed at the mouths of many southern hemisphere estuaries during the drier periods of the year. These systems then are only opened by high riverine discharge or artificial methods for breaching the berm (Fromme 1985). During the often lengthy periods when they are closed, these so-called ‘blind’ estuaries do not have the free connection with the open sea, a factor considered to be crucial in Pritchard’s definition.

In order to accommodate the peculiarities of the above systems, Day (1980) redefined an estuary as “a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage”. However, this definition excludes estuaries such as Lake St Lucia that regularly experience hypersaline conditions, during which period the rivers cease to flow and little or no freshwater enters the system.

Heydorn (1989) defined an estuary as “that portion of a river system entering the sea where there is, within the boundaries of the land, a gradual transition in physical, chemical and biological characteristics from fresh water to sea

water”. Because most southern African estuaries are closed for much of the year and reversed salinity gradients can be a regular feature in several systems, the above definition is also of marginal use to estuarine scientists in the region.

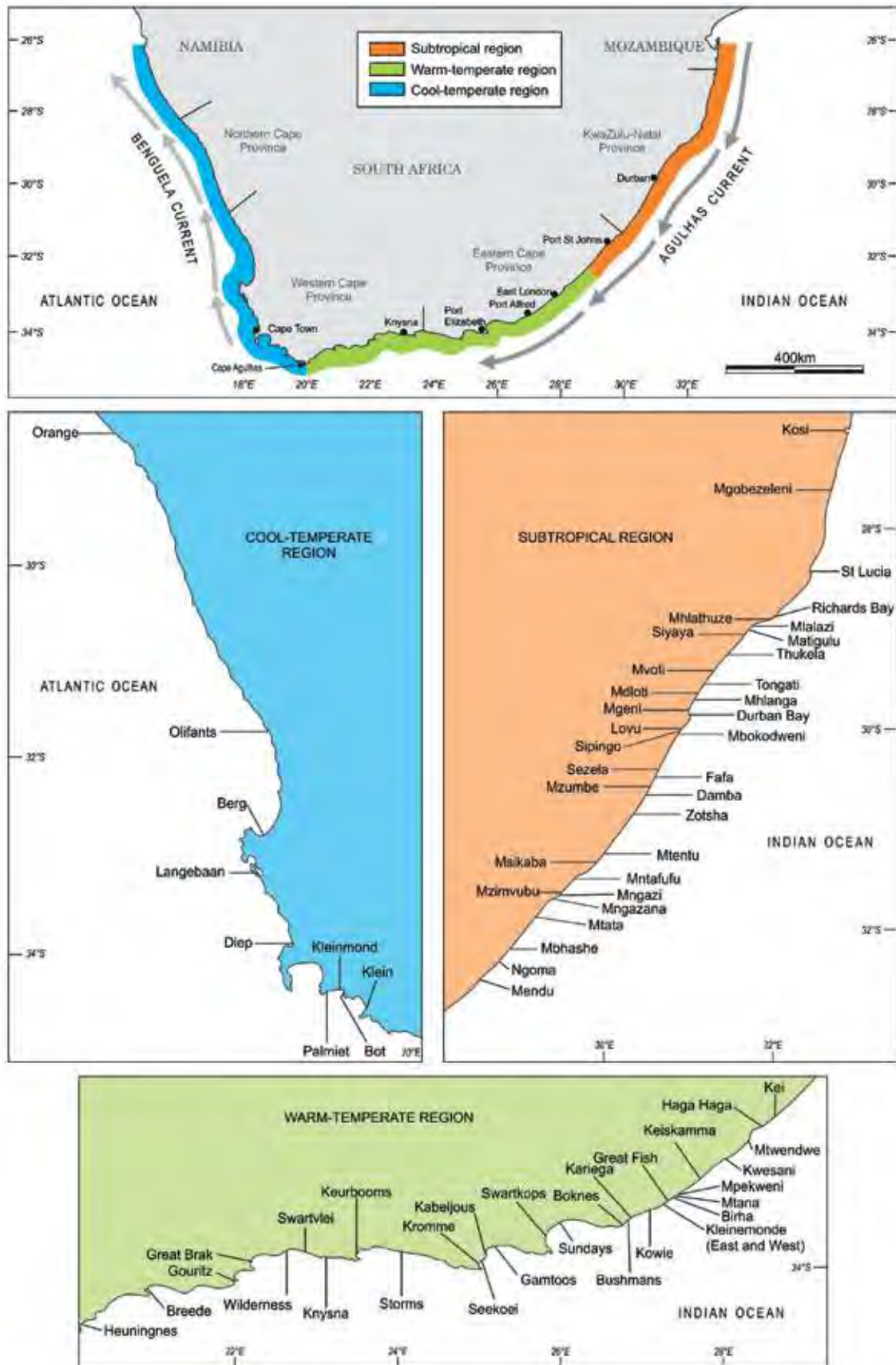
According to the South African National Water Act (No. 36 of 1998) an estuary is defined as “a partially or fully enclosed water body that is open to the sea permanently or periodically, and within which the seawater can be diluted, to an extent that is measurable, with fresh water drained from land.” Again this definition does not cater for those estuarine systems that show little or no dilution of seawater for extended periods and may even become hypersaline during prolonged droughts, e.g. Lake St Lucia.

Similar types of estuaries occur in Australia and this led Potter et al. (2010) to propose the following definition – “An estuary is a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which at least receives periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural seawater and varies along its length, it can become hypersaline in regions when evaporative water loss is high and fresh water and tidal inputs are negligible.”

More recently Whitfield & Elliott (2011) proposed the following global definition for estuaries – “An estuary is a semi-enclosed coastal body of water which is connected to the sea either permanently or periodically, has a salinity that is different from that of the adjacent open ocean due to freshwater inputs, and includes a characteristic biota.” This definition encompasses those estuaries that close and are therefore not tidal, as well as those that are sometimes hypersaline. It also includes coastal systems (e.g. certain estuarine lagoons and bays) that do not have inflowing rivers but where groundwater inputs provide estuarine conditions that support a typical estuarine biota (Whitfield 2005a).

### **Water flow and estuary mouth dynamics**

Three factors play a major role in the type and structure of estuary mouths; namely freshwater discharges from river catchments, tidal flow through the mouth, and sediment transport



**Figure 3.** Regional maps of southern Africa based on zoogeographical breaks for fishes recommended by Harrison (2002) and showing the localities of selected estuaries mentioned in the text.



processes within the marine environment. The local geomorphology, particularly the presence or absence of rocky reefs in the estuary mouth region are also an important determinant of the size and shape of the mouth.

Sediment suspended in sea water near the estuary mouth may be carried into the system by flood tidal currents. The material then settles in the calmer estuary waters and is only partially removed during the ebb tide. This results in an accretion of sand inside the estuary mouth and, in larger permanently open estuaries, may eventually result in the formation of a flood tidal delta that can constrict and eventually result in closure of the mouth, especially if there is a major reduction in the tidal prism.

River flow also has a marked influence on the amount of marine sediment deposited in an estuary. Reduced river flow tends to result in greater influx of marine sand into the lower estuary, whereas episodic river flooding (in conjunction with ebb tides) normally transport large quantities of accumulated sand back to the sea (Rossouw et al. 1991).

Due to variation in the quantities of sand near the mouth, and changes in the deposition

and erosion rates, there is a tendency for the mouth to migrate. Changes in position of up to a kilometre over several years can occur if nothing restricts this movement (e.g. Keurbooms), but most permanently open estuary mouths are stabilised by rocky areas on at least one bank. If tidal exchange and river flow are insufficient to maintain the mouth depth, a sand bar forms. The bar will increase in size until it eventually cuts off all tidal exchange with the sea.

Estuary water levels after closure are determined mainly by the balance between evaporation and the rate of freshwater inflow. However, seepage of estuarine water into the sea and wave overwash of the sandbar due storm sea events can also have an influence on water levels and salinities in certain temporarily closed systems.

Breaching of closed estuaries occurs when the water level behind the sandbar overtops the berm and scours a new mouth (Figure 4). The duration of the open mouth phase varies considerably from one estuary to another. In some cases the estuary may be closed for most of the year and only opens after an extended wet season or after river flooding. In other cases the mouth is usually open for most of the year. In large estuaries where the



**Figure 4.** Outflow phase of the Bot Estuary following mouth breaching due to river flooding from the catchment (Photo: Steve Gildenhuys).



mouth is permanently open, water levels are more predictable, fluctuating with the tides and rising even further during river flooding. The salinity of these systems is controlled by the water exchange at the seaward end, evaporation from the estuary, and freshwater inflow. During periods of low run-off, the salinity throughout such estuaries can approach that of sea water.

During major floods, salinities decline considerably, but the duration of the oligohaline conditions is limited because tidal exchange rapidly replaces the river water after the flood has dissipated. Silt, sand and debris that are brought down by the rivers during floods is usually carried directly out to sea but if a marked reduction in flow velocity occurs within the estuary, part of the sediment load then settles out in the system, mostly in the upper reaches where both coarse and fine material is usually deposited.

There are a number of coastal systems on the subcontinent that dry up periodically, especially during prolonged droughts and zero stream or riverine input. These systems are not considered as estuaries for the purposes of this monograph, even though they may possess typical estuarine biota at certain times. The prevalence of such systems is highest on the Cape west and northern coasts into Namibia.

The occurrence of micro-estuaries and micro-outlets around the southern African coast has not been properly documented. This is because the nature and functioning of these small systems has not been determined on a regional scale. Although micro-estuaries may contribute some estuarine biota to the subcontinent, micro-outlets appear to have very limited connections to the sea and a restricted number and variety of estuarine biota (Magoro 2018).

## 1.2 DESCRIPTIONS OF SOUTHERN AFRICAN ESTUARIES

It is important to note that a description of any estuary is subject to the inevitable changes that occur in all systems through time. These changes are usually driven by sea level fluctuations but will also be influenced by climatic shifts, especially where such shifts have an influence on sediment transport and deposition rates. For example, the present day estuarine lake at Botrivierlei did not exist 18 000 years B.P. when the mouth of the Bot River was situated in a palaeo-valley approximately 40 km south-west of the existing estuary (Rogers 1985). The recent history of the Botrivierlei mouth also reflects major changes, from a system that allowed free interchange of marine and fluvial waters, into an estuary which is now seldom open to the sea (van Heerden 1985). Similarly, about 5 000 years ago the mean sea level was some 2.5 m above present and the Swartvlei Estuary was probably served by a 2 km wide tidal inlet (Whitfield et al. 1983).

During its lifespan a typical southern African estuary goes through various stages of development, from a youthful, newly drowned river valley to a mature system where the valley is filled with

sediment (Reddering & Rust 1990). Channel dimensions of a mature estuary are determined by the flood discharge and slope of the river, geomorphology of the floodplain, cohesion of the sediment bed, and by the tidal influx of marine sediment during periods between river flooding. Mature estuaries establish an equilibrium whereby tidally accumulated sediment is eroded from the estuary only during episodic floods (Reddering 1988a). This equilibrium is likely to be altered as a result of changes described below.

According to Reddering & Rust (1990) modifications to the structure and functioning of southern African estuarine systems can be placed into two major categories; firstly changes that have been driven by global forces such as climatic and sea level fluctuations, and secondly changes that have resulted from direct human interference and are of a local or regional nature. Both the above categories will determine the rate and magnitude of morphological and hydrodynamic changes within these estuaries, and therefore have a major impact on the characterization of individual systems.



**Figure 5.** Aerial photograph of the Kariega Estuary showing the development of a large flood tidal delta inside the mouth and extending above the road bridge (Photo: Alan Whitfield).

River inflow is perhaps one of the most critical factors influencing estuaries on the subcontinent because of its role in sedimentary and hydrodynamic processes within individual systems (van Heerden 1986, Cooper 1993a). The increasing retention of fresh water in dams has a distinct effect on estuaries, and includes the removal of an essential element in their natural cycle, namely the normal flood events (Whitfield & Wooldridge 1994). Dams can cause not only a decrease in the overall number of floods but also reduce the volume of water per flood (Reddering & Rust 1990). The extent to which river water is impounded varies, but in some catchment basins the combined capacity of existing dams already exceeds the mean annual runoff of the river system.

The potential deleterious effects on estuaries so affected are obvious and take the form of an increase in the size of sand shoals situated in the lower estuarine reaches (Reddering & Esterhuysen 1984). This modification may have two further effects. Firstly, the development of large flood tidal deltas (Figure 5) tend to constrict the channel of the lower estuary, so that tidal exchange

between the sea and the estuary becomes gradually less efficient, and consequently the tidal prism cannot maintain an open tidal inlet as before. Secondly, when a flood of sufficient discharge does occur, the sediment in the delta would have a larger than normal volume and therefore take longer to be scoured to a specific base level (Figure 6). In the case of muddy estuaries, the sediment would attain a higher degree of erosion resistance (Reddering 1988a) and be much more difficult to remove. Consequently, a river flood would not be able to scour the estuary channel to its normal dimensions as easily as a flood under natural conditions. As an overall result, smaller estuary channel dimensions are established under prolonged conditions of reduced freshwater discharge.

Apart from the scouring action of freshwater, rivers are also important in the prevention of hypersaline conditions. For example, during the 1989 drought in the Eastern Cape Province, salinities in the middle and upper reaches of the Great Fish Estuary seldom rose above 10 because of a perennial freshwater input, whereas salinities in the upper reaches of the nearby Kariega Estuary



**Figure 6.** Rapid water flow out of the Swartvlei Estuary showing plumes of sand from the flood tide delta being lifted into suspension by the ebb tide and then carried out to sea (Photo: Alan Whitfield).



**Figure 7.** Exceptional high seas entering the temporarily closed East and West Kleinemonde estuaries give some idea of the sort of changes that will result from a major sea level rise (Photo: Paul Cowley).



attained 42 due to an absence of river flow for a prolonged period (Whitfield & Bruton 1989). In some small temporarily closed estuaries, the salinity extremes during the 1989 drought were even more marked, ranging from 98 in the Seekoei system (excessive freshwater abstraction in the catchment) to 29 in the adjacent Boknes Estuary (no major dams in the catchment). Salinity in shallow estuarine lakes can fluctuate widely and in the St Lucia system this can range from <5 during wet cycles to >100 during major droughts (Perissinotto et al. 2013). Such extreme hypersalinity values would not have occurred in the pristine St Lucia system.

Coastal waves are known to be an important factor controlling the closure of estuaries. Estuaries on open, wave-exposed coasts tend to close more often than counterparts on sheltered, embayed coasts (Reddering 1988b). If wave energy increases as a result of global warming then it is likely that the tidal inlets of southern African estuaries will become more constricted.

Conversely if climatic change were to reduce wave energy, then the effect of tidal scour in estuaries would increase, particularly if the tidal prisms were substantially expanded by a rise in sea level (Reddering & Rust 1990).

It has been suggested that southern African estuaries, which are fairly sheltered from the open sea and have their tidal signal significantly dampened by the frictional characteristics of the mouth, may become more vulnerable to storm water ingress as a result of sea level rise (Hughes & Brundrit 1992). In addition, higher coastal water levels during storms (Figure 7) would be capable of penetrating even the most restrictive inlet, provided the event was of sufficient duration. Increased marine domination of estuaries on the subcontinent will also lead to higher salinities within these systems, especially in the lower and middle reaches (Figure 8).

Estuaries are usually classified by salinity characteristics, physiography, hydrography, sedimentation patterns, geomorphology, and even



**Figure 8.** View of the lower Kosi estuarine system, with traditional fish traps in the foreground. This region of the estuary in particular will undergo increasing tidal exchange and higher salinities under a sea level rise scenario (Photo: Alan Whitfield).



**Table 1.** Some generalised physical characteristics of southern African estuarine systems (modified from Whitfield 1992). The mean salinity ranges do not take into account artificial high salinities during droughts caused by excessive freshwater abstraction from the catchments.

System type	Riverine/marine balance	Spring tidal prism	Mixing process	Mean salinity
Estuarine bay	Marine dominance	Large ( $> 10 \times 10^6 \text{ m}^3$ )	Mainly tidal	25-35
Permanently open estuary	Marine dominance	Moderate ( $1-10 \times 10^6 \text{ m}^3$ )	Tidal/Riverine	15-35
River mouth	Riverine dominance	Small ( $< 1 \times 10^6 \text{ m}^3$ )	Riverine	1-15
Estuarine lake	Variable	Negligible ( $< 0.5 \times 10^6 \text{ m}^3$ )	Wind	5-35
Temporarily open/closed estuary	Variable	Absent when closed	Wind	1-35
Micro-estuary	Stream dominance	Absent when closed	Wind	1-15

ecosystem energetics. Although geologists tend to classify estuaries according to their geomorphology or physiography; and oceanographers according to their hydrography and salinity, there is no reason why a combination of the above features should not be used (Whitfield & Elliott 2011). The classification of estuaries described here (Table 1) draws mainly on the physiographic, hydrographic and salinity characteristics of individual systems, thereby providing a more comprehensive classification system than would be possible if only one or two factors were considered.

Although the definition of an estuary by Day (1980) has been widely used for southern African systems, it does not convey the variety of estuaries occurring on the subcontinent. Indeed, it is this variety that has led to scientists using different terminology when describing similar systems, e.g. Begg (1978) refers to temporarily open / closed estuaries as 'lagoons', Day (1981a) uses the term 'blind estuaries', Cowley & Whitfield (2001a) refer to an 'intermittently open' estuary, and Bennett (1989) differentiates between 'seasonally open' and 'normally closed' estuaries. The term 'intermittently closed' estuary has not been used to describe those systems are predominantly open but this could be a way of distinguishing them from 'intermittently open' estuaries.

Reddering & Rust (1990) suggested that few southern African systems qualify as 'true' estuaries, with only 37 'river mouths' maintaining permanent tidal inlets. According to these

authors, estuaries on the subcontinent have the following features: (i) the majority are small, their tidal prisms being  $10^6 \text{ m}^3$  or less; (ii) most occupy drowned river valleys; (iii) most tidal inlets are constricted or periodically blocked by sand bars; and (iv) flood tidal deltas are well developed compared to ebb tidal deltas.

The maximum tidal range off the southern African coast is approximately 2 m between successive high and low spring tides, with most estuaries having a range considerably less than 1.5 m. This, together with some of the estuarine features described above (e.g. constricted tidal inlets), has led to estuaries on the subcontinent being described as microtidal systems (Whitfield & Elliott 2011). Those that are permanently open are subject to a semi-diurnal tidal cycle, i.e. two high and two low waters per day.

Southern African estuaries are unpredictable environments (Table 2) and the differing nature of these systems makes it even more difficult to place them in specific categories. This applies particularly to salinity stratification that varies with time and location within an estuary (Largier & Slinger 1991). The above authors make a distinction between those systems that are permanently highly stratified and those that display highly stratified phases, factors which have not been fully addressed in past estuarine characterizations. Generally, the mean annual run-off from the catchment (river flow), estuary size (surface area), and tidal prism all act in concert to determine

**Table 2.** Characteristics associated with predictable/unpredictable environments (after Bruton 1989) and applied to southern African estuarine systems (after Whitfield 1990).

Environmental characteristics	Predictable environment	Unpredictable environment	Southern African estuaries
Inertia	High	Low	Low
Elasticity	Low	High	High
Amplitude	Low	High	High
Dynamic property	Fragile	Robust	Robust
Maturity	High	Low	Low
Stability	Resistant	Resilient	Resilient

#### *Definitions*

Inertia: the ability of the system to resist perturbations.

Elasticity: the speed with which a system returns to its original state following perturbation.

Amplitude: the magnitude of the perturbations and the degree of displacement from a previous state.

Dynamic property: the variety and nature of forces operating within a system.

Maturity: the degree to which a system approaches a climax state.

Stability: the tendency of a system to remain near an equilibrium point or to return to it after a disturbance.

whether or not a system remains permanently open.

Salinity is a key factor in characterizing individual estuaries and the description of zones within a particular system. In this monograph the Venice system of classification for describing salinity ranges has been followed, i.e. oligohaline (0.5-4.9), mesohaline (5.0-17.9), polyhaline (18.0-29.9) and euhaline (30.0-39.9). Hyperhaline or hypersaline conditions usually refer to any salinity above 40 but some authors use this term for any salinity above 35. It is perhaps noteworthy that turbidity (Figure 9) does not feature in estuarine classifications.

Despite the fluctuating nature of southern African estuaries described above, it is possible to categorize these systems (Table 1) using the dominant phase prevailing in each estuary type. Based on these criteria, a total of six major categories of estuarine systems can be identified, namely estuarine bays, permanently open estuaries, river mouths, estuarine lakes, temporarily open /closed estuaries and micro-estuaries.

#### **Permanently open estuaries**

Systems that are permanently open to the sea (e.g. Figures 10 and 11) show typical estuarine characteristics, i.e. a moderate tidal prism with a horizontal salinity gradient and vertical salinity

stratification dependent upon factors such as bathymetry, tidal cycle and river inflow (MacKay & Schumann 1990). The catchments of these estuaries are usually larger than 500 km<sup>2</sup> and often greater than 10 000 km<sup>2</sup>, with the rivers having a perennial flow in their natural condition. Although river flow in the form of mean annual run-off (MAR) contributes to the maintenance of an open mouth condition, the tidal prism in these systems is generally large enough to maintain a permanent link with the sea. However, during extreme droughts the mouths of some of these systems can close.

According to Cooper (2001) there are three main types of permanently open estuaries in South Africa. The first type are labelled river-dominated estuaries (same as river mouth estuaries in this monograph) and the second tide-dominated estuaries (same as permanently open estuaries in this monograph). His third category comprises permanently open estuaries that lack a supratidal barrier due to inadequate sediment availability.

Generally there is a wetland area within the lower half of permanently open estuaries, which may be occupied by saltmarshes in the more temperate regions or mangroves in subtropical areas. The eelgrass (*Zostera capensis*) often colonizes intertidal and subtidal zones of low turbidity systems, especially in the lower and middle reaches



**Figure 9.** Aerial photographs showing differences in water turbidity in the lower reaches of (a) the Great Fish Estuary and (b) the nearby Kariega Estuary, with both systems being photographed on the same day. Note the absence of submerged vegetation in (a) and its widespread prevalence in littoral areas in (b) (Photos: Alan Whitfield).





**Figure 10.** Aerial view of the mouth region of the permanently open Kariega Estuary on the Eastern Cape coast. Note the stabilization of the estuary mouth by a rocky reef running along the northern bank. (Photo: Alan Whitfield).



**Figure 11.** The permanently open Mbashe Estuary is in the biogeographical transitional zone between warm-temperate and subtropical systems of the Eastern Cape Province. The high water clarity when this photograph was taken indicates low freshwater input by the highly turbid Mbashe River, in conjunction with a flood tide bringing clear marine water into the estuary (Photo: Alan Whitfield).

(Talbot & Bate 1987). However, in systems where the flow of fresh water has been curtailed, eelgrass extends its distribution into the upper reaches (Adams & Talbot 1992).

Tidal currents provide the ultimate driving force for most of the turbulence and mixing in stratified and well mixed estuaries (Kennish 1986). Although Day (1981a) has subdivided 'normal' (i.e. permanently open) southern African estuaries into salt wedge, highly stratified, partially mixed and vertically homogeneous systems, evidence suggests that the degree of stratification is very variable on both a spatial and temporal scale (MacKay & Schumann 1990), and that many estuaries move from one state to another depending upon factors such as river flow, tidal range and mouth state.

Some systems such as the Kariega Estuary seem to be able to remain in an open state despite the loss of river flow for prolonged periods, sometimes in excess of a year. Although the tidal prism in this system currently appears to be sufficient in maintaining a permanently open mouth, there is also evidence of a slow but gradual increase in the size of the flood tidal delta above the road bridge due to marine sand deposition (Figure 5) and therefore a gradual decrease in the magnitude of the tidal prism. A similar progressive growth of the Sundays Estuary flood tidal delta occurs, which is indicative of incoming tidal dominance and the ability of the lower reaches to act as a sink for marine sand (Reddering & Esterhuysen 1981). However, in contrast to the Kariega system, episodic river flooding is more common in the Sundays Estuary and therefore flushing of marine sediments out to sea occurs more frequently than in the Kariega Estuary.

Largier & Slinger (1991) described estuarine circulation patterns in the highly stratified Palmiet system and emphasized the importance of internal hydraulic control of exchange through the narrow mouth, buoyancy-driven landward intrusion of sea water, upward shear-driven entrainment, and ebb tidal outflow. They also drew a distinction between those estuaries that are normally highly stratified, such as the Palmiet, and those that display highly stratified phases. An example of the latter can be found in the Sundays Estuary

which is highly stratified during neap tides but becomes completely mixed during spring tides (MacKay & Schumann 1990). Although tidal currents dominate mixing processes in these estuaries under low and even moderate river flow conditions, floods can result in a complete reversal of the situation, with riverine energy driving water movements within the system until a tidal regime is re-established (Table 1).

Intense stratification is often present in deeper areas of permanently open estuaries where isolated 'pockets' of higher salinity water are trapped. For example, in the fjord-like Msikaba Estuary, surface and bottom salinities of 20 and 35 respectively were measured during the low flow winter season, while the equivalent readings in spring during higher river flows were 2 and 35. The marked salinity stratification in summer leads to dissolved oxygen depletion of bottom waters, with a concomitant negative influence on the sessile biota below 6 m depth (Blaber et al. 1974). Similar highly stratified and anoxic conditions have been recorded in deep regions (>10 m) within the upper Keurbooms Estuary.

Average salinities in permanently open estuaries tend to fluctuate between 15 and 35 but are usually greater than 25, especially during the dry season. Hypersaline conditions (>40) have been recorded in the upper reaches of certain Eastern Cape systems during extreme droughts, primarily due to very low or zero river inflow and high summer evaporation rates (Whitfield & Bruton 1989). Oligohaline (0.5-4.9) and highly turbid conditions can extend into the lower reaches of these estuaries for brief periods during major flood events. The sudden decline in salinities and high silt loads during floods may even cause extensive mortalities of the estuarine biota (McLachlan & Grindley 1974, Whitfield & Paterson 1995).

Estuarine water temperatures are highly variable. Generally, temperatures tend to reflect riverine conditions during floods, with the sea having a stronger influence during normal river flows or droughts. For example Read (1983) found that the Keiskamma Estuary was vertically isothermal during a dry summer (halocline absent), whereas during wet summers a thermocline (halocline present) was recorded in the water column.

A comparison of the vertical temperature structure in the Keiskamma Estuary during stratified winter conditions revealed that the water above the halocline was cooler than that below, whereas in summer the opposite pattern occurred. These differences emphasize the influence of both the marine and riverine components on estuarine water temperatures, and verify the fact that rivers in the warm-temperate region are usually cooler than the sea in winter and warmer during summer.

The role of river flow in supplying nutrients to estuaries is well illustrated by the work of Allanson (1999) in the Great Fish Estuary. He demonstrated that both nitrate and phosphate mixing plots had almost linear relationships with salinity, i.e. the highest values for both nutrients was in river diluted estuary water and declined as the salinity increased towards the mouth. Conversely low river flow results in reduced estuarine nutrient values (Grange et al. 2000).

#### **Temporarily open /closed estuaries**

These systems are blocked off from the sea for varying lengths of time by a sand bar at the mouth

(Figure 12). This occurs during low river flow combined with longshore sand movements in the nearshore marine environment (Day 1981b). Most of these estuaries have small river catchments ( $<500 \text{ km}^2$ ) and long periods (several months) when the river flow is minimal or stops altogether. The tidal prism is usually small ( $<1 \times 10^6 \text{ m}^3$ ) when the mouth is open, and absent altogether when the sand bar is fully formed. The latter condition predominates for most estuaries in this category.

During the estuary closed phase, exchanges with the sea virtually cease, apart from occasional wave overwash events when seawater tops the sand bar (Begg 1984a, 1984b) and flows into the estuary in varying quantities depending on the level of the spring high tide and the magnitude of the storm sea event. Barrier overwash can lower the height of the sand berm thus reducing the volume of estuarine water needed to breach the mouth.

Many TOCEs have a high berm, which results in high water levels and a bed level that is elevated above sea level (Cooper 2001). When such estuaries breach, they essentially drain, exposing much



**Figure 12.** An aerial view of the temporarily closed Mtana Estuary in the Eastern Cape Province. Note the submerged macrophyte beds within the littoral zone of this system (Photo: Alan Whitfield).



of the estuary bed, with water levels only increasing again once the bar is re-formed. Non-perched estuaries, characteristic of those in the Eastern Cape Province, are formed behind low barriers and do not have an elevated bed. Although water levels in these estuaries do fall once they breach, they do not drain as drastically as perched estuaries do. Large amounts of sediment are removed from TOCEs during the outflow phase (Figure 13).

According to Cooper (2001) closed estuaries can be placed in one of two categories, perched or non-perched. Perched estuaries have a high berm due to a predominance of coarse grained sand that is deposited at levels higher than most high tides. When the berm is breached little seawater enters such estuaries due to the elevated bed level. The small tidal prism is insufficient to sustain the outlet and these estuaries normally close very rapidly (days to weeks). Non-perched estuaries do not have a high berm and are normally associated with dissipative beaches that are characterised by wide surf zones (Cooper 2001).

Most TOCEs in the subtropical zone are 'perched' when closed (Begg 1984a). Despite some seepage of estuarine water through the sand bar into the sea, the water level and depth of the estuary typically increases substantially from the open mouth state (Perissinotto et al. 2010). When the level of the estuary exceeds the height of the sandbar at the mouth, usually following heavy precipitation in the catchment, the water overtops the bar and erodes a channel which then becomes the new mouth.

Although strong horizontal salinity gradients are sometimes present in temporarily open estuaries during the tidal phase, more uniform oligohaline (0.5-4.9) or mesohaline (5.0-17.9) conditions usually prevail in KwaZulu-Natal systems during the prolonged closed phase (Begg 1984a). During episodic floods, river conditions may briefly dominate the estuary, but during extreme droughts salinities in some of the Eastern Cape systems can exceed 50 (Whitfield & Bruton 1989) but this rare.



**Figure 13.** Outflow phase following breaching of the sand bar in the temporarily open East Kleinemonde Estuary. Note the sediment scour and transport created by the rapidly outflowing estuarine water (Photo: Bernard Mackenzie).

The circulation in these estuaries is driven by both tidal and river flow when the mouth is open and wind when the mouth is closed. Cooper (1989) recorded current velocities of up to  $60 \text{ cm s}^{-1}$  during a river flood in the Mhlanga Estuary, but tidal conditions soon dominated circulation during the open phase due to the short-lived flood peak.

Water temperatures during the open phase are strongly driven by both riverine and marine conditions, but are normally independent of these influences when the estuary is closed and river flow is either minimal or zero. During the closed phase solar heating and evaporative cooling of the estuarine water body are the prime determinants of the prevailing temperature regime.

Nutrients are transported into these systems and can accumulate during the closed phase where they are recycled internally by sequestration in sediments and subsequent release after bacterial breakdown (Perissinotto et al. 2010). Mouth breaching and subsequent scour of the system releases large quantities of these accumulated nutrients into the nearshore marine zone which may therefore be an important nutrient source for the oligotrophic waters of the southern African east coast (van Ballegoyen et al. 2007).

Macronutrients in temporarily open /closed estuaries in urban or peri-urban areas (e.g. Mdloti and Mhlanga) often have much higher macronutrient levels than systems with more natural catchments (e.g. Mpenjati and East Kleinemonde). It is frequently found that there is a marked increase in macronutrient levels during the open mouth phase when compared to the closed phase (Snow & Taljaard 2007). Indeed, after prolonged periods of mouth closure the water column may even become depleted in macronutrients, probably as a result of sustained algal uptake (Perissinotto et al. 2010).

### River mouths

These are systems in which the river usually dominates physical processes within the estuary (Figure 14), with salinities tending towards oligohaline in both the upper and middle reaches. Although the mouths of these estuaries are permanently open, the tidal prism is relatively small, with sea

water seldom penetrating any major distance upstream during high or even moderate river flow periods. When river flooding occurs, freshwater conditions can extend well into the marine environment. During such flood events the system ceases to behave like an estuary and essentially becomes an extension of the river.

Southern African river mouths generally have relatively large catchment areas ( $>10\,000 \text{ km}^2$ ) and the rivers are often characterized by high flows and heavy silt loads, a portion of which is deposited in the estuary (van Heerden 1986). Consequently river mouths are usually shallow ( $<2 \text{ m}$  deep) despite the large volume of water which passes through these systems. The large sediment loads carried into the marine environment have the potential of creating unique coastal environments for fishes and invertebrates, e.g. the Thukela Bank off the KwaZulu-Natal coast that covers an area of approximately  $300 \text{ km}^2$  (Bosman et al. 2007) and is of major importance to certain fish and penaeid prawn species (Lamberth & Turpie 2003).

Episodic floods can result in scour depths of up to  $15 \text{ m}$  being recorded during peak flooding in the Orange River estuary mouth (Swart et al. 1988). These floods are very important in removing accumulated sediment from the estuary, thus dictating the morphometry and ecology of the system (Seaman & van As 1998). Flood deltas may form on the outside of the mouth following major sediment deposition, e.g. the 1988 Orange River flood created an ephemeral flood delta up to  $1.2 \text{ km}$  offshore with an estimated mass of  $3.6$  million tonnes (Bremner et al. 1990).

River dominated estuaries have a cyclical pattern of sedimentation that is mediated by severe river flooding that promotes vertical erosion of the bed material in the estuary (Cooper 1993b). As mentioned above, eroded sediments are usually deposited as an ephemeral delta in the adjacent marine environment, provided water currents and wave action allow such a development. Once the flood waters have dissipated the river and estuarine gradient is rapidly restored (within a few months) through fluvial deposition and the formation of shallow braided channels (Figure 14) near the mouth (Cooper 1993b).



**Figure 14.** Aerial view of the lower Thukela system during a winter low flow period, showing the shallow nature of the estuary and large ebb tidal delta in the mouth region (Photo: Tris Wooldridge).



Large amounts of macronutrients, mainly by virtue of the considerable water volumes involved, are transported through river mouths into the sea. Because these types of estuaries tend to be relatively short when compared to permanently open estuaries, very little of the nutrients settle or are removed from the water column in transit. These nutrients are particularly important in stimulating coastal productivity, especially on the oligotrophic east coast (de Lecea & Cooper 2016).

The current mean annual river flow in the Orange and Thukela River mouths still exceed 6 000 and 3 000 million m<sup>3</sup> respectively, with most of the flow occurring during summer and relatively low flows in winter (Seaman & van As 1998, de Lecea & Cooper 2016). Indeed both estuaries have a tendency to sometimes close during the winter dry season, and would have done so even in their natural state. Current river flows in both systems have been curtailed considerably, with the natural flow pattern and large water volumes having been lost mainly to irrigation, urban use and inter-basin transfers.

Mixing of the water column in river mouth type estuaries is usually dominated by turbulence derived from river flow. Under moderate or high river flow conditions, the fresh water will flow over the top of any marine water that may be present in the lower or middle estuary. Water temperatures are closely linked to those in the river, although the sea will sometimes influence bottom waters in the lower and sometimes middle reaches, especially during spring high tide.

In terms of estuarine function, these systems offer a greater amount of habitat for typical estuary-associated organisms when river flow is minimal. High river flows during summer limit the actual estuarine area to the mouth region at high tide, with major river flooding precluding occupation of these systems by estuarine biota (Brown 1958). The exceptional variation in physico-chemical conditions each year means that these systems are not priority nursery areas for estuary-associated invertebrates or fishes.

River mouths along the Tsitsikamma coast do not reflect many of the features described above. Systems in this region comprise perennial rivers that carry negligible sediment loads. Due

to the geology of the area, river mouths along this section of the coastline are generally short and situated in narrow, steep sided valleys with limited sedimentary deposits on the rocky base. Although sea water may be present in deep scour holes in these systems, surface salinities are usually oligohaline or even fresh, especially at low tide.

### **Estuarine lakes**

Most estuarine lakes in southern Africa evolved from drowned river valleys (Hill 1975) that were largely filled in by reworked sediments to varying degrees and are now separated from the sea by vegetated sand dune systems. In some instances the dune barrier has completely isolated the lake, which then loses its estuarine character and is then referred to simply as a coastal lake (Whitfield & Elliott 2011). The present morphometry of most southern African estuarine and coastal lakes is directly linked to sea level changes and sedimentary patterns during the Holocene when extensive ice sheets in the northern hemisphere melted as a result of global warming and the sea level rose by more than 100 m over a period of approximately 10 000 years (Botha et al. 2013).

Estuarine lakes, all of which have a water surface area >1000 ha, may have a permanent marine connection (e.g. Kosi), or may be seasonally linked to the sea (e.g. Swartvlei), while others are seldom linked to the sea (e.g. Botrivierlei). In the case of Kosi it is the tidal prism that maintains the open mouth, for Swartvlei it is a combination of river flow and tidal prism that determines mouth status, whereas for Botrivierlei, river flooding is the primary determinant of an open mouth state.

Although the mouth of estuarine lakes are often open, tidal prisms within these systems are usually negligible due to the narrowness of channels linking them to the sea and the large size of the lakes relative to the tides. In some cases segmentation has resulted in a very tenuous connection with the marine environment, especially for the lakes at the end of each chain, e.g. Lake Nhlanga in the Kosi system (Begg 1978) and Rondevlei in the Wilderness Lakes system (Hall et al. 1987).

Salinities in estuarine lakes are spatially and temporally variable (Hutchison & Midgley 1978)

and depend primarily on the balance between freshwater input, evaporation and the periodicity of the marine connection (Bally & McQuaid 1985). These interactions are exemplified by the situation at Lake St Lucia (Figure 15). During prolonged droughts when direct precipitation, river and groundwater flow are insufficient to counter the effects of evaporation on the lake water level, sea water flows up the system, increasing in salinity as it flows northwards. If the estuary mouth is closed during the drought then the potential exists for Lake St Lucia to gradually evaporate, with increasing hypersalinity and eventually loss of water from certain lake compartments (Whitfield & Taylor 2009).

In wet years, the opposite occurs at Lake St Lucia; high river flow and rainfall increases the lake level to the point where saline estuarine water is lost to sea, being replaced by fresh riverine water entering the lake compartments. Evaporation is more than countered by the increased rainfall and other freshwater inputs (e.g. groundwater seepage), resulting in a major salinity decline

throughout the system (Perissinotto et al. 2013).

A primary reason why Lake St Lucia is so susceptible to salinity fluctuations is the high surface to volume ratio of the system (Hutchison & Midgley 1978). Much of the lake has been filled in by riverine sediments over the millennia and the average water depth of the lake is now only 1 m. Deeper estuarine lakes such as Swartvlei (Figure 16) and Nhlanga are more resilient to the effects of evaporation, with their depth profiles being related to low riverine sediment loads.

Meromixis is common in some of the deeper (>5 m) estuarine lakes but seldom occurs in the shallower systems. Wind is the dominant mixing force, even in the deeper lakes where it may take several months to break down the halocline (Allanson & Howard-Williams 1984). Spatial and temporal salinities within estuarine lakes can vary from oligohaline to hypersaline, e.g. Lake St Lucia salinities often range from one to more than 100 (Taylor 2013) whereas salinities in Swartvlei lake vary between 2 and 20 (Allanson & Howard-Williams 1984). Water temperatures in



**Figure 15.** An aerial view of a small portion of the shallow and turbid Lake St Lucia in KwaZulu-Natal, with high vegetated dune cordons abutting onto the sea in the background (Photo: Ricky Taylor).

these systems are directly related to solar heating and radiation, and are little influenced by either rivers or the sea.

Estuarine lakes are natural traps for macronutrients from inflowing rivers since they are large water bodies linked by narrow channels to the sea. Although dissolved inorganic phosphorous and inorganic nitrogen levels in river water flowing into Lake St Lucia were lower than the levels of those nutrients within the lake, evidence from sediment pore-water nutrient concentrations suggest cycling of nutrients between the substratum and overlying lake (Perissinotto et al. 2013).

In contrast to permanently open estuaries, the input of marine derived macronutrients is likely to play much less of a role in the productivity of estuarine lakes that are more strongly linked to riverine and lake recycling processes. However, rivers flowing into Swartvlei have extremely low levels of nutrients (Howard-Williams 1977) and the water column of this lake is therefore oligotrophic (Howard-Williams & Allanson 1981). Nevertheless, river flooding usually results in

elevated nutrient levels entering these systems (Allanson & Whitfield 1983).

#### **Estuarine bays**

Only four estuarine bays occur in southern Africa, with three in the subtropical zone and one in the warm-temperate region. These systems are either natural (e.g. Knysna, Figure 17) or partly artificial due to dredging activities (e.g. Durban Bay) but retaining some biological significance (Forbes et al. 1996). In its natural state, Richards Bay was more of an estuarine lake than a bay (Millard & Harrison 1954). With the advent of harbour developments in the 1970s this system took on the characteristics of two marine dominated estuarine bays, the northern one still being referred to as Richards Bay and the southern one as a new system, the Mhlathuze Estuary (Begg 1978).

Langebaan Lagoon in the cool-temperate region (Figure 18) has now been classified as a coastal embayment type estuary and has many of the attributes of an estuarine bay, except that its freshwater inflow is via an aquifer and not a river



**Figure 16.** View of Swartvlei, a meromictic estuarine lake in the Western Cape Province, with the Outeniqua Mountain range in the background (Photo: Alan Whitfield).





**Figure 17.** The mouth of the Knysna Estuary is 230 m wide and has an average channel depth of approximately 10 m. The Outeniqua Mountain range is visible in the background (Photo: Alan Whitfield).



**Figure 18.** The Langebaan Lagoon in the Western Cape Province has been classified as a coastal embayment that is estuarine in character due to freshwater inputs from aquifers (Photo: Alan Whitfield).

(Whitfield 2005a). There is no distinct salinity gradient in the Langebaan system but the aquifer inputs into the upper reaches of this embayment prevent salinities from becoming hypersaline.

Estuarine bays tend to have large tidal prisms ( $> 10 \times 10^6 \text{ m}^3$ ) that result in the regular replacement of marine water in the lower and middle reaches. Mixing of the water column is tidally driven, and strong salinity stratification is a feature only in the upper and sometimes middle reaches of the Knysna system (Grindley 1985). Even under high river flow conditions, seawater salinities persist in the bottom waters of the lower reaches (Largier et al. 2000). The mouth is up to 10 m deep at spring high tide and tidal height fluctuations within the estuary are normally similar to those in the marine environment, e.g. in the Knysna Estuary a spring tidal range of 1.8 m persists into the upper reaches of this system (Day 1981c).

Salinities in the lower reaches of estuarine bays tend to exceed 30 due to the large volume of sea water entering these systems on each tide. Salinities below 30 are usually recorded in the upper and middle reaches, with reduced salinity conditions extending into the lower reaches only during river flooding. Euhaline conditions can extend into the upper reaches of certain estuarine bays during drought periods when river input is low. Hypersaline conditions have not been recorded in these systems due to the efficient exchange of water between the marine and estuarine environments. An example of the lack of salinity gradient is the Durban Bay salinity value of 27 near incoming rivers compared to approximately 35 for the rest of the bay (Begg 1978).

Water temperatures in both the lower and middle reaches of estuarine bays are strongly influenced by marine conditions (Day 1981c). At the head of the Knysna Estuary the water temperatures usually range between a minimum of 13°C in winter to a maximum of 28°C in summer. However, the moderating influence of the sea is evident in the lower reaches of the estuary where the annual range is usually 15–23°C (Day 1981c). Surface heating in the extensive shallows during summer and radiation in winter causes overall

water temperatures in Durban Bay to be warmer than the sea during summer and slightly cooler in winter (Day & Morgans 1956).

Coastal upwelling of waters adjacent to the Knysna Estuary can cause a sudden drop in water temperatures to 11.5°C in the mouth region of this system (Day 1981c). Indeed, summer upwelling is a regular feature affecting this estuary following persistent easterly winds and Schumann (2000) recorded a temperature decline of over 13°C in 2 hours.

An indication of physico-chemical changes brought about by transformation of the Richards Bay estuarine lake into an estuarine lake are as follows (Begg 1978). The original lake area of approximately 3 000 ha was subdivided into a harbour of 1 500 ha and Mhlathuze Estuary of about 1 300 ha. The original estuary mouth width of approximately 100 m was increased to 750 m for the harbour and 300 m for the estuary. Water depth was increased substantially in the harbour to approximately 19 m. Salinities in the lake were mainly mesohaline in the vicinity of the inflowing rivers to polyhaline towards the estuary mouth. Following transformation both new estuarine systems were euhaline over much of their water area. Because of the change from an estuarine lake into two estuarine bays, the surrounding vegetation is now dominated by mangroves rather than reeds, sedges and papyrus.

Water temperatures in the main body of the original Richards Bay estuarine lake ranged between 18°C in winter to 28°C in summer, whereas after harbour development these temperatures closely followed the adjacent coastal sea temperatures. Turbidities in the estuarine lake were generally high (Secchi disc readings = 0.1 m) due to disturbance of the shallow silty sediments by wind generated water currents. Following harbour development estuarine water clarity increased considerably due to marine domination in terms of water volume and therefore closely reflected seawater values (Begg 1978).

### Micro-estuaries

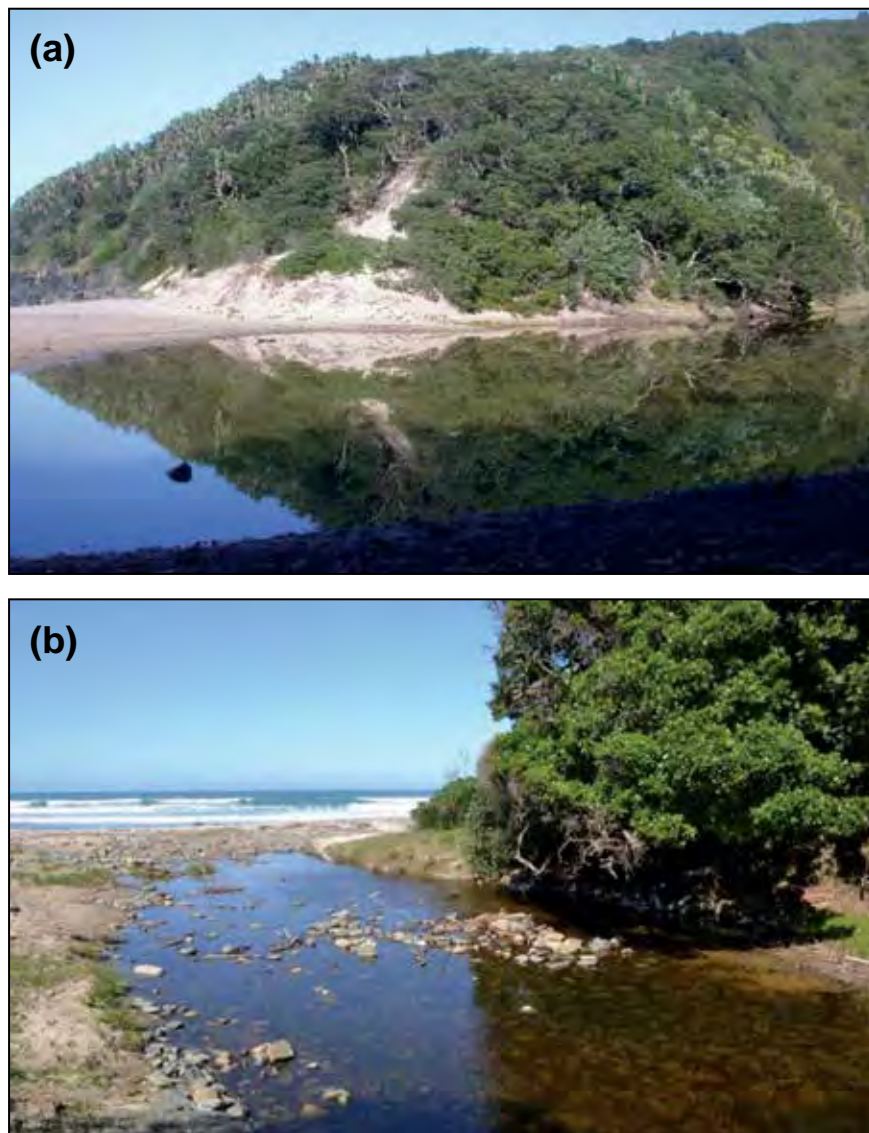
There are hundreds of coastal stream catchments entering the sea, giving rise to both micro-estuaries and micro-outlets (Figure 19), with the latter

systems not qualifying as estuaries (Magoro 2018). Micro-estuaries have been provisionally defined by Bate et al. (2017) as “A feature that displays a small but obvious water body draining into the sea that was likely to have water exchange with the sea at some point in time, thus indicating a high degree of permanency.” Apart from the small surface area of micro-estuaries (<5 ha), they also receive limited stream inflow on an annual basis and are characterized by being very shallow (mean depth = 0.1-0.5 m), regardless of mouth phase.

Marine inputs to micro-estuaries occur during very high spring tidal events, often resulting in sudden increases in salinity over the entire system.

However, in the period following such surges, salinities quickly decline and usually become oligohaline once persistent stream flow dilutes the salts (Magoro 2018).

Water temperature is strongly affected by adiabatic heating and cooling, being warm in summer (>25°C) and cool in winter (<12°C) due to the absence of any buffering linked to water depth. Turbidities are generally low (<10 NTU), except when river or stream flooding occurs. Dissolved oxygen values are relatively high due to the shallow nature of these systems, with a high water surface to volume ratio and major exposure to wind mixing (Magoro 2018).



**Figure 19.** View of the lower Mtwendwe Micro-estuary (a) and lower Black Rock Micro-outlet (b), with both systems being located in the Eastern Cape Province (Photos: Alan Whitfield).

### 1.3 HISTORY OF ESTUARINE ICHTHYOLOGY IN SOUTHERN AFRICA

The origins of estuarine ichthyology on the sub-continent can be traced back to the early 20<sup>th</sup> century and the perceived problems being experienced by anglers in the Swartkops Estuary. They claimed that the netting of fishes in this estuary, which was permitted by an Act promulgated in 1883, was causing marked reductions in the fish available to recreational fishermen. In 1912 it was resolved to close the estuary to netting for three years “to attempt to discover by a series of experimental nettings and other observations what were the real facts of the case” (Gilchrist 1918).

Towards the end of 1913 “it was represented to the Government that there had been a great falling off of the fish in the river, and this was alleged to be so marked as to necessitate some restriction even on angling operations” (Gilchrist 1918). At a meeting of anglers and netters at Swartkops town in June 1915, “it was mutually agreed that the estuary should remain closed to netting for a period of twelve months, during which regular experimental netting should take place”. Two days later the first comprehensive ichthyological survey of a South African estuary commenced (Figures 20 and 21).

Between 1919 and 1945 very little estuarine fish research appears to have been conducted. However, well-known ichthyologists Dr K.H. Barnard and Professor J.L.B. Smith sampled a number of estuaries during this period so that the documentation of marine fish diversity could be as comprehensive as possible. Early sampling of fishes in estuaries focused on the use of seine and gill nets but became increasingly diversified over the next few decades (Figures 22-35).

#### Period 1946-1955

This decade marked the beginning of a number of estuarine surveys undertaken by Professor John Day and his research team from the University of Cape Town (Day 1977). Fishes were one of many components covered during these surveys and in some cases only very limited information was obtained. In the Knysna Estuary, for example, Day et al. (1952) stated “We ourselves have done

a certain amount of netting, but our nets were small and the catches accordingly restricted to small species or the fry of larger ones”. Indeed, a characteristic of most of these early estuarine ecological surveys was a strong emphasis on benthic macro-invertebrates, with much less effort being applied to the ichthyofauna.

In contrast to the lack of even a species checklist for the Knysna Estuary (Day 1967), the later survey of the St Lucia system (Day et al. 1954) did contain a list of over 70 fish taxa together with notes on the relative abundance, distribution, breeding and feeding biology of the more common species. Already these authors had identified the importance of freshwater inputs to a healthy lake ecology and suggested that “Unless the circulation through the lakes is maintained, the salinity may rise to such high values that the fish and bottom fauna may die”. Richards Bay was next on the Zululand list of major estuaries to be covered, with Millard & Harrison (1954) conducting a detailed survey of this system, long before it was transformed into a harbour.

In the Western Cape Province, Scott et al. (1952) investigated the fishes of the Klein Estuary and this was followed by an estuarine survey of the Diep /Milnerton system on the Atlantic west coast (Millard & Scott 1954). Once again attention was given to the distribution, diet and recorded salinities of the various fish species. During this period the first autecological study on an estuary-associated fish species was conducted by Talbot (1955) in the Klein Estuary, covering the feeding, growth and breeding biology of the white stumpnose *Rhabdosargus globiceps*.

#### Period 1956-1965

The trend of collecting increasingly useful ichthyological information during the University of Cape Town estuarine studies was carried over into the Durban Bay survey (Day & Morgans 1956), primarily because the Natal Parks Board financed the study and specifically requested that the scientists to pay special attention to the fish fauna. Thousands of fish were caught, identified, measured and weighed. The dominant species





**Figure 20.** “Netting No. 20 at Telegraaf Spruit” in the Swartkops Estuary (after Gilchrist 1918).



**Figure 21.** “Results of Netting No.1 at Modder Spruit” in the Swartkops Estuary (after Gilchrist 1918).

were dissected to determine what they had been feeding on, the size at sexual maturity and the spawning season. Altogether, 186 taxa were collected and a preliminary analysis of the habitats occupied by the major fish components was attempted, viz. pelagic, demersal and mangrove fish groups. Biological notes on all the important species appeared in Day & Morgans (1956) but the “voluminous statistical data” arising from this study was never published.

The detail gleaned from the Durban Bay study contrasted to that in the Orange River Estuary (Brown 1958) where only limited information

on the fish species was collected. Similarly, the fish survey by Broekhuysen & Taylor (1959) of the Kosi estuarine system was incomplete and limited to “a little seining when time permitted”. However, by combining the above information with that of Campbell & Allanson (1952), a Kosi Estuary checklist of more than 60 fish species was compiled.

#### **Period 1966-1975**

This decade was characterised by increasing involvement in estuarine fish research by universities and institutions beyond the Western Cape

Province. Dr Burke Hill, published the first detailed checklist of fish species from the Mlalazi Estuary (Hill 1966) and hypersaline conditions in the nearby St Lucia system resulted in Millard & Broekhuysen (1970) being commissioned to conduct another detailed survey, with emphasis being placed on the recorded salinity ranges of fish species.

In the late 1960s a small group of young scientists from the Oceanographic Research Institute, under the leadership of Dr John Wallace, embarked on a major estuarine fish research programme centred in KwaZulu-Natal. These ichthyologists presented a detailed analysis of the species composition, reproduction, recruitment, migrations, length distribution, seasonal abundance and ecology of estuary-associated marine fishes along the east coast of South Africa (Wallace 1975a, 1975b, Wallace & van der Elst 1975).

The pioneering autecological research of Talbot (1955) on the white stumpnose *Rhabdosargus globiceps* was followed in 1970 by Dr Steve Blaber's field and laboratory study on another estuary-associated sparid, the Cape stumpnose *Rhabdosargus holubi*. Dr Blaber's investigation focused on the salinity and temperature tolerance, population dynamics, growth, food and feeding ecology of *R. holubi* in the temporarily closed West Kleinemonde Estuary (Blaber 1973a, 1973b, 1974a, 1974b, 1974c, 1975). For the first time, comprehensive information was available on the juvenile life-history stages of an estuarine-dependent fish species and served as an important benchmark for further studies on this and other estuary-associated taxa.

### Period 1976-1985

The autecological and synecological approach of the previous decade gained momentum, with major studies being initiated in all the coastal provinces. The family Mugilidae came under the spotlight, with particular emphasis on the feeding ecology of this group of fishes (Masson & Marais 1975, Marais & Erasmus 1977a, 1977b, Blaber 1976, 1977, Blaber & Whitfield 1977a, Marais 1980). This focus was broadened at Lake St Lucia where the food and feeding ecology of detritivorous, planktivorous and piscivorous

fish species was investigated (Whitfield & Blaber 1978a, 1978b, 1978c, Blaber 1979). In addition, the diet of piscivorous birds in Lake St Lucia was assessed for the first time (Whitfield & Blaber 1978d, 1979a, 1979b).

Studies by Cyrus & Blaber (1982a, 1982b, 1983a, 1983b, 1984a, 1984b, 1984c) on the Gerreidae, Martin & Blaber (1983, 1984) on the Ambassidae, and Blaber & Cyrus (1983) on the Carangidae, resulted in detailed biological and ecological information being collected on these important estuary-associated families. During this period, single species studies were continued, with *Rhabdosargus sarba*, *Gilchristella aestuaria* and *Sphyrna barracuda* all receiving research attention (Blaber 1982a, 1984, Blaber et al. 1981, Melville-Smith et al. 1981, Coetzee 1982a, Talbot & Baird 1985a, 1985b).

Fish assemblage studies in a wide variety of southern African estuaries (e.g. Whitfield 1980a, 1980b, Marais 1981, 1983a, 1983b, Begg 1984a, Beckley 1984a, Hanekom & Baird 1984, Plumstead et al. 1985, 1989a, 1989b) also gathered momentum, with increasing attention being given to aspects such as distribution, food and feeding ecology, habitat utilization and the seasonality of fish species within estuarine environments.

A number of more specific biological and general ecological issues were also addressed during the latter part of the decade (e.g. Marais 1982, 1984, Whitfield 1984, 1985, Beckley 1985a, Bennett 1985, Bennett et al. 1985), thus providing the basis for a more comprehensive understanding of the factors influencing fish assemblages in estuaries (Blaber 1981a, 1985, Whitfield 1983, Begg 1984a, Marais 1988).

### Period 1986-1996

Earlier work on fish larvae in the Swartkops Estuary by Melville-Smith & Baird (1980) and Beckley (1985a) gained momentum, with emphasis being placed on the composition, distribution and abundance of these early life stages in warm-temperate and subtropical estuaries (Whitfield 1989a, Harrison & Whitfield 1990, Martin et al. 1992, Harris & Cyrus 1995, 1999, 2000, Harris et al. 1995). Attention was also given to recruitment processes of 0+ fishes entering estuaries, including





**Figure 22.** Alan Whitfield and Steve Blaber seine netting at Lake St Lucia during the 1970s for a range of fish species required for dietary studies (Photo: Digby Cyrus).



**Figure 23.** Paul Cowley preparing to fin clip fish held in the seine net bag (foreground) during a mark-recapture study in the temporarily closed East Kleinemonde Estuary (Photo: Alan Whitfield).



**Figure 24.** Cast netting for fish in the upper reaches of the temporarily closed Haga Haga Estuary in the Eastern Cape Province (Photo: Alan Whitfield).

factors influencing their abundance (Hall et al. 1987, Whitfield 1988a, 1989b, 1989c, 1994a, 1996a, 1991a, Harrison & Cooper 1991, Paterson & Whitfield 1996).

Work conducted by Blaber (1981a) suggested that many southern African estuary-associated fishes are essentially 'turbid-water' species. This hypothesis was tested in a series of field and laboratory studies which showed that the distribution of juvenile marine fishes in estuaries are significantly influenced by turbidity (Cyrus & Blaber 1987a, 1987b, 1987c, Cyrus 1988a). That work was followed by Hecht & van der Lingen (1992) who investigated the influence of turbidity on the feeding strategies of certain fish species in estuaries.

Major river flood events were linked to possible mass mortalities of fishes in estuaries (Whitfield & Paterson 1995) and interactions between salinity, temperature, dissolved oxygen and suspensoids were also highlighted in triggering fish kills (Whitfield 1995a). Documentation of fish mortalities in estuarine lake systems was also recorded (Russell 1994).

Fish community studies continued to receive attention during this period (Whitfield et al. 1989,

Clark et al. 1994, 2009), with emphasis being placed on resource utilization (Whitfield 1988a, Bennett & Branch 1990), anthropogenic impacts (Cyrus 1991b, Plumstead 1990, Bennett 1994), fish recruitment and seasonality (Bennett 1989, Whitfield & Kok 1992, Harrison & Whitfield 1995). There were also a number of studies dealing with the influence of river flow on the structure and functioning of estuarine fish communities (Whitfield et al. 1994, Russell 1996, Ter Morshuizen et al. 1996a, 1996b).

There was a decline in single family studies during this period, with Martin (1988, 1989, 1990) concluding his earlier work on the Ambassidae. The 1990s represented a 'coming of age' for estuarine ichthyology in southern Africa (Whitfield 1996b). Life-history styles of fishes in estuaries on the subcontinent were reviewed by Potter et al. (1990), Blaber (1991), and Whitfield (1990, 1994b), with the question of estuarine dependence being investigated by Cyrus (1991c) and Whitfield (1994c). The 1990s also saw a renewed interest in fish standing stocks (Whitfield 1993, Whitfield & Harrison 1996) and the modelling of energy flow through a fish assemblage formed part of a broader study using





**Figure 25.** Monofilament gill net and *Pseudomyxus capensis* fish catch, with the net in the horizontal position showing the float line at the right of the picture and the lead line at the left (Photo: Alan Whitfield).

estuarine network analyses (Heymans & Baird 1995, Baird & Heymans 1996).

A major leap forward in the practical use of estuarine ichthyological data occurred with the development of indicators of estuarine 'health' (Ramm 1990; Cooper et al. 1994). These developments resulted in the CSIR, funded by the Department of Environment and Tourism (DEAT), undertaking a nationwide survey of the country's estuaries. This program, which lasted six years (1993-1998), included water quality, geomorphological and ichthyofaunal surveys. Data were collected on some 250 estuaries, which greatly enhanced the state of information on South African estuaries, many of which had very little or no available information.

#### **Period 1997-2007**

The results of the above CSIR survey were used to apply an Estuarine Health Index for a National State of the Environment Report (Harrison et al. 2000). Several regional publications on the estuarine fish fauna of various coastal sectors were also produced as a result of these surveys (Harrison 1997a, 1997b, 1998, 1999a, 1999b), information which was widely used by estuarine scientists in the region. The study also provided the foundation and data for the development of a multimetric fish index to assess the environmental condition of estuaries (Harrison & Whitfield 2004, Harrison & Whitfield 2006a). The data also allowed aspects of the biogeography of South African estuarine fish communities to be investigated (Harrison



**Figure 26.** Block nets being set up in a saltmarsh as part of Angus Paterson's PhD study on the fishes of this habitat type in the Kariega Estuary (Photo: Alan Whitfield).



**Figure 27.** Seine netting in the temporarily closed Mtana Estuary as part of the nationwide estuary survey by Trevor Harrison (Photo: Alan Whitfield).





**Figure 28.** Nadine Strydom preparing a WP2 plankton net for a larval fish study in the Kromme Estuary (Photo: Alan Whitfield).



**Figure 29.** A fine mesh fyke net set to record the recruitment of late larvae and early juvenile fish into the Sundays Estuary (Photo: Paula Pattrick).



2002, 2005). The relationship between estuary typology and their fish communities was investigated both regionally and nationally (Harrison & Whitfield 2006a) as was the influence of temperature and salinity on the structuring of estuarine fish assemblages (Harrison & Whitfield 2006b).

The above use of fishes as indicators of estuarine 'health' stimulated related work in this field (Quinn et al. 1999) and also resulted in a review by Whitfield & Elliott (2002). There were also important papers on the influence of river flow and the vital role of fresh water on the structure and functioning of fish assemblages in southern African estuaries (Quinn et al. 1999, Grange et al. 2000, Bate et al. 2002, Strydom et al. 2002, Whitfield & Harrison 2003, Whitfield & Paterson 2003, Whitfield 2005b).

A renewed emphasis on small temporarily open /closed estuaries (Cowley & Whitfield 2001a, 2001b, 2002, James et al. 2007a, 2007b) included a new topic of investigation, i.e. post-larval fish recruitment over the sand berm during marine overwash events (Bell et al. 2001, Cowley et al. 2001, Vivier & Cyrus 2001, Kemp & Froneman 2004). Fish larval work in estuaries also continued to gain momentum (Strydom 2003a, 2003b, Strydom et al. 2002, 2003, Strydom & Wooldridge 2005, Patrick et al. 2007). In addition, attention was given to fish recruitment to nursery habitats in estuarine bays (Weerts & Cyrus 2002a, 2002b).

Isolation of the St Lucia system from the sea during a major long-term drought and high lake salinities marked the beginning of what was to become a stream of papers being published on fish responses to a major environmental perturbation (e.g. Whitfield et al. 2006, Cyrus & Vivier 2006a, 2006b, Mann & Pradervand 2007, Cyrus et al. 2010a, 2010b, Vivier et al. 2010).

The increasing availability of estuarine fish data on a country wide scale led to some significant papers (e.g. Maree et al. 2000, Paterson & Whitfield 2000, Harrison & Whitfield 2006b, 2006c). There were also a number of reviews (Whitfield & Bok 1998, Whitfield 1999, Whitfield & Marais 1999, Harrison 2002, Pradervand & Baird 2002, Whitfield 2005a, 2005b), including papers supporting fish

conservation in estuaries (Whitfield 1997, 1998; Turpie et al. 2002).

### **Period 2008-2018**

This period was marked by the introduction of new technologies to study fishes in estuaries. The availability of underwater video cameras to study the habitat use and behaviour of estuary-associated fish species was used very successfully in small and large estuaries in the Eastern Cape Province but was limited to clear systems for obvious reasons (Becker et al. 2010, Becker et al. 2012, Leslie et al. 2017). This was followed by the use of DIDSON sonic images of fishes that allowed a wide variety of ichthyological questions to be answered over diel cycles in both open and closed estuaries, as well as clear and turbid systems (Becker et al. 2011a, 2011b, Becker et al. 2013a, 2013b, Becker et al. 2016).

The implementation of acoustic tracking technology resulted in a number of fish movement studies on important fishery species (e.g. Kerwath et al. 2005, Næsje et al. 2007, 2012, Cowley et al. 2008, Childs et al. 2008a, 2008b, 2008c, Bennett et al. 2011, 2012, 2013, 2015, 2017a, 2017b, Maree et al. 2016, Dames et al. 2017, Grant et al. 2017a, 2017b). This facilitated assessments of the home ranges of targeted species and therefore highlighted their vulnerability to fishing activities whilst in estuaries. These studies also greatly improved our understanding of aspects of the biology and ecology of a range of marine species in estuaries, as well as the degree to which estuaries are used as nursery areas by juveniles and adults of these taxa.

Regional review papers arising mainly from the earlier CSIR estuarine fish survey continued to be generated for the various coastal sectors (James & Harrison 2008, 2010a, 2010b, 2011, 2016) as well as regional and national assessments of estuary fish functional guilds and trophic structure (Harrison & Whitfield 2008, 2012). The CSIR dataset was also used to assess the possible role that grey mullet (*Mugilidae*) could play as indicators of global warming around the coast (James et al. 2016).

Stable isotope studies were used to interpret the role of different fish species in the estuarine



**Figure 30.** Retrieval of a small otter trawl from the Kariega Estuary, Eastern Cape Province. The otter boards which hold the net in the open position can also be seen (Photo: Alan Whitfield).



**Figure 31.** Deployment of the shoeless beam trawl, especially designed for use in estuaries, by Trevor Harrison, the creator of this particular sampling gear (Photo: Alan Whitfield).

ecosystem. Earlier work in the Kariega (Paterson & Whitfield 1997) and Mngazi and Mngazana estuaries (Mbande et al. 2004) was followed by studies in other systems in an attempt to gain further insights into carbon flow within these estuaries (Sheppard et al. 2012, Bergamino et al. 2014, Magoro et al. 2015, Costalago et al. 2015, Carassou et al. 2016, 2017). What became apparent from this work was that saltmarshes and mangroves contribute relatively little carbon to the functioning of estuarine fish assemblages and that benthic and epiphytic microalgae in particular are very important to the bionomics of southern African estuaries. However, the structural importance of littoral macrophyte habitats as refuges for small fish was also emphasized (Paterson & Whitfield 2000b, 2003, Whitfield 2017, Nel et al. 2018).

Biomarker research on fishes in estuaries, using the omnivorous *Rhabdosargus holubi* as the indicator species, was attempted for the first time in order to measure stress arising from anthropogenic impacts in three Eastern Cape systems (Richardson et al. 2010). This led to the development of a broad index that included the Estuarine Fish Community Index (EFCI) and could be used to determine fish health at both the individual and community level in estuaries (Richardson et al. 2011).

Genetic studies also gathered momentum, targeting recreationally important taxa so that the information could also be of use from a stock management perspective (Mirimin et al. 2016, Oosthuizen et al. 2016). In addition, rare and endangered fish species, such as the Knysna seahorse *Hippocampus capensis* were also studied from a conservation perspective (Teske et al. 2003). Similarly, the relevance of life-history styles, and genetics for the conservation of two estuary-associated pipefish species was investigated (Whitfield et al. 2017a). Population genetics were used to assess the degree of connectivity of an estuarine fish species (Phair et al. 2015) and, for the first time in southern Africa, RNA/DNA ratios provided a new method to assess the nutritional condition of fish larvae in selected Eastern Cape estuaries (Costalago et al. 2014, 2015).

The increased knowledge of larval fishes in temperate southern African estuaries increased

considerably over this period (Montoya-Maya & Strydom 2009a, Kruger & Strydom 2010, Strydom & Wooldridge 2012, Strydom et al. 2014, Sutherland et al. 2012) and culminated in a major review on the diversity, abundance and distribution of larval fishes within these systems (Strydom 2015). The level of understanding in terms of marine /estuarine recruitment processes for both larvae and early juveniles also increased substantially, mainly as a result of work done in Eastern Cape systems (James et al. 2008a, Patrick & Strydom 2008, Kruger & Strydom 2011, Strydom et al. 2015, Kisten et al. 2015, 2017).

The possible impacts of global change, and climate change in particular, became a major focus of estuarine ichthyological research during this period (James et al. 2008b, 2008c, 2011, 2013, 2016, 2018a, Whitfield et al. 2016). Changing river flows and the impact that this has on estuary-associated fishes also continued to be a major area of research (James et al. 2008d, 2018b, Lamberth et al. 2008, Vorwerk et al. 2008a, 2008b, 2009, Whitfield & Taylor 2009, Wasserman & Strydom 2011, Whitfield et al. 2013, Nodo et al. 2017, 2018, Mbandzi et al. 2018).

Synthesis and review type papers continued to be generated on both a national and regional basis using the ever increasing database covering fishes in southern African estuaries (Harrison & Whitfield 2008, 2012, James & Harrison 2008, 2009, 2010a, 2010b, 2011, 2016, Whitfield & Cowley 2010, Whitfield et al. 2012a, 2012b, Whitfield & Becker 2014, Whitfield & Patrick 2015, Whitfield 2015, 2016a, 2016b, Whitfield 2017, Whitfield et al. 2017b, 2018).

### The future

Although considerable progress has been made over the past four decades in particular (Figure 36), much work remains to be done before we can say that we have a comprehensive understanding of the biology and ecology of fishes in southern African estuaries. Indeed, for most fish species occurring in estuaries there is no available dietary or other basic biological information (e.g. growth and reproduction). More than 60% of southern African estuaries have no comprehensive fish species checklist, let alone seasonal information, and





**Figure 32.** Ryan Palmer and Nikki James assessing the influence of climate change on estuary-associated fish species in the Sundays system (Photo: Alan Whitfield).



**Figure 33.** Small seine net sampling of the Kwesani Micro-estuary as part of Mandla Magoro's PhD study on the ecology of Eastern Cape micro-estuaries and micro-outlets (Photo: Tatenda Dalu).



less than 10% of the systems on the subcontinent can be described as well studied. Remote Eastern Cape estuaries have been particularly neglected by past research efforts, despite the subtropical / warm-temperate biogeographical transition zone occurring within this region.

A similar 'window of opportunity' has been identified for poorly-studied micro-estuaries and micro-outlets around the subcontinent, with a research team from the South African Institute for Aquatic Biodiversity, Nelson Mandela University and Rhodes University having recently completed an Eastern Cape research programme on these systems (Figure 37). This work, which has identified the sensitivity of these small systems to even minor catchment perturbations, needs to be expanded on a national basis.

During the next decade, new demands will be placed on estuarine scientists, with funding being increasingly linked to societal priorities rather than broader environmental issues. However, these demands should also be seen as a challenge, and our research should be geared towards providing the type of information required for the maintenance of vital ecological processes within estuaries, as well as supporting recreational and subsistence fisheries, ecotourism and boosting coastal employment. Much effort and financial investment is being made in the new 'Operation Phakisa' initiative – estuarine fish biologists and ecologists need to link the importance of their work in making the Blue Economy sustainable for generations to come. Without a fundamental understanding of the link between estuarine nursery areas and primary and secondary productivity under various global change scenarios, there can be no wise management of coastal fishery resources.

The involvement of socio-economic specialists in the ichthyological research field has become an imperative, with funding from most government sources now demanding that these aspects form a major and integral part of any major scientific proposal. Research on the rehabilitation

or restoration of natural estuarine functioning, especially where systems have become severely degraded, is also gaining momentum (Elliott et al. 2016).

The urgent need for estuarine research in Mozambique, Angola and further north remains. The reason for prioritizing East African estuarine studies is because most of the southern African fish species are tropical Indo-Pacific in origin but have been little studied in this important biogeographical region. Indeed, there are large areas along this coast where even preliminary checklists of fish species are lacking and where recently pristine systems are being rapidly transformed by intensive resource exploitation. International funding and estuarine research support from both developed countries and South Africa will be imperative for the success of such initiatives.

The current generation of estuarine ichthyologists is extremely fortunate in having access to technologies that researchers in the last century could only dream about. For example, the use of stable isotope and fatty acid analyses, underwater video and sonic imagery technology, acoustic and pit tag implants, biomarker and genetic studies, all provide opportunities for answering questions that were not possible only three decades ago. In addition, the increasing use of non-destructive sampling methods such as underwater video technology and eDNA, and the increasing avoidance of destructive sampling methods such as rotenone and gill netting, is to be strongly commended.

The ability to simulate estuary functioning using rapidly evolving ecosystem models, driven by high-powered computers, is a research avenue that also needs to be pursued with vigour. However, the basic information that these models require is often not available and there is a limit to how many 'assumptions' can be made before the model loses its value. Clearly government and associated research institutions are currently not investing sufficient financial and human resources to obtain such information and thus the challenge will remain into the future.

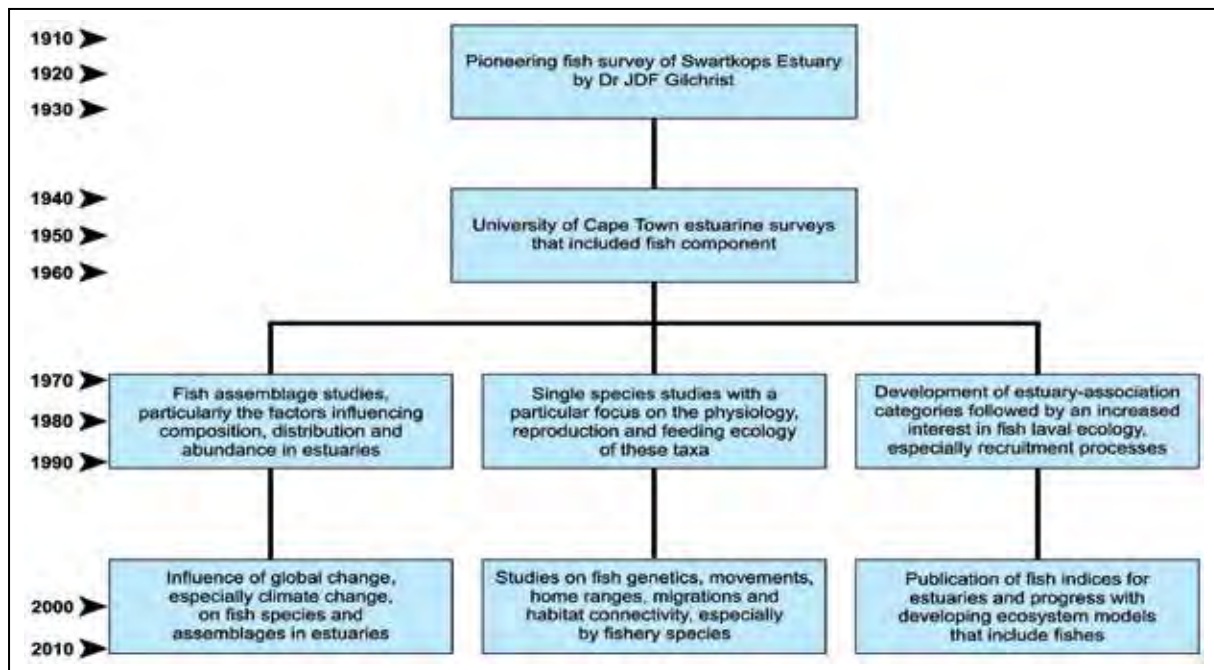


**Figure 34.** Rhett Bennett handing Alistair Becker a DIDSON for placement in the Kowie Estuary to record fish abundance and behaviour during both the day and night (Photo: Alan Whitfield).



**Figure 35.** Taryn Murray and Dylan Howell retrieving an acoustic 'listening station' that had been recording the movements of acoustically tagged fish in the Bushmans Estuary (Photo: Paul Cowley).





**Figure 36.** Diagrammatic representation of major phases in past South African estuarine fish research (1910-2010) (after Whitfield 2010).



**Figure 37.** The Eastern Cape micro-estuaries team, an independent research initiative (2015-2017) led by Alan Whitfield and Renzo Perissinotto to examine the structure and functioning of micro-estuaries and micro-outlets (Photo: Tatenda Dalu).





## Chapter 2

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### Fishes of southern African estuaries

#### 2.1 INTRODUCTION

ESTUARIES ARE REGIONS where marine and fresh waters meet, where environmental gradients are steep, and where exceptionally high levels of production are often recorded. These factors have a major influence on the numbers, variety and biomass of fishes that can live in these systems. In particular, the often abrupt changes in salinity, temperature, turbidity and other variables place considerable physiological demands on the fishes that utilize estuaries. However, those species which are broadly tolerant of biotic and abiotic variability are at a considerable advantage over those fishes that cannot survive such fluctuations.

In this chapter the attributes required by fishes utilizing southern African estuaries are reviewed. Particular attention is given to the recruitment mechanisms of postlarvae entering estuaries, as well as the movements of the juveniles of certain marine species within these systems. Evolutionary processes that have structured fish assemblages in estuaries on the subcontinent are examined and a brief comparison between the fishes of Devonian and Holocene estuarine lakes is undertaken. The question of estuarine association and dependence is discussed and there is also a detailed review of fish biomass and productivity. The chapter concludes with an examination of fish foraging and food webs in estuaries on the subcontinent.

In order to contextualise the estuary-associated fish assemblages of southern Africa, we have to assess the ichthyofauna on a continent wide basis (Figure 38). Using lists of fish species and families sampled in cool-temperate, warm-temperate, subtropical and tropical African estuaries, it was determined that both species and family diversity declined between tropical and temperate sub-Saharan estuaries (Figure 39). Eastern and western tropical estuaries had similar numbers of species and families, with the ratio of species to families increasing from temperate to

tropical systems. Although the genera of many tropical fish families were represented on both sides of the continent, the species were very different, probably due to initial connectivity and then isolation and speciation (Whitfield 2005c).

The Sparidae and Mugilidae were the two most diverse fish families in the temperate biogeographic regions, the Gobiidae and Mugilidae in tropical and subtropical eastern African regions, and Carangidae and Gobiidae in western African tropical regions. In terms of species richness, the families Mugilidae and Sparidae often exceeded 10 species and the Gobiidae sometimes exceeded 20 species. Only the Gobiidae and Mugilidae featured in the top five families in all the biogeographic regions surveyed (Whitfield 2005c).

Species and family composition comparisons between the different regions were undertaken using the Bray-Curtis Similarity Coefficient. Results indicated that although family similarities between the different regions were generally high, this was often not the case at the species level (Whitfield 2005c). Temperate zones along the southern and southwestern coast of Africa prevent mixing of east and west coast tropical fish species, thus causing the low species similarity between the ichthyofauna in the two tropical regions. Differentiation of these 'geminant' species on the eastern and western African coasts appears to have commenced at least 12 million years ago and coincided with the development of the Benguela upwelling system along the southwest coast of Africa that isolated tropical fish species on either side of the continent.

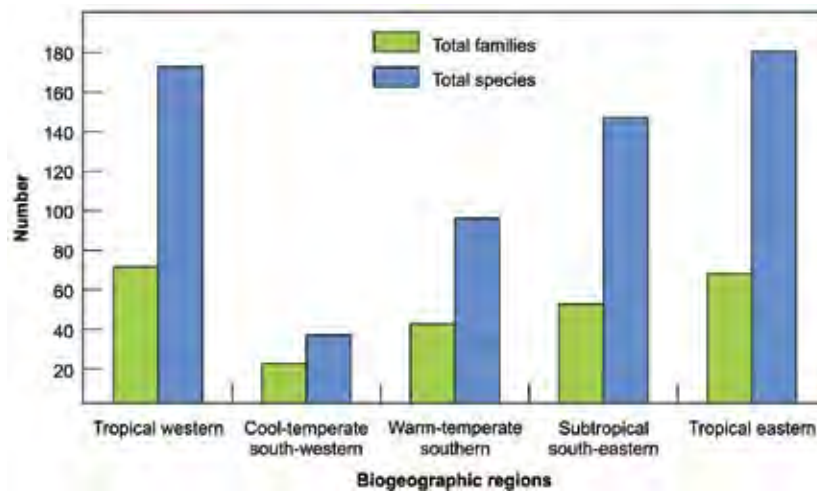
Fish species in the different biogeographic regions were divided into guilds based upon their origins (Whitfield 2005c). Preliminary results showed that marine taxa provided between 68% and 75% of the fish species richness recorded in sub-Saharan estuaries, with estuarine resident

taxa accounting for between 10% and 25%. Freshwater taxa comprised less than 7% of fish richness on the east and south coasts of Africa compared to more than 21% in the west. The greater representation of freshwater forms in

central /west African estuaries is probably related to the high flows from tropical central and western African rivers, and the extensive lagoonal conditions prevailing within these coastal zones (Whitfield 2005c).



**Figure 38.** Map showing the biogeographic regions used to assess fish assemblages in sub-Saharan African estuaries (after Whitfield 2005c).



**Figure 39.** Fish richness (number of species and families) in sub-Saharan African estuaries (after Whitfield 2005c).

## 2.2 LIFE-HISTORY STYLES

The fishes inhabiting estuaries may be divided into two major groups according to their ability to breed within the estuarine environment. The first group is dominant in terms of biomass and comprises euryhaline marine species that spawn at sea but make extensive use of estuaries during juvenile and sometimes the adult life stages (Dando 1984). The second group spawn within the estuarine environment, although certain species may also breed at sea or in fresh water (Whitfield 1998). For the purposes of this book, the former group has been classified as marine and the latter as estuarine. Although catadromous anguillid eels do not utilize estuaries to any significant extent for foraging, these systems are vital conduits to complete the life history of these species and they are therefore included in this analysis.

The main feature of the life cycle of most marine species utilizing southern African estuaries is a division into a juvenile phase that is mainly estuarine and an adult life stage that is predominantly marine (Wallace 1975b). The proportion of juveniles entering estuaries varies according to species. Marine juveniles usually enter estuaries at 10-60 mm SL, although most species have completed their active recruitment phase by the time a length of 20 mm is attained (Wallace & van der Elst 1975). After a residence period of approximately 1-3 years these fish then return to the sea where they join adult stocks when mature. Although some species may attain sexual maturity within the estuarine environment, most do not and spawning generally occurs in the sea (Wallace 1975b).

There are relatively few fish species that can complete their entire life cycle within southern African estuaries and these are invariably small species (Table 3). Sexual maturity usually occurs at less than 50 mm SL, in contrast to marine taxa where most mature above 200 mm SL (Table 4). Wallace (1975b) has suggested that the small size of estuarine species would reduce their physical ability to undertake mass migrations to and from the sea, and also make them vulnerable to predation by large piscivorous fishes that are abundant

in the marine environment. However, some estuarine species (e.g. *Atherina breviceps* and *Syngnathus temminckii*) are known to breed in both estuaries and the sea.

More recently, the guild approach originally developed by Elliott et al. (2007) for the ways in which fish use estuaries has been further refined by Potter et al. (2015) to comprise four categories, i.e. marine, estuarine, diadromous and freshwater, with each containing multiple guilds. Examples of southern African fish species from all four categories, and comprising a total of 10 guilds, are illustrated in Figure 40.

The question as to which fish guilds are strictly estuarine-dependent has been asked on a number of occasions, most recently by Potter et al. (2015). Recognition that many commercial fish species are found in estuaries at some stage of their life cycle has led to numerous authors categorizing them as 'estuarine dependent' or 'estuarine species' when discussing and quantifying the importance of estuaries to such species. Thus, McHugh (1976) calculated that these species contributed 69% to the weight of the total commercial fishery catch in the United States in 1970.

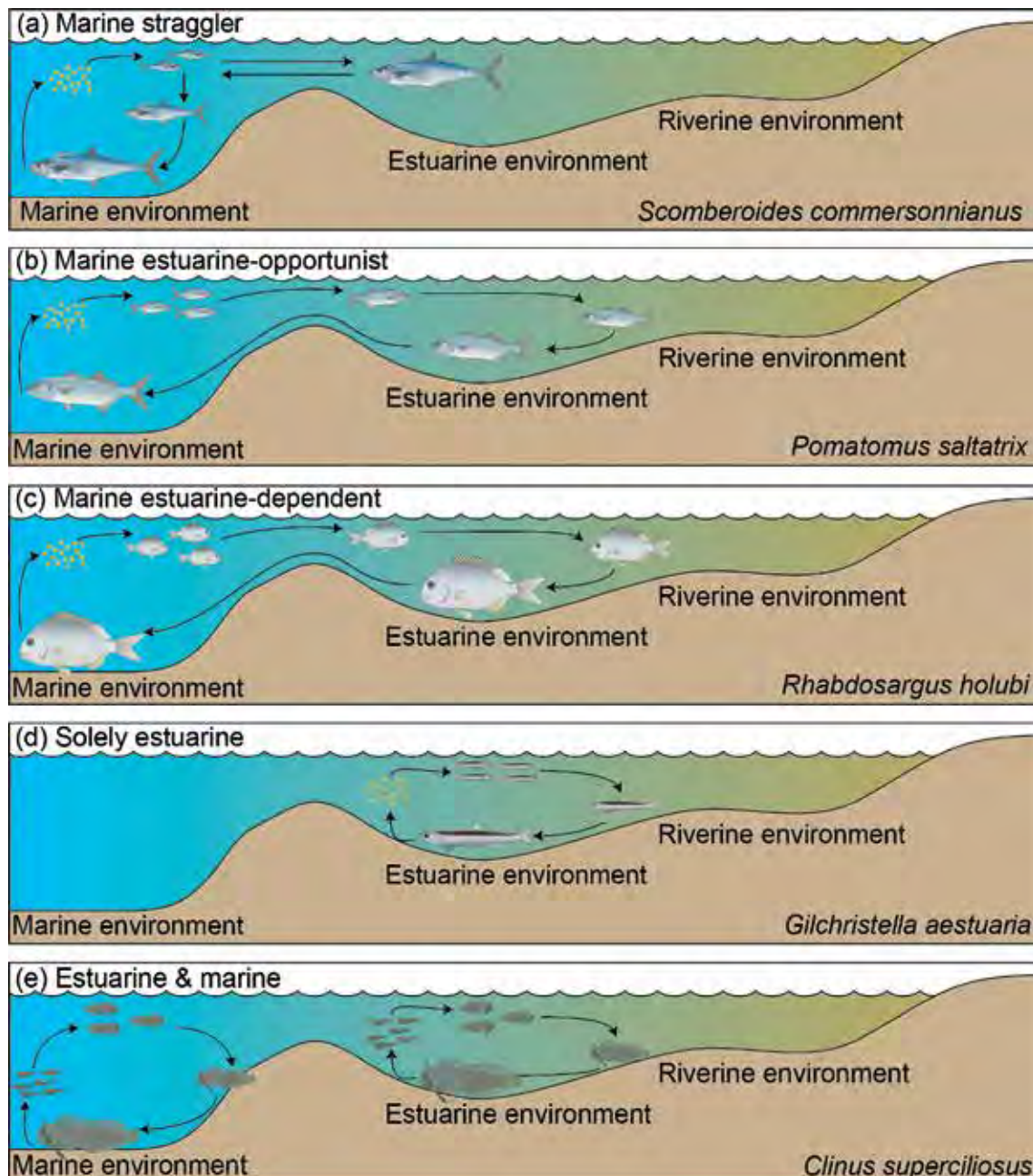
It must be emphasized that the groupings used for the above assessments covered both 'estuarine dependent' and 'estuarine' species belonging to marine taxa, estuarine residents and diadromous species. The marine category included some species that are not strictly dependent on estuaries in the formal sense of the word, i.e. estuaries are essential for the survival of the species. Indeed, the conclusion by Able & Fahay (2010) that "estuarine dependent has become a part of resource managers' lexicons, despite a lack of critical testing or exacting definition" needs to be emphasized if estuarine ichthyologists are to retain credibility on this topic. Although similar calculations have not been done for southern African estuary-associated fish species, contributions to commercial catches are likely to be low but high for recreational and subsistence fisheries.

The view of Able (2005) that species using estuaries extensively are best regarded as either obligate or facultative users is fully supported. Thus, species

belonging to the marine estuarine-dependent guild, the solely estuarine guild, the estuarine migrant guild, and the diadromous guild, as defined by Potter et al. (2015), are obligate users of estuaries and therefore likely to show severe declines in abundance should this environment be unavailable or badly polluted. In contrast, fish species in the marine estuarine-opportunist and freshwater estuarine-opportunist guilds constitute

facultative users of estuaries (Potter et al. 2015), and can make extensive use of the marine neritic zone or inland freshwater areas should estuarine habitats become unavailable due to prolonged mouth closure or environmental degradation.

The African subcontinent has four obligate catadromous fish species, all belonging to the family Anguillidae (*Anguilla bicolor*, *A. labiata*, *A. marmorata* and *A. mossambica*), and no recorded

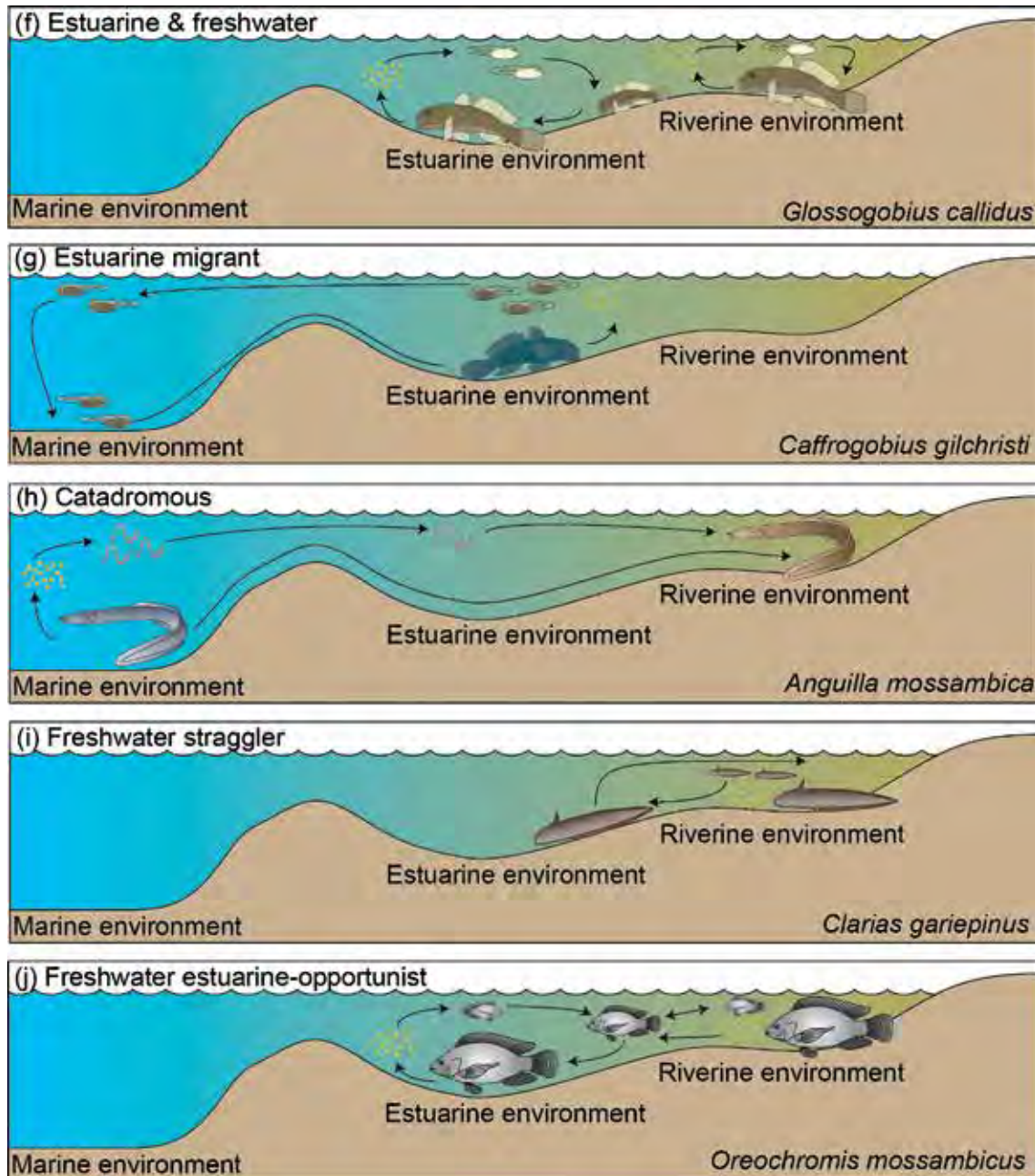


**Figure 40.** Guilds of fishes in southern African estuaries using the estuarine usage functional group approach (see Potter et al. 2015 for more details). (a) Talang queenfish *Scomberoides commersonnianus*, (b) Elf *Pomatomus saltatrix*, (c) Cape stumpnose *Rhabdosargus holubi*, (d) Estuarine roundherring *Gilchristella aestuaria*, (e) Super klipfish *Clinus superciliosus*. The technical assistance of James Tweedley in compiling this figure is gratefully acknowledged.



anadromous taxa. Of these four species, only *Anguilla. mossambica* is both abundant and widespread in southern African waters. According to Bruton et al. (1987) the probable reasons for the paucity of diadromous fishes on the subcontinent are the unstable nature of the rivers due to mostly low rainfall and frequent droughts, together with the unreliable availability of resources such as food and space when compared with the ocean.

*Pseudomyxus capensis* is one of the few marine fish species that makes extensive use of the riverine environment as a nursery area (Bok 1979). Although spawning occurs at sea, *P. capensis* lives mainly in estuaries, with large numbers also making use of rivers. Carassou et al. (2017) have suggested that interspecific competition with other mugilids may be an important factor accounting for the virtual absence of *P. capensis* from the



**Figure 40 (continued).** Guilds of fishes in southern African estuaries using the estuarine usage functional group approach. (f) River goby *Glossogobius callidus*, (g) Prison goby *Caffrogobius gilchristi*, (h) Longfin eel *Anguilla mossambica*, (i) Sharptooth catfish *Clarias gariepinus*, (j) Mozambique tilapia *Oreochromis mossambicus*. The technical assistance of James Tweedley in compiling this figure is gratefully acknowledged.

Table 3. Approximate standard length (SL) at first sexual maturity of some southern African estuarine fish species that have been recorded breeding within these systems. Where different values are given in the literature for males and females of a particular species, these are shown.

Fish species	Family	SL (mm)	Reference
<i>Ambassis ambassis</i>	Ambassidae	50	van der Elst (1988)
<i>Ambassis natalensis</i>	Ambassidae	35	Wallace (1975b)
<i>Atherina breviceps</i>	Atherinidae	40	Ratte (1989)
<i>Caffrogobius gilchristi</i>	Gobiidae	50	Bennett (1989)
<i>Caffrogobius nudiceps</i>	Gobiidae	45	Day et al. (1981)
<i>Clinus spatulatus</i>	Clinidae	65	Bennett (1983)
<i>Clinus superciliosus</i>	Clinidae	50	Prochazka (1994)
<i>Croilia mossambica</i>	Gobiidae	30	Blaber & Whitfield (1977b)
<i>Gilchristella aestuaria</i>	Clupeidae	30	Blaber (1979)
<i>Glossogobius callidus</i>	Gobiidae	35	Boullé (1989)
<i>Hippocampus capensis</i>	Syngnathidae	89	Lockyear et al. (1997)
<i>Hyporhamphus capensis</i>	Hemiramphidae	80	Wallace (1975b)
<i>Periophthalmus argentilineatus</i>	Gobiidae	50	Stebbins & Kalk (1961)
<i>Psammogobius knysnaensis</i>	Gobiidae	30	Bennett (1989)
<i>Redigobius dewaali</i>	Gobiidae	30	Kramer et al. (2015)
<i>Syngnathus temminckii</i>	Syngnathidae	130 (m) 120 (f)	Mwale et al. (2014)
<i>Syngnathus watermeyer</i>	Syngnathidae	120 (m) 100 (f)	Mwale et al. (2014)

saline parts of certain Eastern Cape estuarine systems.

According to Bok (1983), the relatively wide range in size and age at sexual maturity is an insurance by this species against consecutive dry years due to isolation in fresh water reaches during droughts. Other life-history traits of *P. capensis* suited for riverine use include reduced gonadal development in fresh water which minimizes the risk of energy wastage if ripe fish are isolated in freshwater reaches for protracted periods. The catadromous life-history style of *P. capensis* therefore differs from that of other southern African mugilids, with the exception of *Mugil cephalus* which also makes use of riverine habitats in some regions.

The cichlid *Oreochromis mossambicus* is the only abundant freshwater species in southern African estuaries. It occurs in large numbers in coastal lakes and temporarily closed estuaries, but is usually absent from the lower reaches of permanently open estuaries (Whitfield & Blaber 1979c). When temporarily closed estuaries are breached,

this species usually retreats into the upper reaches.

Widespread breeding has been recorded in several estuaries during the closed mouth phase, with parental care enhancing survival of offspring within these environments. Young are released by mouth-brooding adults when they attain about 10 mm SL (Bruton & Bolt 1975), by which time they can avoid being swept out to sea when the estuary mouth opens. In small subtropical estuaries, which are seldom open to the sea, this species is often a dominant component of the ichthyofaunal community (Begg 1984a).

The paucity of freshwater fish species in southern African estuaries, even during periods of elevated freshwater input, may be partially attributed to the abundant estuarine and marine fish assemblages found within these systems (Ter Morshuizen et al. 1996a, 1996b). Exclusion of freshwater taxa from estuaries is likely to be due to competition with the latter groups, as well as predation by the comparatively large number of piscivorous fish found in estuarine versus freshwater systems on the subcontinent. However, in

Table 4. Approximate standard length (SL) at sexual maturity of some marine fish species recorded in southern African estuaries. Where different values are given in the literature for males and females of a particular species, these are shown.

Fish species	Family	SL (mm)	Reference
<i>Acanthopagrus vagus</i>	Sparidae	170	Wallace (1975b)
<i>Argyrosomus japonicus</i>	Sciaenidae	780 (m) 900 (f)	Griffiths (1996)
<i>Caranx ignobilis</i>	Carangidae	580	van der Elst (1988)
<i>Caranx sexfasciatus</i>	Carangidae	420	van der Elst (1988)
<i>Chanos chanos</i>	Chanidae	870	van der Elst (1988)
<i>Chelon dumerili</i>	Mugilidae	180	Wallace (1975b)
<i>Chelon richardsonii</i>	Mugilidae	180	de Villiers (1987)
<i>Chelon tricuspidens</i>	Mugilidae	380	Wallace (1975b)
<i>Crenimugil buehneri</i>	Mugilidae	170	Wallace (1975b)
<i>Diplodus capensis</i>	Sparidae	190	Mann & Buxton (1998)
<i>Diplodus hottentotus</i>	Sparidae	240	Mann & Buxton (1998)
<i>Galeichthys feliceps</i>	Ariidae	260 (m) 240 (f)	Tilney & Hecht (1993)
<i>Gerres longirostris</i>	Gerreidae	110	Cyrus & Blaber (1984a)
<i>Gerres methueni</i>	Gerreidae	110 (m) 140 (f)	Cyrus & Blaber (1984a)
<i>Hilsa kelee</i>	Clupeidae	150	Blaber (1979)
<i>Johnius dorsalis</i>	Sciaenidae	100 (m) 130 (f)	Day et al. (1981)
<i>Leiognathus equula</i>	Leiognathidae	130	Wallace (1975b)
<i>Lichia amia</i>	Carangidae	580	van der Elst (1988)
<i>Lithognathus lithognathus</i>	Sparidae	540	Bennett (1993)
<i>Lutjanus argentimaculatus</i>	Lutjanidae	490	van der Elst (1988)
<i>Lutjanus fulvivittatus</i>	Lutjanidae	130	van der Elst (1988)
<i>Megalops cyprinoides</i>	Megalopidae	250	Mann (2000)
<i>Monodactylus argenteus</i>	Monodactylidae	130	Day et al. (1981)
<i>Monodactylus falciformis</i>	Monodactylidae	140	Beckley (1984a)
<i>Moolgarda cunnesius</i>	Mugilidae	170	Wallace (1975b)
<i>Mugil cephalus</i>	Mugilidae	340	Whitfield & Blaber (1978e)
<i>Otolithes ruber</i>	Sciaenidae	230	Wallace (1975b)
<i>Planiliza macrolepis</i>	Mugilidae	230	Wallace (1975b)
<i>Platycephalus indicus</i>	Platycephalidae	360	Wallace (1975b)
<i>Pomadourys commersonii</i>	Haemulidae	300 (m) 360 (f)	Wallace (1975b)
<i>Pomadourys olivaceus</i>	Haemulidae	120 (m) 130 (f)	Joubert (1981)
<i>Pomatomus saltatrix</i>	Pomatomidae	190 (m) 200 (f)	van der Elst (1976)
<i>Pseudomyxus capensis</i>	Mugilidae	190 (m) 230 (f)	Bok (1983)
<i>Rhabdosargus globiceps</i>	Sparidae	230 (m) 190 (f)	Talbot (1955)
<i>Rhabdosargus holubi</i>	Sparidae	150	Wallace (1975b)
<i>Rhabdosargus sarba</i>	Sparidae	200	Wallace (1975b)
<i>Sarpa salpa</i>	Sparidae	130 (m) 150 (f)	Joubert (1981)
<i>Sphyraena barracuda</i>	Sphyraenidae	600	Blaber (1982a)
<i>Terapon jarbua</i>	Teraponidae	130	Day et al. (1981)

those small lagoons or river mouth type estuaries where marine species are rare due to prevailing oligohaline conditions, freshwater fish taxa may assume greater significance (Begg 1984a). Also of significance is the scarcity of large piscivorous fishes in small TOCEs. The topic of why there are so few freshwater fish species in estuaries is covered in more detail by Whitfield (2015).

### Fish early life histories

Southern African estuaries are prone to temperature, salinity, turbidity and water current variations, all of which will affect the breeding of resident fish. Reproductive specializations to reduce the mortality of eggs, embryos and larvae are therefore very evident in the estuarine group of fishes. Both *Clinus superciliosus* and *C. spatulatus* are viviparous and their young exceed 15 mm in length when released into the estuarine environment (Veith 1979, Bennett 1983). The elimination of pelagic eggs and embryo stages, which are susceptible to a wide variety of mortality factors, appears to have enabled the clinids to reduce the number of young produced, e.g. *C. superciliosus* produces a maximum of 450 embryos per spawning season (Veith 1979).

Among estuarine spawning species, relatively few complete their entire life cycle within estuaries, with some of the estuarine spawners appearing to require a marine phase in their life cycle. For example, the gobies *Psammogobius knysnaensis* and *Caffrogobius gilchristi*, and the blenny *Omobranchus woodi*, have a marine larval phase that is achieved by a synchronised hatching of the embryos at the turn of the high tide, thus facilitating a mass export of hundreds of thousands of mainly goby larvae to the sea during each nocturnal ebb tide (Whitfield 1989a, Strydom & Wooldridge 2005). These taxa then recolonise estuaries following completion of the larval stage in the marine environment. The reason why the early larval stages are spent in the marine environment are unknown but may be related to the more predictable neritic conditions when compared to estuaries.

In contrast to the life cycles of the above taxa, most estuarine resident species have reproductive specializations that facilitate the retention

of eggs, embryos and larvae within the estuarine environment. For example, the males of both *Syngnathus watermeyer* and *Hippocampus capensis* have a brood pouch in which the offspring are carried until they have reached an advanced developmental stage, thus avoiding the rigours of the estuary (Whitfield 1995b, Mwale et al. 2014).

The spawning of *Atherina breviceps* is also closely associated with submerged macrophyte beds. This species has relatively large eggs with glutinous filaments that are used for attachment to aquatic plants and other objects (Neira et al. 1988), thus aiding their retention within the estuarine environment. Although the eggs of *Gilchristella aestuaria* are free-floating (Wooldridge & Bailey 1982), this species spawns in the upper reaches of open estuaries (Talbot 1982), thereby reducing losses of embryos and larvae to the sea (Figure 41).

Evidence suggests that the spawning of most marine species found in estuaries occurs close inshore (van der Horst & Lasiak 1989), often in the vicinity of estuary mouths (Wallace 1975b, Lasiak 1983a, Harris & Cyrus 1996). Inshore currents along the KwaZulu-Natal coast also retain eggs, embryos and larvae within the region (Wallace 1975b), thus reducing the distance between breeding and nursery areas. According to Heydorn et al. (1978), the retention of these early life stages inshore prior to migration into KwaZulu-Natal estuaries is favoured by the slow overall movement of the water mass between the Agulhas Current and the coast, frequent current reversals parallel with the shore, and onshore water movements.

Within Algoa Bay and other bays along the Eastern Cape coast, cyclonic within-bay circulation occurs (Harris 1978). It has been suggested that in Algoa Bay preflexion larvae become entrained within this cyclonic circulation and, upon attainment of the postflexion stage of development, would not have to swim great distances to recruit into coastal nursery areas (Beckley 1986, Figure 42). Thus, species which spawn close inshore are likely to be retained within the bay until the onset of the estuarine phase in the life cycle (Lasiak 1984a).

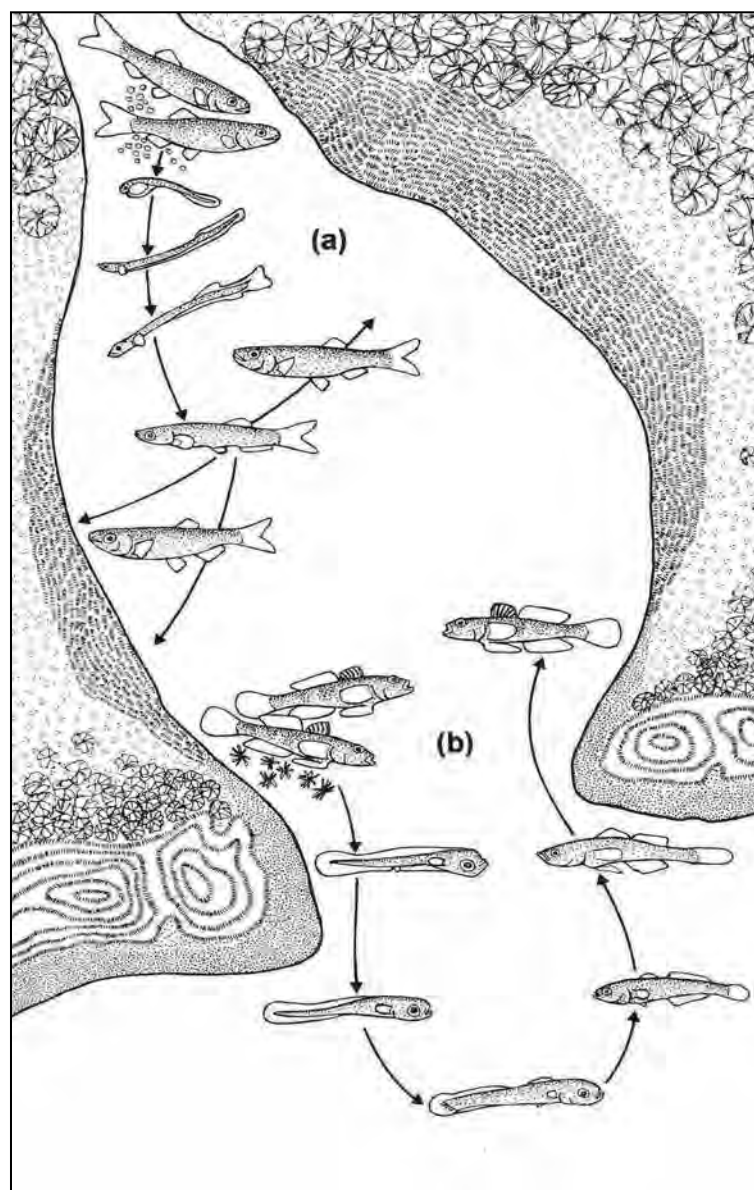
Some marine species do occasionally spawn in estuaries but this appears to be a rare occurrence.



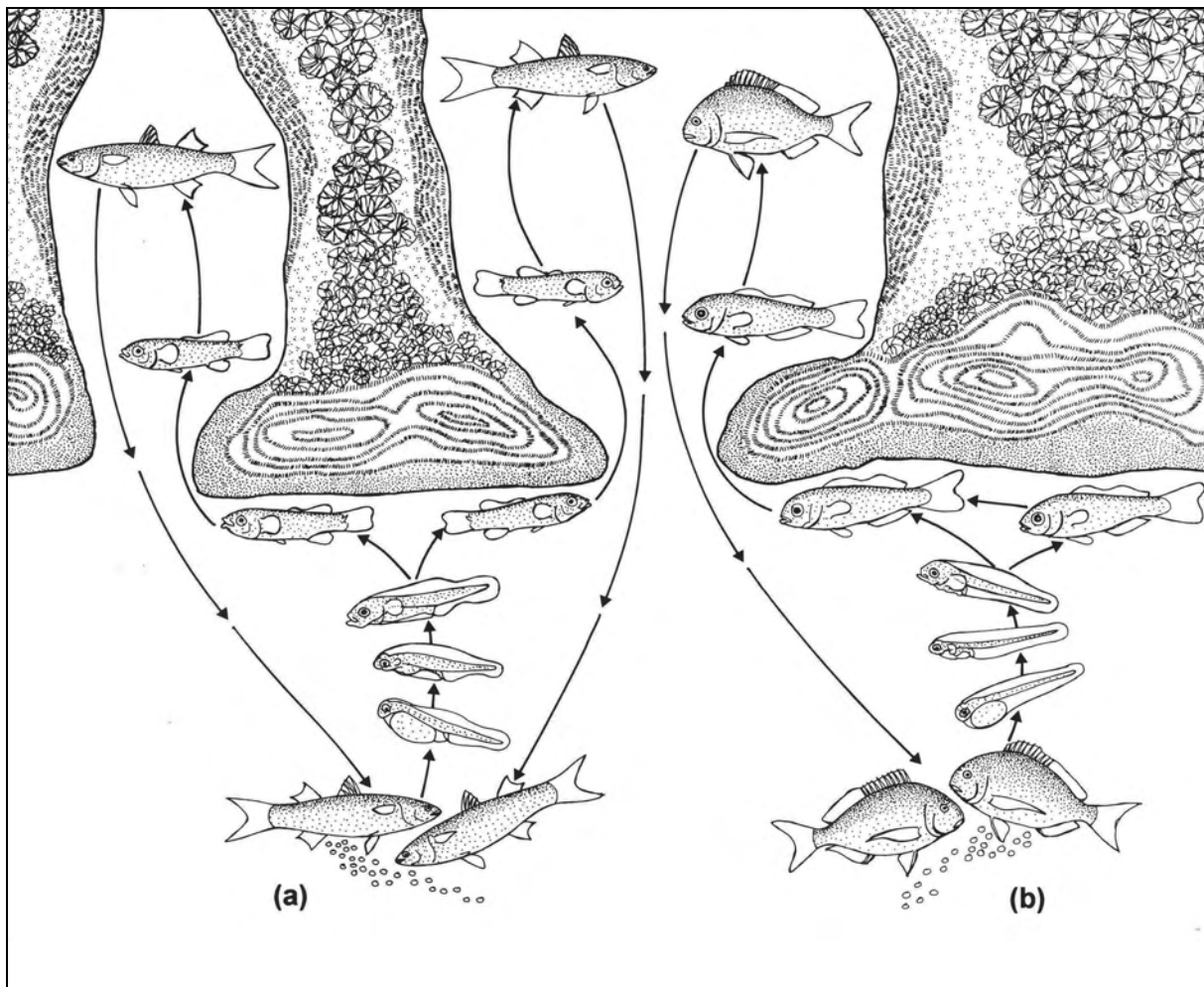
The sparid *Acanthopagrus vagus* has been recorded spawning in the mouth region of the Kosi estuary at night, with the eggs being transported out to sea during the nocturnal ebb tide (Garratt 1993). *Solea turbynei* breeds in Lake St Lucia when conditions are suitable (Cyrus 1991a) but this species has not been recorded spawning in other KwaZulu-Natal estuaries. The fertile eggs of this and other marine species have been found in the closed St Lucia system under euhaline conditions, and include *Acanthopagrus vagus*, *Ambassis* sp., *Crenidens crenidens*, *Planiliza macrolepis*, *Pomadasys comersonnii* and *Stolephorus holodon* (Connell 1996).

However, the success or otherwise of egg and larval development under such conditions has not been determined.

*Galeichthys feliceps* are mouth brooders (Tilney & Hecht 1993) and adult males have been recorded carrying eggs and young in Eastern Cape estuaries (Marais & Venter 1991), thus providing juveniles with direct access to estuarine nursery habitats. In contrast, the eggs of other marine species are mainly pelagic (Brownell 1979), with larvae drifting in ocean currents and the postlarvae being required to locate and enter estuaries without parental assistance (Wallace & van der Elst 1975).



**Figure 41.** Diagrammatic representation of the life cycles of two main types of estuarine spawners. The examples shown here are (a) the estuarine roundherring *Gilchristella aestuaria* and (b) speckled sandgoby *Psammogobius knysnaensis*.



**Figure 42.** Diagrammatic representation of the predominant life cycles of estuary-associated marine spawners, e.g. (a) flathead mullet *Mugil cephalus* and (b) Cape stumpnose *Rhabdosargus holubi*.

### Recruitment mechanisms and cues

The egg, embryonic and larval stages of marine species are retained within the nearshore environment by cyclonic circulation patterns and predominantly onshore surface current components (Heydorn et al. 1978). Once the preflexion larval stage of development has been completed, fish movement becomes active and metabolic activity increases (Edworthy et al. 2018), with individuals then entering the surf zone which may be used as an interim nursery area (Table 5). More than 60% of the ichthyoplankton found in the Swartvlei Bay and St Lucia surf zones belonged to estuary-associated taxa (Whitfield 1989b, Harris & Cyrus 1996). The increase in fish densities towards both the Swartvlei and St Lucia estuaries suggests that there is an active onshore and longshore movement towards estuary mouths.

Further support for the interim nursery hypothesis has been provided by Strydom & d'Hotman (2005) who found that 68% of all ichthyoplankton species captured in the Cape Padrone surf zone were estuary-associated taxa and 98% of all individuals collected were in the same category. A similar result was recorded in the Kwaaihoek surf zone of the Eastern Cape, and troughs within the surf with slower water currents were the preferred habitat for these postflexion larvae (Watt-Pringle & Strydom (2003)).

How do the postlarvae locate the estuary mouth once they have entered the surf zone? Blaber & Blaber (1980) have suggested that turbidity gradients in the marine environment (Figure 43) may aid juvenile fishes to locate estuarine nursery areas, and Harris & Cyrus (1996) present evidence to support this hypothesis for

Table 5. Some possible processes and behaviour influencing marine fish immigration to southern African estuarine nursery areas.

Habitat:	Nearshore marine	Surf zone	Estuary mouth	Estuary
<b>Physical processes</b>	Coastal currents	Longshore transport	Tidal flux transport	Estuarine currents
<b>Fish development</b>	Egg/embryo/larval preflexion stages	Postflexion/early juvenile stages	Early juvenile stages	Juvenile stages
<b>Fish movement</b>	Mainly passive	Mainly active	Active and passive	Active
<b>Orientation to estuarine cues</b>	No	Yes	Yes	Yes

the St Lucia region. However, Whitfield (1994a) compared the recruitment of larval and juvenile fishes into three Eastern Cape estuaries with differing turbidities and showed that both the Sundays (average turbidity 10 NTU) and Great Fish (average turbidity 65 NTU) had similar ichthyonekton recruitment and abundance. These results suggest that in warm-temperate southern African estuaries, turbidity gradients do not play a major role in postlarval abundance within these systems.

Whitfield (1994a) also found that the abundance of newly-recruited marine fishes in permanently open Eastern Cape estuaries showed a significant positive correlation with longitudinal salinity gradients within these systems. However, detectable salinity gradients within the marine environment are usually absent, and it is most likely that riverine and estuarine olfactory cues associated with ebb tidal waters attract the post-larvae into estuaries. This view is supported by the study of Strydom (2003a) which showed



**Figure 43.** Turbidity and olfactory gradients in the sea may aid the recruitment of marine estuary-associated fish postflexion larvae towards the coast and then into estuaries (Photo: Alan Whitfield).

major increases in the abundance of postflexion estuary-associated marine fish larvae in the surf zone following estuary opening events. The postlarvae of most marine fish species are likely to wait until river flooding ceases before entering estuaries, e.g. Engraulidae entering the Mhlathuze Estuary showed maximum recruitment when river flow was minimal (Viljoen & Cyrus 2002).

Indirect evidence to support the olfactory hypothesis also comes from the observation that marine postlarvae are able to enter temporarily closed estuaries when marine overtopping of the mouth sandbar occurs (Whitfield 1998) and no salinity gradient between the estuary and sea is detectable. Olfactory cues associated with seepage of estuarine water through sand bars (Figure 44) could provide the key to locating the mouth area of temporarily closed estuaries, and thus facilitate the safe transfer of postlarvae over these barriers and into the estuary during overwash events. Additional evidence to support this hypothesis can be found in the concentration of postflexion larvae of estuary-associated species adjacent to sand bars at the closed Swartvlei and St Lucia

mouths, thus suggesting that olfactory rather than turbidity cues are attracting these fish to the area (Whitfield 1989b, Harris & Cyrus 1996).

Experimental evidence which suggests that estuary-associated marine fish species do use olfactory cues to locate and enter estuaries is provided by James et al. (2008a) and shows that postflexion *Rhabdosargus holubi* larvae recognize water from different origins and are most attracted to water containing riverine and /or estuarine cues. The source and nature of the attractant is unknown but it is likely to be dissolved organic material from more than one source. Since estuarine water also contains river water, the origin of the major attractant for these postlarval fishes may well be from the catchment but distinctive estuarine cues cannot be ruled out. This view is supported by the results from Whitfield (1994a) which showed some early marine juvenile recruitment in the absence of river flow into the Kariega Estuary.

The swimming abilities of marine postflexion larvae seeking estuaries is not to be underestimated. Experimental tests on wild caught settlement stage sparids *Diplodus capensis* and *Sarpa*



**Figure 44.** Seepage of estuarine water through the sand bar at the mouth of TOCEs may provide olfactory cues to postflexion marine fish larvae in the sea to locate temporarily closed estuaries (Photo: Alan Whitfield).



*salpa* revealed a maximum swimming speed for the former species of  $19 \text{ cm s}^{-1}$  and  $18 \text{ cm s}^{-1}$  for the latter (Patrick & Strydom 2009). The mean endurance distance covered was also similar for the two species, with *D. capensis* swimming 6 km and *S. salpa* 8 km during a single event. These swimming abilities provide ample evidence of the potential for postflexion fish larvae to strongly influence their dispersal trajectories and ultimately reach preferred coastal and estuarine nurseries.

The immigration of larvae and postlarvae into southern African estuaries usually takes place on the flood tide (Figure 45) and they are then retained by rapidly settling along the banks or on the bottom where water movements are reduced (Beckley 1985a). Indeed, Harris & Cyrus (1995) found that fish larvae of estuary-associated species used selective tidal stream transport to facilitate retention within large KwaZulu-Natal estuaries, with larval densities being significantly higher on flood tides and in bottom waters. They also recorded postflexion larvae of estuary-associated marine fish species accumulating near the mouth of the St Lucia Estuary at low tide, and

subsequently using flood tidal currents to enter the estuarine environment. Furthermore, the postflexion larvae of species such *Chelon richardsonii* and *Pseudomyxus capensis* are closely associated with estuarine frontal systems which can play an important role in plankton accumulations entering estuaries (Kruger & Strydom 2011).

Motile postflexion larvae can, however, easily enter estuaries on the ebb tide by keeping to the margins where current speeds are attenuated (Whitfield 1989a, Strydom & Wooldridge 2005, Patrick & Strydom 2014). In the Zotsa Estuary, postlarval marine fish were recorded moving into the system through the bottom of standing waves, swimming upstream in a series of steps (Harrison & Cooper 1991). Once inside the estuary the postlarvae are attracted to the littoral zone where they avoid higher water currents associated with the channel and also obtain shelter from large piscivorous fishes (Strydom 2003a).

Yet another fish recruitment mechanism involves the larvae and juveniles entering temporarily closed or closing estuaries during marine overwash of the sand bar at the closed mouth



**Figure 45.** Fish recruitment of postflexion larvae from the marine environment usually occurs on the flood tide while the estuary mouth is open (Photo: Alan Whitfield).

(Figure 46). Preliminary indications are that largescale ichthyonekton migration into temporarily closed estuaries may occur in this manner (Cowley et al. 2001, Vivier & Cyrus 2001, Tweddle & Froneman 2017).

Whitfield (1989b) has quantified marine ichthyoplankton recruitment into the Swartvlei Estuary and found up to 315 000 fish larvae and postlarvae entering the system over a 24 h period. This study also documented that there was a net loss of larvae belonging to certain estuarine spawners which subsequently returned to the estuary as postlarvae. Movements of larvae and postlarvae between the estuary and sea occurred mainly during twilight and nocturnal hours when predation rates would probably be lower than during the day. Nevertheless, the magnitude of the above immigration figures in relation to juvenile and adult densities within the estuary suggests that high mortalities of these early recruits occurs.

Once the juveniles have entered an estuary, they usually continue to move up the system (Figures 47 and 48), often in concert with flood tidal currents. Hall et al. (1987) found that more than 99% of the juvenile fishes captured in the

Serpentine Channel (Wilderness lakes system) were moving upstream on flood tidal currents. There was also a strong positive correlation between the number of fish moving upstream per hour and mean water depth. Furthermore, the highest numbers of migrating fish were recorded during daylight hours but several species only moved up the channel during the night. Altogether 52 000 juvenile marine fishes, comprising at least seven species, were estimated to have migrated up the Serpentine Channel during February 1984.

Similarly large numbers of larval and early juvenile stages of estuarine resident and estuary-associated marine fish species were recorded in the headwaters of a range of permanently open Eastern Cape estuaries (Wasserman & Strydom 2011). According to these authors the species diversity and composition of fish catches in the headwaters further emphasizes the attraction and potential importance of these transitional areas for young fish.

Several cues are available within an estuary to assist fish orientation towards specific nursery areas. Salinity gradients are perhaps the most



**Figure 46.** Marine overwash of the estuarine sand berm provides opportunities for postflexion larval recruitment into temporarily closed estuaries (Photo: Alan Whitfield).

obvious but have been largely discounted by Blaber (1987) on the basis of experimental and field evidence. Temperature is an unlikely cue, as thermal gradients within estuaries are irregular and highly variable, depending upon tidal regime, river flow, oceanic upwelling, etc. However, the juveniles of a number of fish species are attracted to warm littoral areas, so the use of water temperatures, possibly in conjunction with other cues, cannot be discounted.

Turbidity gradients are usually strongly developed within estuaries, and Blaber (1987) is of the opinion that both vertical and horizontal gradients may be important to certain species. Studies by Cyrus & Blaber (1987a, 1987b, 1987c) have shown that the juvenile marine fishes of KwaZulu-Natal estuaries can be divided into five main groups according to their occurrence in various turbidities. The above field and laboratory studies indicate that turbidity plays a major role, either singly or in combination with other variables, in determining the fine scale distribution of juvenile marine fishes within estuaries.

In contrast to the marine migrants, larvae of species such as *Gilchristella aestuaria* do not have to enter the estuary. Instead, they need to remain within the system during the vulnerable embryonic and larval stages. Melville-Smith et al. (1981) have described how *G. aestuaria* larvae in the Sundays Estuary utilize tidal transport in order to avoid being swept out to sea. Evidence suggests that these larvae remain in the middle and upper reaches of the estuary where zooplankton food resources are most abundant (Sutherland et al. 2012, 2013), and avoid the more marine areas near the mouth until at least the juvenile stage has been attained. Nevertheless, large numbers of *G. aestuaria* larvae are sometimes flushed from estuaries during river flood events.

### **Spatial and temporal fish larval patterns**

The migration of marine larvae and juveniles into KwaZulu-Natal estuaries occurs mainly during late winter and spring when river flow is often at a minimum (Wallace & van der Elst 1975). Although all of the permanently open estuaries and bays are always available for colonization, most of the smaller systems along the KwaZulu-Natal

coast are closed during the winter and only open after spring rains in October (Whitfield 1980c). Recruitment into these temporarily closed estuaries is therefore only possible when increased water flow forces open the mouths of the above systems. The prolonged period of larval and juvenile immigration (Figure 49), which is a function of the extended spawning season of most species, may therefore be regarded as a strategy against unseasonal river flooding which could open blind estuaries prematurely, and droughts that would delay mouth opening until mid-summer.

In Eastern and Western Cape estuaries, a similar prolonged recruitment pattern is evident, but in these cases the peak immigration phase occurs during early summer when most temporarily closed estuaries in the region are already open. In addition, the late winter and early spring rains send pulses of fresh water into the Cape estuaries, thereby ensuring the replenishment of nutrients needed to stimulate summer primary productivity. Thus, in both KwaZulu-Natal and Cape estuaries, juvenile fishes are able to exploit the abundant summer food resources and warm temperatures to grow rapidly before the onset of winter. Refuges in the form of submerged aquatic vegetation are also most prolific during summer and higher turbidities due to increased river flow aid predator avoidance by juvenile fish.

Spawning by estuarine fish taxa occurs mainly during spring, with the larvae and juveniles being particularly abundant during summer (Figure 50). The spring and summer rains in warm-temperate South African estuaries creates freshwater pulses that stimulate spawning by various resident goby species, e.g. both *Glossogobius callidus* and *Redigobius dewaali* are more prevalent in estuaries where perennial river flow occurs (Strydom & Neira 2006). Other researchers have shown that mouth status, which is a function of river flow, also has a strong influence on the populations of estuarine resident fish species such as *Atherina breviceps* (Tweddle & Froneman 2015).

Larval fish assemblages in cool-temperate estuaries are dominated by *Gilchristella aestuaria*, and ichthyoplankton is most abundant during summer, especially in the mesohaline zone (Montoya-Maya & Strydom 2009a). Estuary-resident fish larvae





**Figure 47.** Early juvenile mugilids (10-20 mm SL) associated with the sandy littoral in the mouth region of the Swartvlei Estuary (Photo: Alan Whitfield).



**Figure 48.** Early juvenile sparids (10-20 mm SL) associated with an eelgrass bed in the lower reaches of the Swartvlei Estuary (Photo: Alan Whitfield).



usually dominate ichthyoplankton assemblages in estuaries throughout the subcontinent and often comprise more than 90% of the overall catch (Kruger & Strydom 2010, Sutherland et al. 2012).

Estuarine larvae and postlarvae grow very rapidly in the warm, highly productive waters over summer and, with the onset of winter, have already attained sexual maturity. For example, *Gilchristella aestuaria* consume approximately 12% of body mass per day in summer and mature within seven months of hatching (Talbot & Baird 1985a). Daily food consumption then declines to <2% of body mass in winter when water temperatures decline and zooplankton resources become increasingly scarce.

A major factor influencing the composition of ichthyoplankton in southern African estuaries is sea temperature, which is linked not only to season but also to latitude. Species diversity (number of taxa) generally declines from the subtropical systems in the northeast to the cool-temperate region in the southwest. The subtraction of the larvae of fish species represented in subtropical versus cool-temperate estuaries declines by approximately 50%, with the fish families represented in the St Lucia Estuary almost double those present in Eastern and Western Cape systems. The decline becomes even more apparent if the Kosi Estuary diversity is compared with that of more temperate estuaries.

In both KwaZulu-Natal and Cape systems, ichthyoplankton densities fluctuate widely and are generally much higher in summer than in winter (Melville-Smith & Baird 1980, Whitfield 1989a, Harrison & Whitfield 1990, Harris & Cyrus 1995). Similarly, in Eastern and Western Cape estuaries, larval and postlarval fish densities showed a strong positive correlation with water temperature (Whitfield 1994a, Montoya-Maya & Strydom 2009a).

### **Larvae and postlarvae in estuaries**

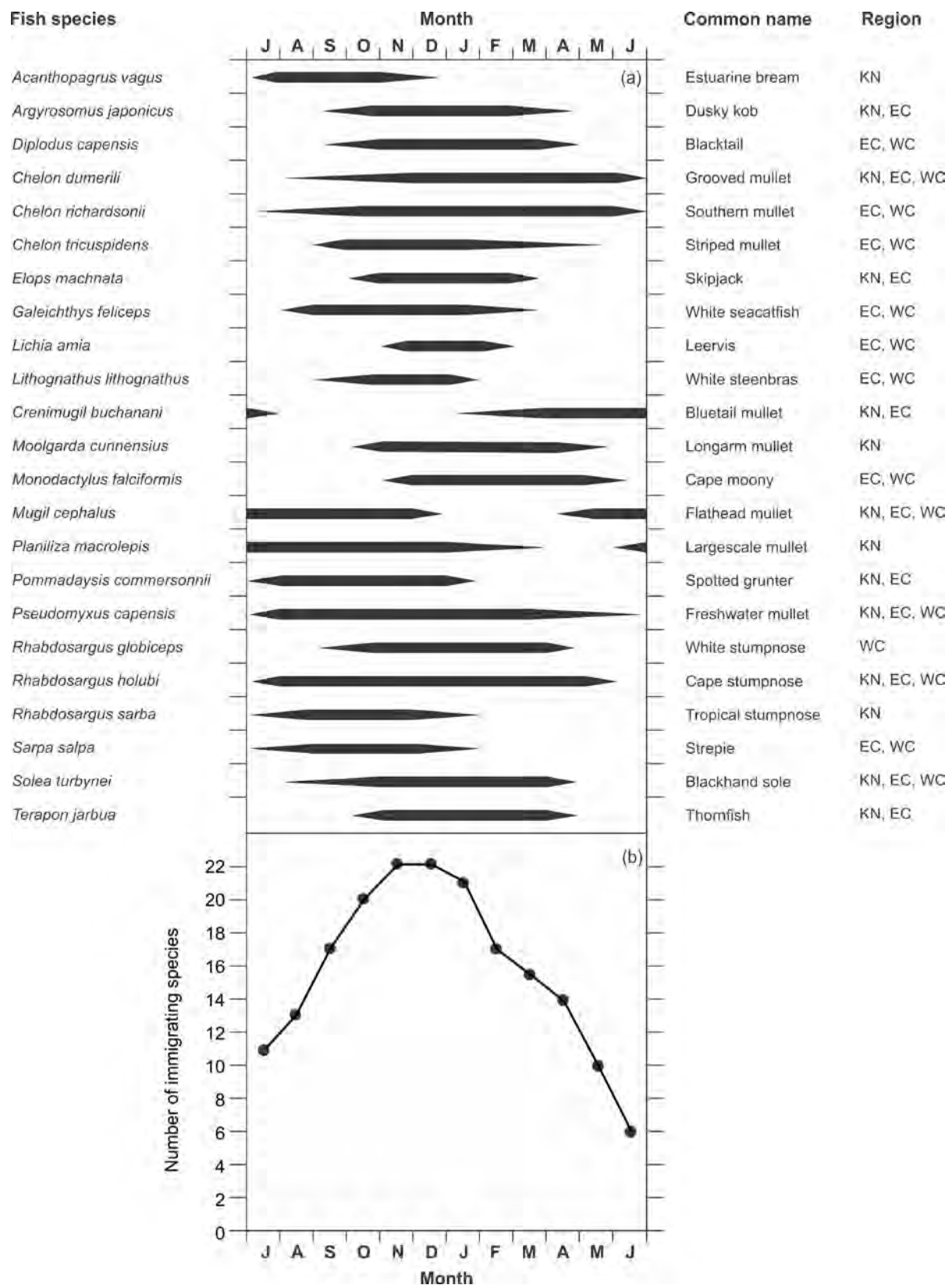
Juveniles of a number of marine fish species are dependent on estuaries as nursery areas but their preflexion and flexion larvae are usually absent from these systems (Figure 51). The available evidence suggests that abiotic constraints to the survival of larval stages in estuaries, including

fluctuating salinity, temperature and dissolved oxygen regimes, could be problematical. In addition, tidal currents could easily transport embryos and non-motile larvae into unfavourable reaches of an estuary. The unpredictable abiotic characteristics of estuaries outlined above contrast to conditions prevailing in the more predictable and stable marine environment.

Despite the supposed advantages of the sea for the larval stages of fishes, the larvae of large numbers of resident clupeids and gobies successfully develop in all types of southern African estuaries (Froneman & Vorwerk 2003, Pattrick et al. 2007, Wasserman et al. 2010). These taxa, together with the postlarvae of certain estuary-associated marine fish taxa are often more abundant in the mesohaline zone of estuaries (Strydom et al. 2003, Montoya-Maya & Strydom 2009a, Strydom 2015), whereas the highest species diversity is generally located in the euhaline zone of open estuaries (Pattrick et al. 2007). This is because maximum estuarine productivity is usually associated with mesohaline areas whereas marine fish species richness is often highest in the lower reaches.

The biotic environment within estuaries may also present problems for the survival of large numbers of fish larvae. Ichthyoplankton feed mainly on microzooplankton, whereas postlarval fishes utilize both micro- and meso-zooplankton. Since zooplankton are the dominant primary consumers of large phytoplankton stocks in oceanic waters, fish larvae are more likely to find a suitably sized and reliable planktonic food supply in the sea. Furthermore, the highest zooplankton biomass usually occurs within a few kilometres of the coast, a region usually occupied by fish larvae of estuary-associated marine species (Heydorn et al. 1978).

Zooplankton food availability, and therefore larval fish survival, is strongly linked to river flow. Those estuaries with either extensive habitat variability and/or a good supply of fresh water were the systems with the highest species richness and diversity of larval fishes (Strydom 2015). Additionally, the mesohaline zone of estuaries in the temperate region was characterized by the highest density of larval and postlarval fishes



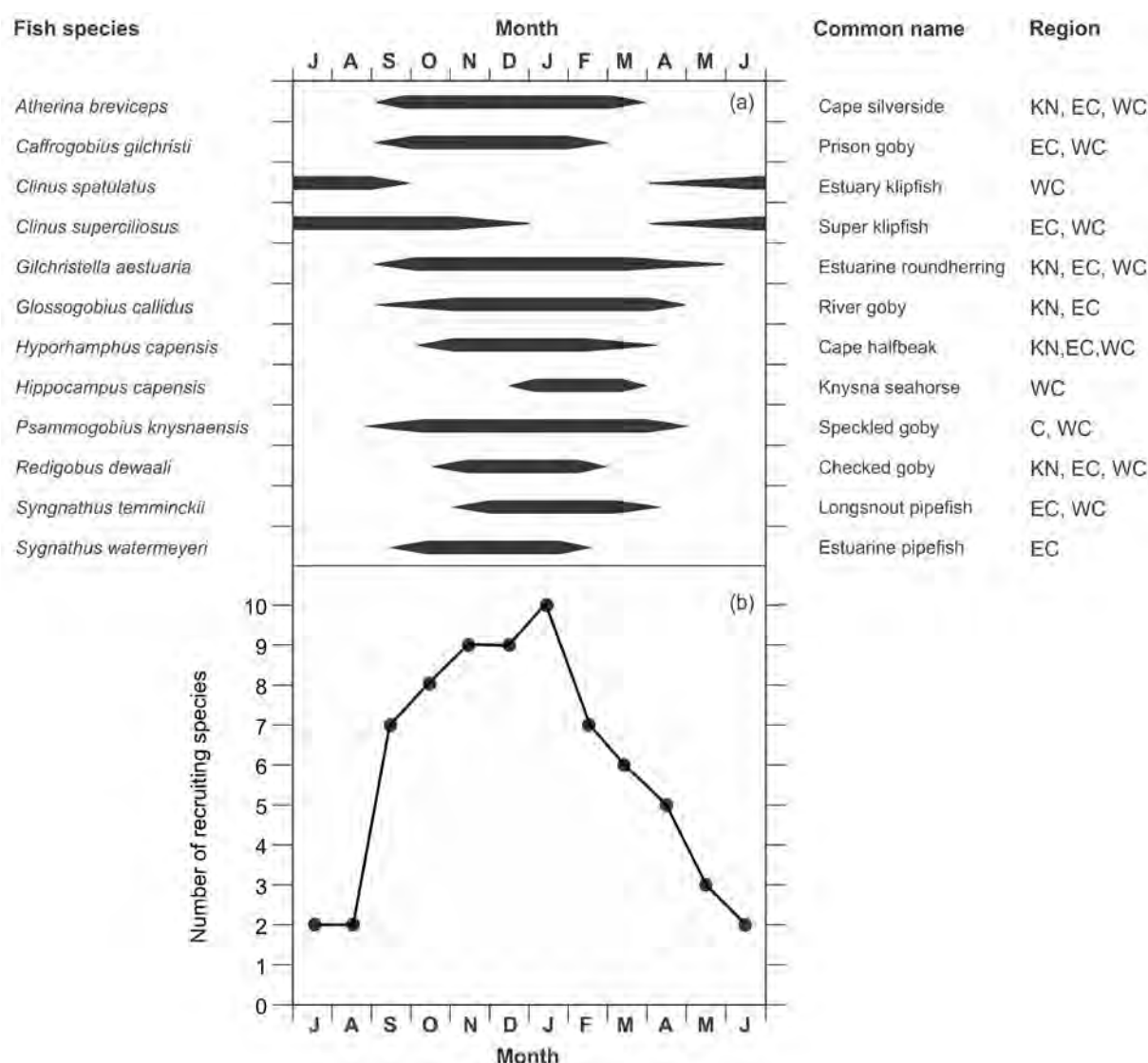
**Figure 49.** (a) Diagrammatic representation of the immigration periods of some estuary-associated fish larvae and early juveniles from the marine environment. Regional information used; KN = KwaZulu-Natal, EC = Eastern Cape, WC = Western Cape. Data from Wallace & van der Elst (1975), Bok (1979), Melville-Smith & Baird (1980), Whitfield (1990), Whitfield & Kok (1992) and Harris & Cyrus (1995). (b) Monthly variation in the numbers of species entering southern African estuaries, as derived from bar representations shown in (a).

(Montoya-Maya & Strydom 2009a), probably due to the peak in zooplankton stocks usually encountered within or near this salinity zone (Montoya-Maya & Strydom 2009b). Indeed, a model developed to predict postflexion larval occurrence of *Rhabdosargus holubi* in South African estuaries highlighted the importance of lower salinity in attracting high densities of this species to particular systems (Kisten et al. 2017).

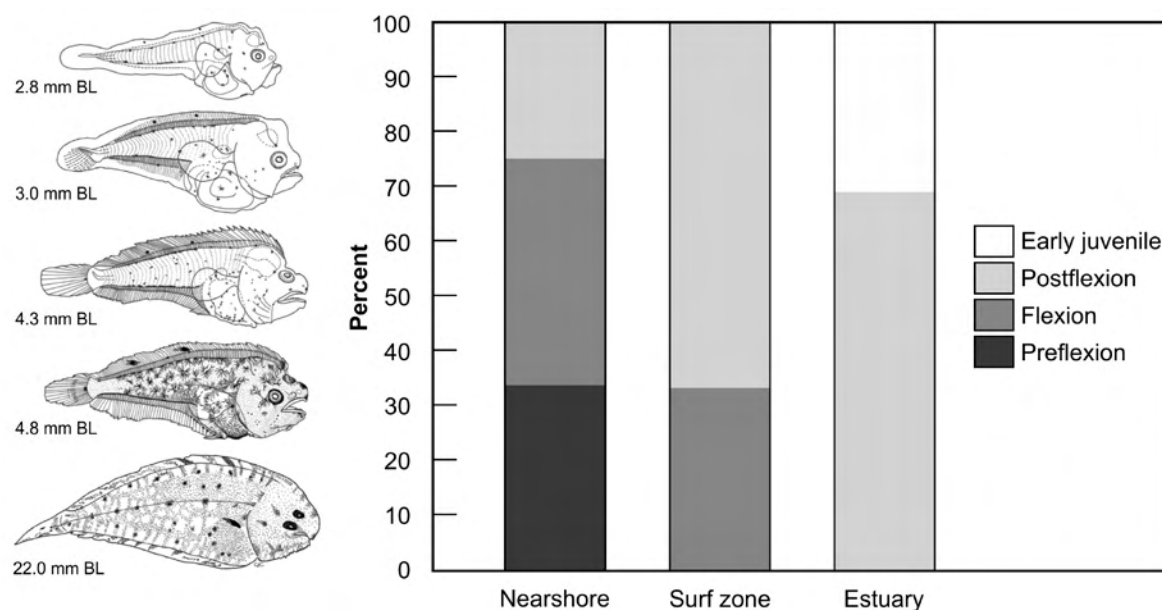
Zooplankton abundance in southern African estuaries is spatially highly variable, with east coast systems tending to have a higher biomass than south coast estuaries (Grindley 1981). In addition,

the unpredictable nature of estuarine zooplankton on a temporal basis, even in those systems with characteristically large stocks, mitigates against the consistent use of this environment by larvae of marine fish species.

Virtually all the marine fish postlarvae which enter South African estuaries initially feed on zooplankton (Whitfield 1985, Strydom et al. 2014), regardless of their ultimate juvenile or adult diet. Calanoid copepods in particular are important for newly-recruited ichthyoplankton, with zooplankton numbers being particularly high in the mesohaline zone where fish larvae densities are



**Figure 50.** (a) Diagrammatic representation of the periods of abundance of larvae spawned within southern African estuaries. Regional information used; KN = KwaZulu-Natal, EC = Eastern Cape, WC = Western Cape. Data from Melville-Smith & Baird (1980), Whitfield (1990), Harris & Cyrus (1995) and Strydom & Neira (2006). (b) Monthly variation in the numbers of species represented by larvae in southern African estuaries, as derived from bar representations shown in (a).



**Figure 51.** Habitats occupied by various early developmental stages of *Solea turbynei* in Algoa Bay (after Strydom et al. 2015). The larval stages of *S. turbynei* illustrated on the left hand side of the figure are (from top to bottom) preflexion, flexion, postflexion, metamorphosis and early juvenile respectively (drawings by Crystal Coetzer).

often highest (Montoya-Maya & Strydom 2009b). Indeed, postlarval fishes have been shown to influence multiple trophic levels in the estuarine plankton community by feeding on copepods and polychaetes which, in turn, cascaded through the ciliates, micro-flagellates, non-flagellates and bacteria in the water column (Wasserman et al. 2013a, 2013b).

The switch from a predominantly zooplanktonic diet to one dominated by zoobenthos, detritus or aquatic plants is rapid and usually occurs between 10 mm and 30 mm SL. Since most estuarine-associated marine fish species first enter these systems between 10 mm and 20 mm SL, the transition in diet occurs within the estuarine environment. Blaber & Whitfield (1977a) have shown that mugilid postlarvae in estuaries feed initially on zooplankton, then vertically migrating zooplankton and meiobenthos, and finally microbenthos. The role of vertically migrating zooplankton in initiating dietary switches by the postlarvae appears to be particularly important for demersal fish species (Figure 52).

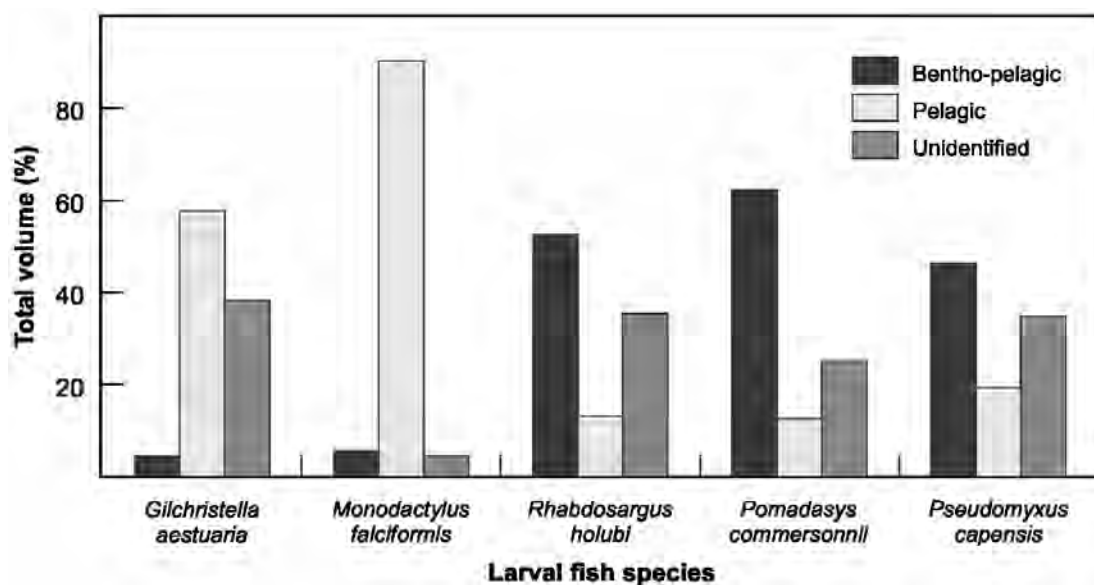
The seasonal abundance of ichthyoplankton in Eastern Cape estuaries is positively correlated with copepod densities (Harrison & Whitfield 1990), thereby increasing the potential growth and survival of larval fish. The summer peak in

zooplanktonic productivity is particularly important to those estuarine fish species whose larvae do not develop within the marine environment (Strydom 2015), with larval nutritional condition directly related to zooplankton abundance (Costalago et al. 2015). Hence, it is perhaps not surprising that peak ichthyoplankton stocks are highest in summer and lowest in winter (Patrick et al. 2007).

River flooding can, however, disrupt the build-up in zooplankton and this is likely to have a negative influence on both larval and planktivorous fish abundance in estuaries (Mbandzi et al. 2018). Nevertheless, the recovery of zooplankton stocks following river flooding is likely to be rapid, given the life cycle characteristics of the dominant copepod species (Wooldridge & Mellville-Smith 1979).

Available evidence suggests that estuaries with large zooplankton stocks also have high densities of resident planktivores such as *Gilchristella aestuaria*. In Swartvlei, an estuarine lake that has limited phytoplankton and poor zooplankton resources (Coetzee 1981a), *G. aestuaria* larvae averaged 26 individuals per 100 m<sup>3</sup> during 1986/87 (Whitfield 1989a). In contrast, the Sundays Estuary, which has a rich zooplanktonic food resource (Wooldridge & Bailey 1982),





**Figure 52.** Diet of fish larvae (% volume) belonging to two eventual (juvenile and adult stages) pelagic or midwater fish species (*G. aestuaria* and *M. falciformis*) and three eventual demersal fish species (*R. holubi*, *P. commersonnii* and *P. capensis*) from the Sundays Estuary. Note the high dependence of the demersal species on benthopelagic invertebrate species that facilitate the eventual switch from pelagic to benthic foraging (after Strydom et al. 2014).

*G. aestuaria* larvae averaged 204 individuals per 100 m<sup>3</sup> during 1986/87 (Harrison & Whitfield 1990). In addition, larval *G. aestuaria* from the Swartvlei system are narrower bodied than those from the Sundays Estuary (Haigh & Whitfield 1993), thus reinforcing the suggestion by Blaber et al. (1981) that zooplanktonic prey abundance may influence the morphometrics of this species.

#### Influence of temperature and salinity

Of the main physico-chemical parameters recorded, temperature and salinity appear to be the two main factors affecting the distribution and occurrence of fishes in southern African estuaries (Harrison & Whitfield 2006b). Tropical estuarine-associated species (Group 1) appear to prefer warm, turbid, brackish water conditions with many species being largely restricted to subtropical estuaries (Figure 53). The decline in sea temperatures, as well as upwelling events, limits the dispersal of tropical species into warm-temperate estuaries. Some eurythermal tropical species (Group 2), however, do extend into warm-temperate estuaries (Figure 53).

Warm-temperate estuaries are characterised by cool, more saline waters, with low turbidity and are dominated by endemic taxa. Some warm-water endemic species are common in both warm-

temperate and subtropical estuaries (Group 3) but are generally not a major component of the fish community of cool-temperate estuaries (Figure 53). Other endemic species appear to prefer cooler waters and occur in both warm- and cool-temperate estuaries but are uncommon in subtropical systems (Group 4). Temperate species (Group 5) also occur in warm-temperate systems but are generally absent from subtropical estuaries. Widespread or cosmopolitan species occur in all biogeographic regions (Group 6).

There is a strong positive correlation between tropical fish species (e.g. *Leiognathus equula* and *Thryssa vitrirostris*) and estuarine water temperature around the coast (Harrison & Whitfield 2006b). Similarly, Cyrus & Blaber (1987a) reported a positive relationship between the abundance of a number of tropical fish species and water temperature in Lake St Lucia. Tropical species are sensitive to sudden water temperature declines below 14°C, as evidenced by mass fish mortalities by this group in both Lake St Lucia (Cyrus & McLean 1996) and the Kosi lakes (Kyle 1989).

The majority of fish species in southern African estuaries that exhibit a negative correlation with salinity are tropical species (Harrison & Whitfield 2006b). Within the tropical Indian

Ocean, where many of these species also occur, monsoon rains occur twice a year and salinities are always <35 (Blaber 1981a). The high rainfall in most KwaZulu-Natal catchments often results in low salinities in subtropical estuaries within the region (Harrison 2004) and fortunately tropical fishes occupying these systems are more tolerant of low rather than high salinities (Whitfield et al. 1981).

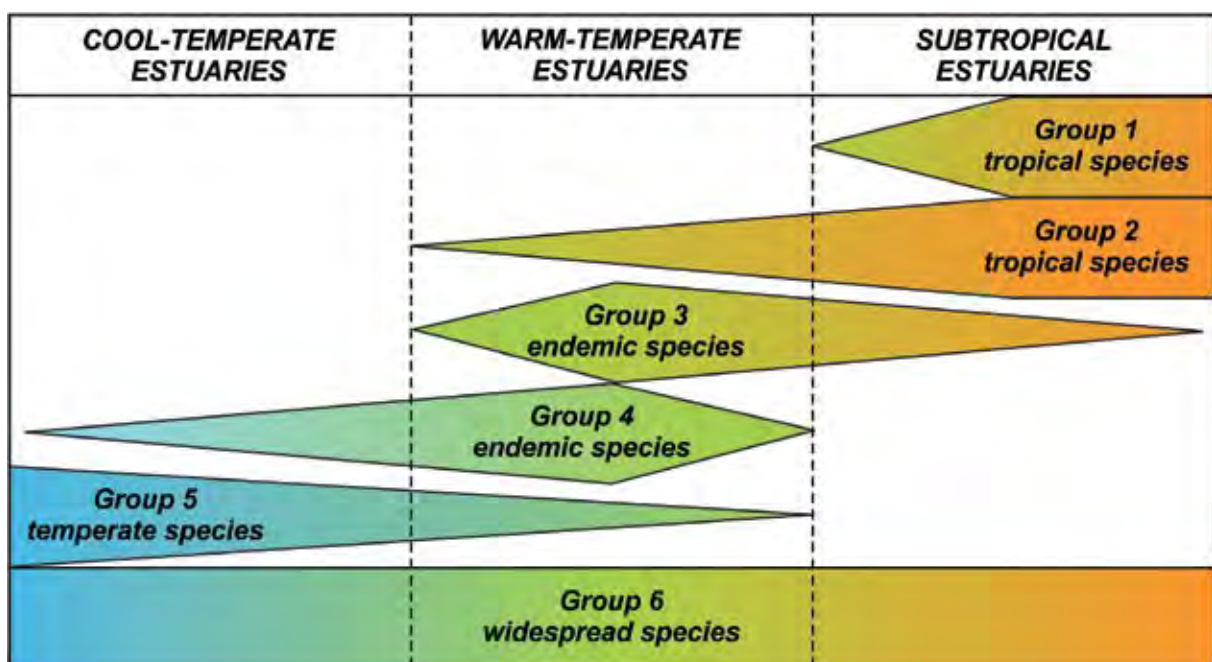
### Estuarine typology and fish composition

Some 190 South African estuaries surveyed by Harrison (2004) can be classified into three basic types based on a combination of mouth state and estuary size (water surface area), viz. small closed estuaries, moderate to large closed estuaries and predominantly open estuaries. The fish communities of the above estuary types have been described and compared by Harrison & Whitfield (2006c). Multivariate analyses revealed that each estuary type contained somewhat distinct fish communities. In addition, the study identified some common patterns in terms of species richness and ichthyofaunal composition. A permanent or near-permanent connection with the sea allows access into open estuaries by all marine migrant species within the region, and these systems have

a relatively high species richness. Intermittent connection with the sea partially limits the recruitment and utilisation of closed estuaries by marine migrant species, and this results in reduced species richness in moderate to large closed estuaries. Small closed estuaries exhibit the lowest species richness and this is probably a result of their limited habitat availability and increased isolation from the sea.

The key fishes that utilise estuaries can also be categorised into a number of groups based on their relative importance within each estuary type (Figure 54). Group A comprises those species that are important in predominantly open systems but usually comprise a minor component of the fish fauna of closed estuaries. Group B consists of taxa that are important in predominantly open estuaries but also occur in moderate to large closed systems. Group C comprises species that are well represented in all estuary types but whose importance is greatest in moderate to large closed estuaries. Group D also comprises species that are well represented in all estuarine types but their importance is higher in small closed estuaries.

In both the subtropical and warm-temperate regions of the southern African coast, MDS ordinations showed that fish communities in



**Figure 53.** Southern African estuarine fish faunal groupings based mainly on temperature and salinity environmental preferences (see text for more information) (after Harrison & Whitfield 2006b).

predominantly those in open estuaries were distinct from large and small closed estuaries. This pattern was supported by ANOSIM tests where the fish faunas of predominantly open estuaries were shown to be significantly different to closed systems (Harrison & Whitfield 2006c).

Results from the above study have shown that southern African fish communities not only reflect estuarine typology but also respond to these differences in a consistent manner that spans all zoogeographic regions. Similar results were presented by Vorwerk et al. (2001, 2003) which showed that fish assemblages in Eastern Cape temporarily open /closed estuaries differed from those in permanently open estuaries in the same region. The prevalence of similar patterns in other parts of the world suggests that estuarine typology is a major driver in the structuring of global estuarine fish communities.

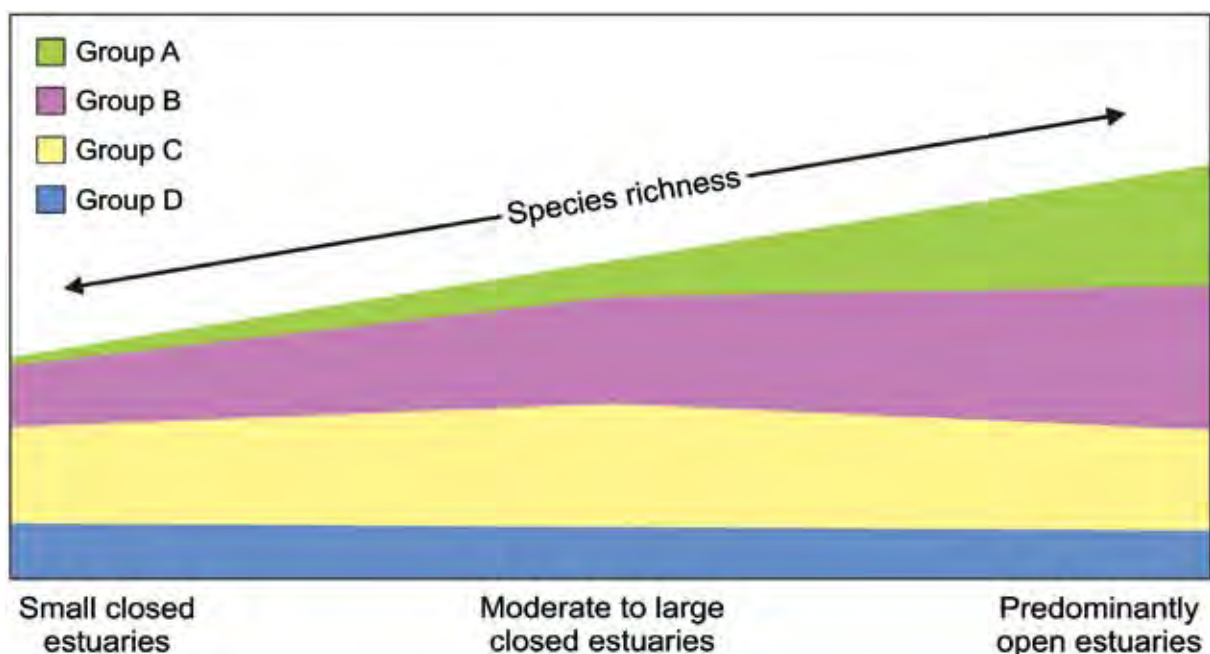
#### Estuarine zoogeography and fish guilds

A comparative zoogeographical analysis of fish estuary-association guilds in southern Africa has also been undertaken (Harrison & Whitfield 2008). This study spanned three zoogeographic regions (Figure 55) and included three broad estuarine types, namely small temporarily open/

closed estuaries (TOCEs), moderate to large TOCEs, and predominantly open estuaries.

Freshwater stragglers were largely restricted to subtropical estuaries. However, the occurrence of this group in predominantly open cool-temperate systems was due to high catches of *Labeobarbus aeneus* in the Orange Estuary. The subtropical region experiences a high summer rainfall and river flow is the main mechanism whereby predominantly open systems in this region maintain an outlet to the sea (Cooper 2001). High river flow results in reduced salinities (<15) in most of these estuaries (Harrison 2004) and this probably allows freshwater fish stragglers to occupy these habitats.

Freshwater migrant species are a minor component of most estuaries in most southern African estuaries but exhibited the highest importance in predominantly closed subtropical systems (Harrison & Whitfield 2008). There is a general decline in importance of this group from the subtropical region toward the temperate regions that parallels the north-south decline in species richness of freshwater fishes (Skelton 2001). The main freshwater migrant or opportunist in most southern African estuaries is *Oreochromis mossambicus* which prefers salinity stability and



**Figure 54.** Conceptual diagram of fish community richness and composition associated with various estuary types on the South African coast (for a description of Group A, B, C and D see above) (after Harrison & Whitfield 2006c).

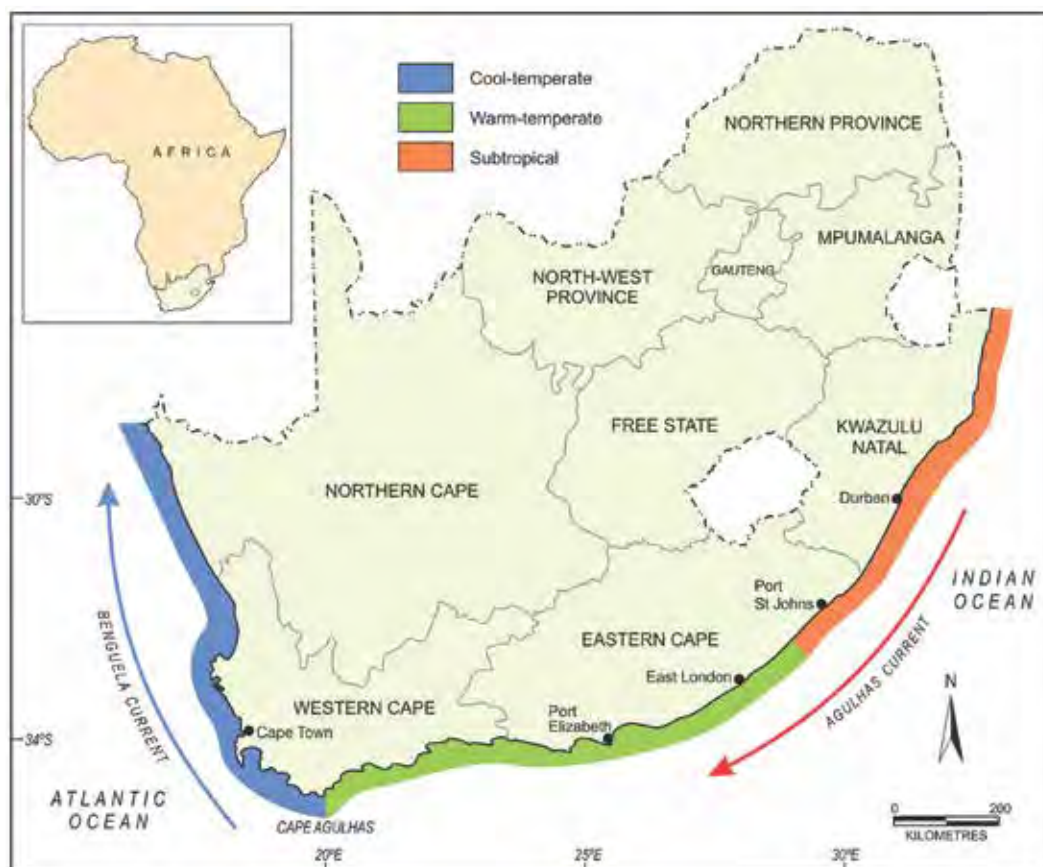
slow water currents (Whitfield & Blaber 1979c). As a consequence, *O. mossambicus* is abundant in many TOCEs and estuarine lakes but is generally absent from open estuaries where tidal action and the presence of large piscivorous fishes are more prevalent (Whitfield & Blaber 1979c).

The relative importance of estuarine resident species is generally highest in warm-temperate estuaries and accounts for some of the dissimilarity between these systems and those in the subtropical and cool-temperate regions (Whitfield & Harrison 2008). Estuarine resident species also exhibit a slightly higher importance in subtropical estuaries relative to those in the cool-temperate region and this also contributes toward the dissimilarity between estuaries from these two regions. Unlike warm-temperate estuaries, both cool-temperate and subtropical systems experience marked seasonal variations in rainfall, runoff and salinity (Harrison 2004), all of which are

likely to impact on estuarine resident taxa.

Estuarine resident species in the subtropical region also exhibit a higher importance in predominantly closed systems relative to predominantly open estuaries and this contributes toward the dissimilarity recorded between these estuary types. It has been suggested that the high contribution made by species that spawn in southern African estuaries may be a reflection of adaptations evolved in response to an intermittent mouth condition. Since most estuaries in southern Africa are predominantly closed systems; there are likely to be strong selection pressures for small species with short life cycles to adapt to spawning within estuaries in those years when their access to the sea is blocked.

The relative importance of estuarine migrant species was generally highest in cool-temperate estuaries and exhibited a decline toward warm-temperate and subtropical estuaries. *Atherina*



**Figure 55.** Map of South Africa showing the three major zoogeographic zones for estuary-associated fish species (after Harrison 2002).



*breviceps* was among the key estuarine migrant species recorded in cool- and warm-temperate estuaries (Harrison & Whitfield 2008), and populations of this species have also been reported in the relatively sheltered bays of the Western Cape (Bennett 1989, Clark et al. 1994). The higher importance of estuarine migrants in warm-temperate estuaries, particularly in predominantly open systems, also contributed toward the dissimilarity observed between these systems and subtropical estuaries. The estuarine gobies *Caffrogobius gilchristi* and *Psammogobius knysnaensis* were among the dominant estuarine migrant species recorded in predominantly open estuaries during this study.

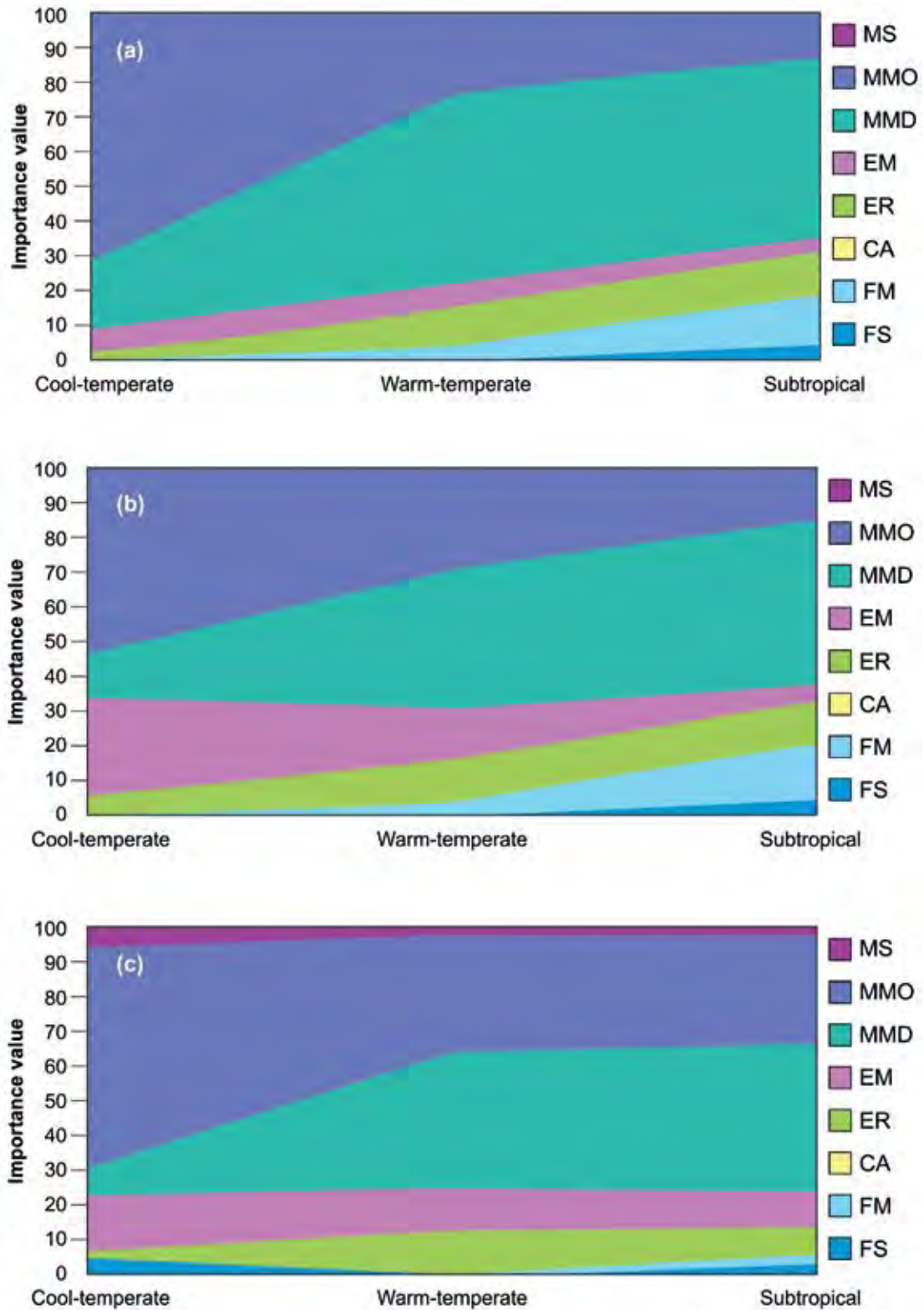
Marine migrant species (both estuarine dependent marine migrants and marine estuarine-opportunists) were the dominant guilds in all estuary types within all biogeographic regions. The importance of estuarine dependent marine migrants was high in subtropical estuaries and declined toward cool-temperate systems. Although marine estuarine-opportunists utilise estuarine nursery areas, they are not entirely dependent on these environments (Elliott et al. 2007). The relative importance of marine estuarine-opportunists was highest in cool-temperate estuaries and declined toward warm-temperate and subtropical systems. This pattern accounted for some of the dissimilarity between cool-temperate estuaries and warm-temperate and subtropical systems (Harrison & Whitfield 2008).

The paucity of estuaries in the cool-temperate region probably favours those species that are not entirely dependent on estuarine nursery areas but are also able to utilise alternate marine nursery areas such as coastal embayments. *Chelon richardsonii*, for example, was a key marine estuarine-opportunist species recorded in cool-temperate estuaries and, although juveniles utilise estuarine nursery areas, they are also abundant in the inshore waters

of fairly sheltered embayments on the Cape coast (de Villiers 1987, Bennett 1989, Clark et al. 1994).

Stenohaline marine fishes generally do not constitute an important component of the ichthyofauna of southern African estuaries (Wallace 1975a). The importance of marine stragglers was highest in predominantly open cool-temperate estuaries and declined toward predominantly open warm-temperate and subtropical systems. Marine stragglers were virtually absent from closed estuaries, probably a reflection of the isolation of these systems from the sea (Harrison & Whitfield 2008). It should be noted that freshwater deprived permanently open estuaries such as the Kariega and Bushmans in the Eastern Cape Province have a wide variety of stenohaline marine teleost and elasmobranch species recorded in low numbers, some of them even extending into the euhaline middle reaches.

A summary of the importance of the various estuary-association guilds within the different estuary types from each biogeographic region is presented in Figure 56. The general pattern to emerge is that cool-temperate estuaries appear to be dominated by migratory species, especially marine estuarine-opportunists. This may be linked to the paucity of estuaries in the region, which would favour species that can utilise alternate marine nursery areas. The frequency of estuaries in the warm-temperate and subtropical regions increases; with species dependent on estuaries, namely estuarine residents and estuary-dependent marine migrant species assuming a greater importance (Figure 56). As a result of high rainfall and runoff, estuaries in the subtropical region are river-dominated and this allows freshwater taxa (freshwater stragglers and freshwater migrants) to occupy and even become abundant in temporarily closed estuaries of this region.



**Figure 56.** Summary of importance of estuary-associated fish guilds in small closed estuaries (a), moderate-to-large closed estuaries (b) and predominantly open estuaries (c), in the cool-temperate, warm-temperate and subtropical zoogeographic regions (MS = Marine stragglers, MMO = Marine estuarine opportunists, MMD = Marine estuarine dependents, EM = Estuarine migrants, ER = Estuarine residents, CA = Catadromous, FM = Freshwater migrants, FS = Freshwater stragglers) (after Harrison & Whitfield 2008).

## 2.3 AN EVOLUTIONARY PERSPECTIVE OF FISHES IN ESTUARIES

Fish are a major component of the nektonic community in estuaries and represent the most mobile element of these systems (Kennish 1990). Their mobility confers them with considerable advantages over sessile organisms, enabling them to avoid unfavourable conditions, exploit a wide variety of habitats and food sources, evade predatory attacks, and move from one estuarine system to another via the marine environment. This latter characteristic allows extensive genetic mixing and may provide the key to an understanding of fish speciation in southern African estuaries.

According to Levinton (1980), studies of several invertebrate and vertebrate taxa in estuaries indicate genetic divergence of estuarine populations from conspecific populations in coastal marine waters. In a southern African context, Ratte (1989) found significant positive genetic autocorrelation over distance among populations of *Atherina breviceps* separated by less than 200 km, and strong negative correlation between populations separated by 300 km or more. This tendency does not appear to have been translated into widespread estuarine speciation, despite the variety of barriers (e.g. closure of estuary mouths for extended periods) to gene flow between the different ecosystems along the coast.

The ichthyofauna of estuaries globally may be characterized by the numerical dominance of relatively few species per system (Kennish 1990). This observation gives rise to questions; (a) why do so few species utilize estuaries compared to adjacent nearshore marine environments and (b) why has fish speciation in estuaries been less extensive when compared to other aquatic habitats? In attempting to answer these questions we need to examine both the organism and its environment in more detail.

### The estuarine environment

As has already been discussed (see Chapter 1 for details), southern African estuaries are highly variable habitats in which conditions such as salinity, temperature, turbidity, water currents and dissolved oxygen concentrations can fluctuate rapidly, both temporally and spatially. In

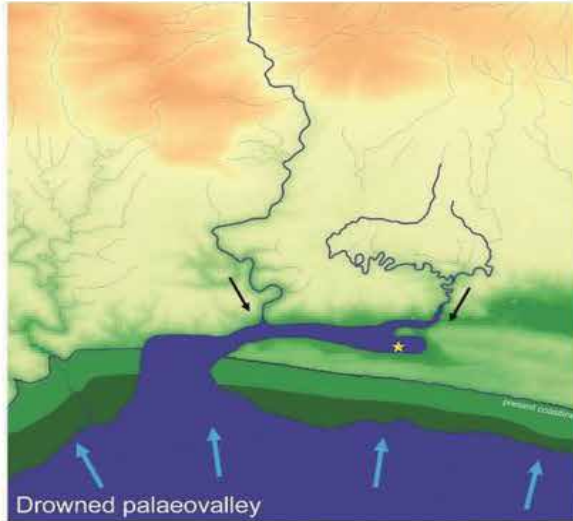
addition, they are variable in terms of size, shape, degree of marine /riverine influence and catchment characteristics. Based on that information, one could characterize estuaries as regions where environmental stress is pronounced and periods of stability are short-lived.

Climatic variations and sea-level fluctuations control the development and distribution of estuaries around the world. During high stands of sea level, estuaries tend to be abundant and relatively large; during low stands they are likely to be less abundant and small (Schubel & Hirschberg 1978). During full glacial periods, declines in the productivity of estuaries has occurred due to their decreased area, reduced capacity for nutrient entrapment, and decreased ability to dampen environmental perturbations (Stone et al. 1978). In addition, the lifetimes of particular estuaries are usually limited to a few thousand years and, according to Schubel & Hirschberg (1978), these systems have been abundant during only 10-20% of the last million years.

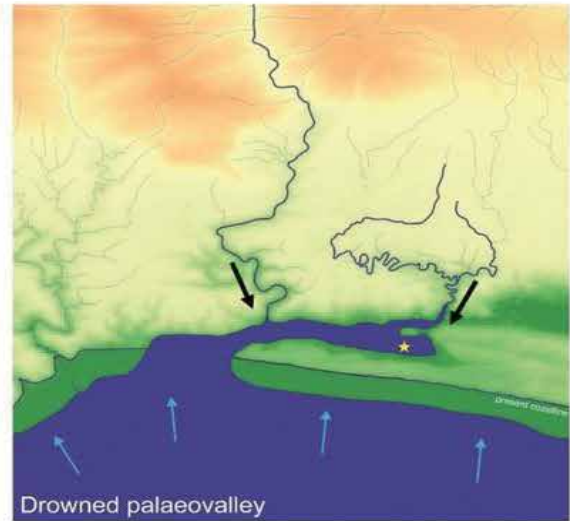
Sea level in southern Africa was approximately 130 m below existing levels at the end of the last glacial period 17 000 years B.P. (Miller 1990) and, as recently as 6 000 years ago, it was about 2-3 m above mean sea level (Marker & Miller 1993). Consequently present day estuarine systems differ considerably from those in the recent past, although estuaries have existed ever since rivers started flowing into the sea. An example of such a change can be seen in the evolution of Lake St Lucia. This estuarine lake did not exist during the interglacial period  $\pm 125\,000$  years B.P. and the western arm of the lake was a marine embayment opening directly to the sea (Orme 1973).

The nearby Lake Sibaya has also undergone major transformation during the last 10 000 years (Allanson 1981), changing from an estuarine lake into a freshwater coastal lake during that period (Allanson et al. 1981). A similar late Holocene transformation of a drowned palaeo-valley into an estuarine bay, and then into an estuarine lake system has been documented on the southern Cape coast (Figure 57). The above ecomorphological changes would have resulted in major

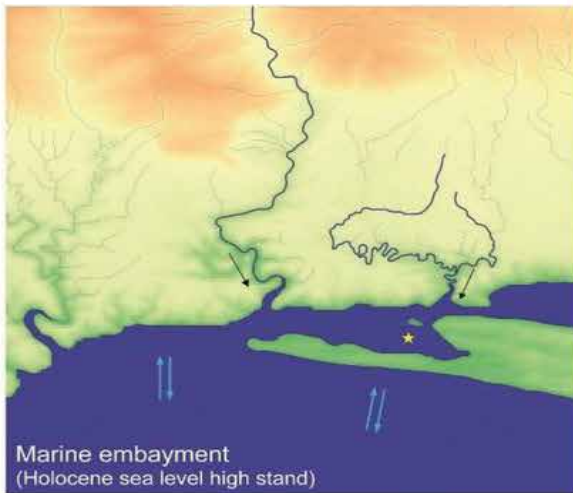
(a) ~8900-7900 years BP



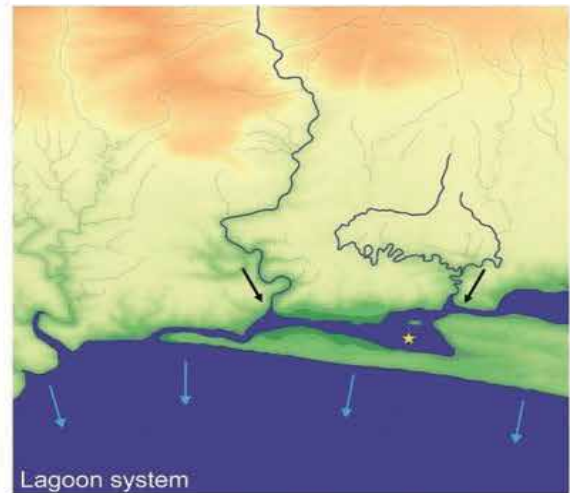
(b) ~7900-6400 years BP



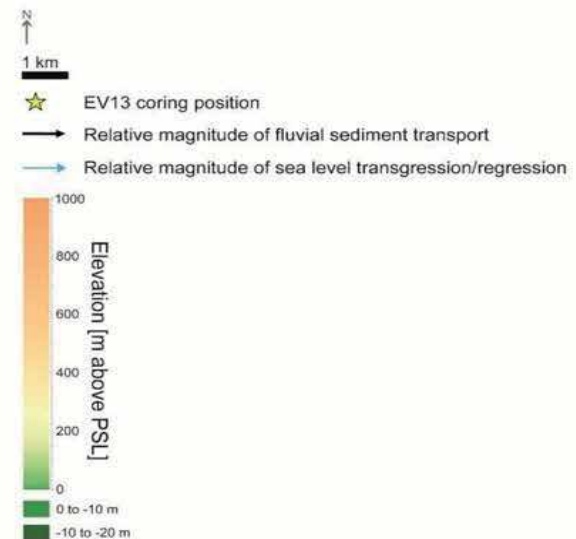
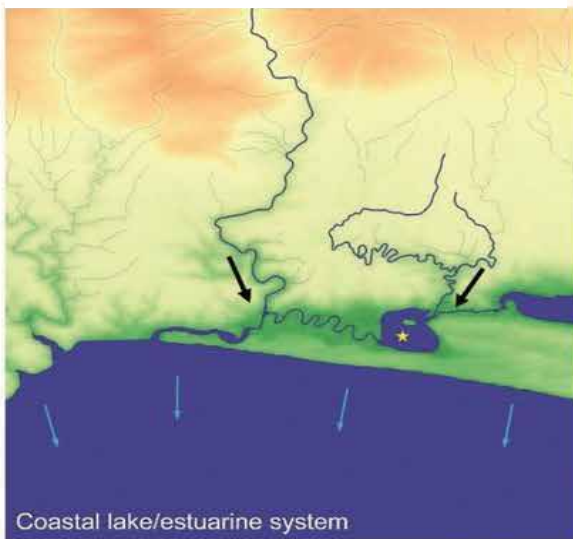
(c) ~6400-4700 years BP



(d) ~4700-1200 years BP



(e) ~1200 cal BP-present



**Figure 57.** Late Holocene changes (9000 years BP to Present) in the morphometry of the lower Wilderness lakes system, from a drowned palaeo-valley (a and b), estuarine bay (c), continuous estuarine lake system (d) and segmented estuarine lake system (e) (after Wündsich et al. 2018).



alterations in the ichthyofauna found within the above systems.

Blaber (1991) has argued that the boundaries between habitats need to be defined according to whether such divisions are important to the species living in these environments. He asks whether the movements of fishes from a marine rocky reef habitat in the sea to an adjacent soft bottom habitat, also in the sea, are not as great a change as the movement of fishes from the sea into an estuary. Horizontal linkages between the sea and rivers through estuaries are also common, but for some fish species the physiological barriers between fresh and salt water are almost as great as between water and land (Blaber 1991).

#### **Ancient estuarine fish communities**

If, on a geological time-scale, individual estuaries are ephemeral features of the coast, perhaps individual estuary-associated fish species should be placed in the same category. How many taxa have become extinct and how have southern African estuarine fish assemblages changed within the last 400 million years? Comparisons between the

ichthyofauna of a Famennian and modern estuary are underway (Gess & Whitfield submitted), with none of the fish species from the Devonian having survived through into the Holocene. Indeed, lampreys were once widespread in the region (Gess et al. 2006) but are now absent from the continent. Similarly, coelacanths were also recorded in the Grahamstown Famennian estuary (Gess & Coates 2015a) but now only occur in the adjacent marine environment.

Fossil fish research in Witpoort Formation black shale deposits in the Grahamstown area has revealed evidence of a fish assemblage that occupied an estuarine lagoon or lake approximately 360 million years ago (Figure 58). Four major groups of Palaeozoic fishes, namely acanthodians, placoderms, chondrichthyans and osteichthyans, are represented in the Witpoort ichthyofauna, with the former two extinct and the latter two extant (Anderson et al. 1994, Long et al. 1997), albeit with a completely different set of species.

Most of the species found at the above site are represented by both adults and juveniles, with the variety of groups present in the deposits suggesting



**Figure 58.** A diagrammatic representation of a section of the Grahamstown (Waterloo Farm) Devonian estuarine ichthyofauna (© Trustees of the Albany Museum, Grahamstown).

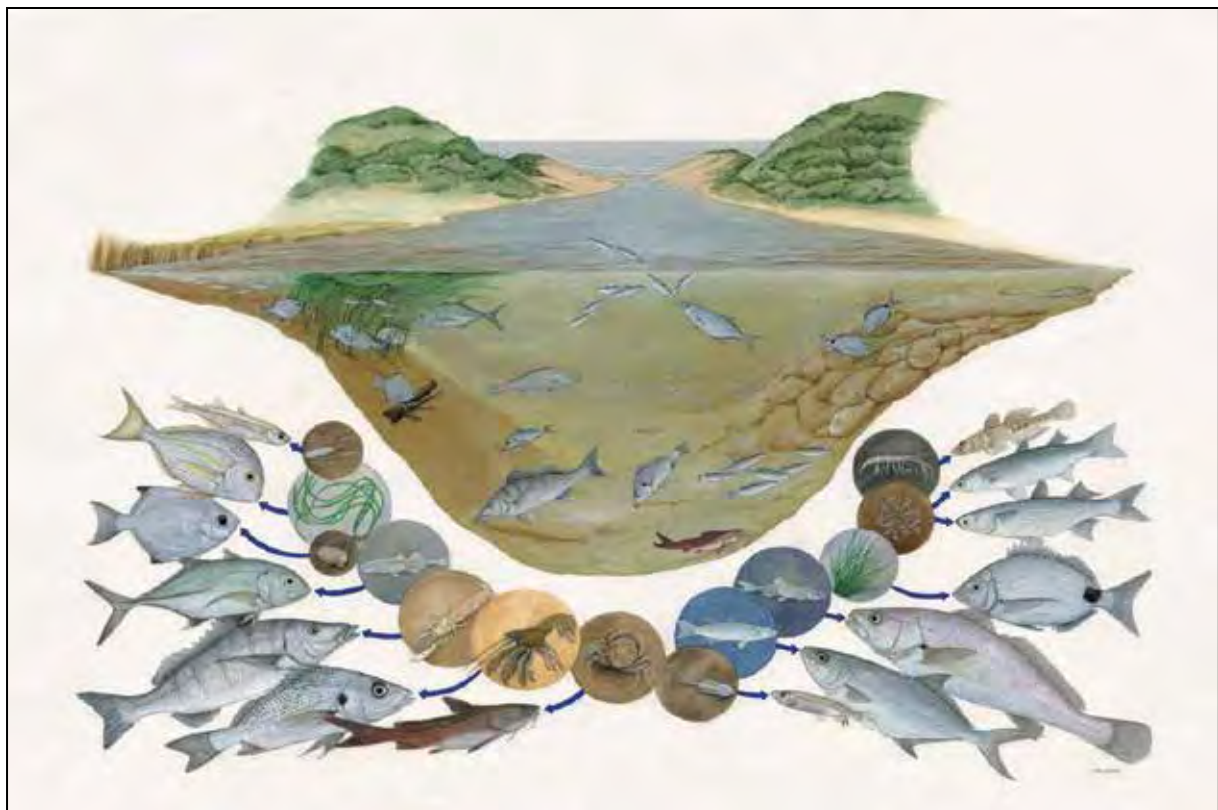
that a range of salinities occurred within the estuary (Gess 1995). The abundance of juveniles indicates that estuaries in the Devonian Period also acted as important nursery areas for small fish (Gess & Hiller 1995a). Indeed, the charophyte meadows that flourished in the Fammennian estuarine lake (Gess & Hiller 1995b) are well represented by modern charophytes in Swartvlei estuarine lake and also act as a nursery area for modern fish species.

As is the case today, large predatory fish were also present. Of particular interest was that approximately 21% of the ichthyofauna represented in the Devonian estuarine lake were viviparous and 79% oviparous. This compares to a 100% oviparous composition in a modern southern African estuarine lake due to total dominance by the Actinopterygii, thus suggesting a strong trend away from vivipary and towards ovipary over the intervening period (Gess & Whitfield submitted).

An acanthodian and a crossopterygian, both approximately 1.5 m in length, have been found at the Grahamstown fossil site and both were

probably piscivorous. Evidence suggests that certain taxa, including both arthrodire and antiarch placoderms, spent their entire life cycle within the estuarine environment (Gess & Trinajstić 2017) whereas others, including the coelacanth *Serenichthys*, only inhabited the estuary as juveniles and sub-adults (Gess & Coates 2015a). Large sharks also entered the estuary to feed and possibly also to bear young (Gess & Coates 2015b). A similar situation pertains to some modern southern African estuaries (e.g. Lake St Lucia and Mzimvubu) that are utilised by bull sharks *Carcharinus leucas* for feeding and pupping purposes.

In general, actinopterygians are not abundant in the ichthyofauna of the Grahamstown fossil site, and are represented by very small juveniles that would almost certainly have been utilising the estuary as a nursery area, with presumed adults foraging in the same system. The proportional scarcity of juvenile actinopterygians in the fossil record from this site, relative to those of other taxa such as the coelacanth, might suggest extensive



**Figure 59.** A diagrammatic representation of a section of a modern Eastern Cape estuarine ichthyofauna together with some dominant food items of selected fish species (© NRF-SAIAB, Grahamstown).

estuarine nursery use by these early coastal marine fishes.

### **Modern estuarine fish communities**

Modern southern African estuaries may differ only slightly from the early Devonian estuaries described above in terms of the physico-chemical and habitat conditions provided. However, the ichthyofauna has changed completely over the above geological time frame, and all the current family and species in estuaries on the subcontinent are new, with all the dominant taxa now belonging to the class Actinopterygii (Figure 59).

In addition, the evolutionary stage of the ichthyofauna will also influence fish composition and diversity within an estuary. Hence one would expect any Holocene southern African system to potentially have a much higher fish species richness than a Devonian estuarine equivalent (Gess & Whitfield submitted). The reason for the loss of some fish groups, such as the lampreys, from modern estuaries on the subcontinent are unknown but may be related to climate change and especially more erratic catchment run-off and decreased river flow rates in the region.

Despite the physical instability of estuaries in southern Africa, the species composition of fish communities within the various biogeographic regions is relatively stable and the fishes have more or less predictable patterns of abundance and distribution. Moyle & Cech (1982) attributed such stability to four principal conditions, namely (1) the regular distribution of fish populations along environmental gradients (2) seasonal movements of fishes into and out of estuaries; (3) the dominance of estuaries by relatively few species; and (4) the robust nature of food webs within estuaries. A fifth condition can be added to those above, viz. the wide physiological and ecological tolerances of fish species utilizing estuaries.

Although the ichthyofaunal communities in southern African estuaries may be relatively stable, they are characterized by a relatively low species diversity when compared to the adjacent marine environment. Wallace et al. (1984a) have shown that, of the approximately 1 500 species of fishes found on the continental shelf of the subcontinent, fewer than 150 species are regularly

found in estuaries of the region, i.e. a less than 10% occurrence ratio.

According to Whitfield (1994c) approximately 100 southern African fish species are wholly or partially dependent on the estuarine environment. A more recent analysis (page 111 in this chapter) revealed that 79 (46%) of the 172 fish species recorded in southern African estuaries are strongly associated with these systems. However, on an individual estuary basis the number of species associated with these systems is much lower. Of the four South African and four Western Australian estuaries reviewed by Potter et al. (1990), all had less than 60 fish species per estuary.

The pattern of declining estuarine species richness with increase in latitude along the African western Atlantic and south-eastern Indian Ocean coasts has already been mentioned. In the western Atlantic this decline was attributed to the increasing disturbance frequency or magnitude (e.g. temperature variations) with increasing latitude (Vieira & Musick 1993). These authors also suggested that the greater fish diversity of tropical estuaries arose from the prolonged coexistence of species whose traits would otherwise lead to competitive exclusion. In a southern African context, temperate estuaries are dominated by relatively few species when compared to more tropical systems, but the extent to which competitive interactions or food resource limitations affect species diversity is not yet known.

According to Kennish (1990), the higher species richness in the mouth region of estuaries is indicative of the osmotic problems many species experience as they progress up an estuary. Osmoregulatory stress may be part of the reason why <10% of marine and freshwater fish species from southern Africa utilize estuaries to any significant extent, but the variable nature of these systems probably plays a greater role (Table 6). In an unpredictable environment (e.g. an estuary) only organisms that can tolerate wide perturbations are present, and the ecosystem tends to be simple but also more robust (Bruton 1989). In contrast, a more predictable environment (e.g. a coral reef) may permit a relatively complex ecosystem, with increased species diversity to evolve (Margalef 1968).

Table 6. Community traits associated with predictable/unpredictable environments as presented by Bruton (1989), compared to the southern African estuarine fish fauna (after Whitfield 1990).

Traits	Predictable environment	Unpredictable environment	Estuaries
Species diversity	High	Low	Low
Breeding guilds	Few	Many	Many
Species interdependence	High	Low	Low
Mutualisms	High	Low	Low
Rare species	Common	Uncommon	Uncommon
Migratory species	Uncommon	Common	Common
Sedentary species	Common	Uncommon	Uncommon
Speciation rates	High	Low	Low
Extinction rates	High	Low	Low?
Species saturation	High	Low	Low

### Successionary trends and fish speciation

Estuaries differ from certain other inland aquatic ecosystems in that they show a weak successionary trend towards a more mature plant and animal community. In Lake Malawi, for example, the fish community is characterised by an increasing proportion of specialised forms with progressively stronger species interdependence. In contrast, the estuarine systems of southern Africa are characterized by wide fluctuations in abiotic conditions, the constant re-organization of biological communities and homeostatic mechanisms, and the frequent resetting of the ecological succession to an earlier state (Whitfield & Bruton 1989). Thus, the fish fauna of these estuaries is characterized by a relatively low species diversity, consisting mainly of migratory forms with weak interspecific connections (e.g. a lack of mutualistic relationships). Although there are a relatively large number of breeding styles employed by the different groups of fishes in southern African estuaries, species saturation may be considered low when compared to the communities present in certain central African freshwater lakes, or the assemblages associated with coral reefs on the subcontinent.

Vrba (1980) has suggested that the environment is the 'motor' of evolutionary change. Similarly, Ribbink (1994) has proposed that the environment plays a major role in the speciation process of African cichlids and it is possible that it performs a similar function in the fish communities of southern African estuarine systems.

Speciation in seasonally stable, uniform environments (e.g. large lakes) was shown by Bruton & Merron (1990) to be greater than that of seasonally unstable, heterogeneous environments (e.g. rivers).

A number of authors (e.g. Eldredge 1979) have suggested that diversification of stenotopes (specialists) is more rapid than that of eurytopes (generalists). Since southern African estuaries are dominated by eurytopes, and these systems are one of the most unstable aquatic environments in the region, it is perhaps not surprising that they exhibit a very low species richness. In addition, the few stenotopes occurring in estuaries are faced with major short and long-term environmental changes, which effectively reduces the potential for speciation. This is because adaptations developed by existing stenotopes in a particular estuarine system may be eliminated as a result of episodic (e.g. river floods) or longer term fluctuations (e.g. sea level rise).

A more detailed examination at the species level reveals that there are several stenotopic taxa (e.g. *Syngnathus watermeyer*, *Clinus spatulatus* and *Hippocampus capensis*) which are restricted to five or fewer estuarine systems altogether, whereas most of the eurytopic species (e.g. *Chelon dumerili*, *Lichia amia* and *Pomadasys commersonnii*) on the subcontinent occur in more than 100 estuarine systems. It is perhaps noteworthy that the two most eurytopic species within the estuarine spawner group, *Atherina breviceps* and



*Gilchristella aestuaria* (Figure 60), breed in both freshwater dominated and hypersaline systems (Day et al. 1981), and are abundant in temperate and subtropical estuaries of the region (Potter et al. 1990).

Although a number of stenohaline marine fish species enter the mouth region of estuaries (Wallace 1975a), these taxa make minimal use of this environment and are usually transient components of the estuarine ichthyofauna, i.e. marine stragglers. The poor numerical representation and transient nature of marine stragglers in southern African estuaries can probably be attributed to their more stenotopic environmental requirements when compared to the marine estuarine-opportunists. For example, 20% of the fishes recorded in the Kosi Estuary were restricted to a rocky reef near its mouth (Blaber 1978), with the species composition fluctuating according to changing biotic (e.g. fish movements) and abiotic (e.g. salinity regime) factors. The absence of these reef-associated marine species from the rest of the system suggests that their presence in this estuary was mainly dependent on the rocky outcrop inside the mouth.

The disappearance of euryhaline marine species from coastal lakes that have become isolated from the sea results in the opening up of these environments to speciation by freshwater and relic estuarine groups, yet very few fish species are found in these habitats. In the warm-temperate Groenvlei for example, which has been isolated from the nearby Swartvlei estuary for less than 5 000 years, the eurytopic *A. breviceps* and *G. aestuaria* were the only two indigenous fish

species recorded from this system (Whitfield et al. 2017b). According to Ratte (1989) these two species are in the early stages of allopatric speciation, with *A. breviceps* and *G. aestuaria* from Groenvlei being separated from their historic populations in the nearby Swartvlei estuarine system by a genetic distance of 0.1 and 0.05 respectively. These genetic differences have not yet reached the subspecies level of divergence, but they were sufficiently different for Ratte (1989) to suggest that the populations of both species in Groenvlei should receive a priority conservation status. This view was later supported by molecular genetic studies on both species by Phair et al. (2015).

When compared to Groenvlei, subtropical Lake Sibaya has a more diverse ichthyofauna (18 species), with five taxa having estuarine affinities. According to Bruton (1980) the most successful and abundant fishes in Lake Sibaya are those species with wide habitat and food tolerances, i.e. eurytopes. Although Lake Sibaya has a more stable aquatic environment when compared to estuarine systems, fluctuations in lake level, either as a result of seasonal or long-term changes in rainfall patterns, have a marked effect on the littoral fish community. At low lake levels the littoral terrace is a barren, harsh environment, inhabited mainly by the eurytopic *Oreochromis mossambicus*, whereas at higher lake levels the more diverse and stable marginal habitats harbour a variety of fishes (Bruton 1980, Bowen & Allanson 1982). It is important to note that Lake Sibaya has been classified as oligo-mesotrophic (Allanson 1979) and this may also have had a negative influence on fish species diversity and richness, e.g. a shortage



**Figure 60.** The endemic estuarine round-herring *Gilchristella aestuaria*, one of the few estuary associated fish species that probably evolved within these systems on the subcontinent (Photo: Alan Whitfield).

of prey fish would reduce the potential for exclusively piscivorous species to maintain viable populations.

Lake Sibaya, like Groenvlei, is a relatively young system (Hobday 1979) and it is unlikely that major speciation could have occurred within a period of less than 10 000 years. However, one species (*Silhouettea sibayi*) was originally thought to be endemic to the lake. This small cryptic goby is present over barren sandy substrata but little is known about its biology or ecological requirements (Bruton & Kok 1980). Did *S. sibayi* evolve in Lake Sibaya or does it represent a relic estuarine species which is either rare or has disappeared from other southern African coastal systems? Recent evidence, especially the presence of *S. sibayi* in certain northern KwaZulu-Natal estuaries, indicates that this species did not evolve in Lake Sibaya but was distributed through a number of Holocene estuaries within this region. Some of these systems (e.g. Lake Sibaya) subsequently became isolated from the sea, as did the local *S. sibayi* population.

According to several authors (e.g. Ribbink 1994) a degree of environmental permanency is necessary for stenotopes to evolve and speciate. In systems that undergo major changes seasonally or over longer periods, eurytopes dominate and speciation is rare. Estuaries do not exhibit the environmental permanency necessary for eurytopes to develop into stenotopes and, although some stenotopic species are found in estuarine systems, these taxa are forced to become 'survivors' rather than 'increasers' using the terminology of Vrba (1980). Thus the barriers to gene flow along estuarine and latitudinal gradients, together with intense natural selection (Levinton 1980), have not resulted in widespread speciation as has occurred in other more stable (and therefore predictable) aquatic ecosystems, e.g. the coral reefs of the Indo-Pacific or the great lakes of central Africa.

The lack of speciation in southern African coastal lakes, which exhibit a greater degree of environmental permanency and predictability than estuaries, can probably be attributed to three principal factors; (a) the recent history of these systems which only became isolated during the Holocene, (b) the eurytopic nature of

the dominant freshwater and relic estuarine fish species, and (c) the lack of opportunities for additional founder species to colonise these systems. In addition, the relatively low species richness of potential ichthyofaunal colonists from the adjacent estuarine and freshwater systems has given rise to species poor communities.

### Reproductive modes

Early developmental modes of southern African estuarine fishes fall into three main categories, namely viviparity, ovoviparity and oviparity. The viviparous (e.g. *Clinus spatulatus*) and ovoviparous (e.g. *Hippocampus capensis*) forms breed within the estuarine environment and have a relatively low fecundity when compared to oviparous taxa (Whitfield 1990). However, the former embryos generally develop to a larger size prior to parturition or hatching and, on average, a high percentage of them survive.

In contrast, oviparous fishes (e.g. *Mugil cephalus*) produce many more eggs, which are unprotected and have limited yolk reserves. Survival is closely linked to the duration of the planktonic egg and /or larval interval (May 1974). The dispersal ranges of these species greatly surpass those of the viviparous or ovoviparous forms (Norcross & Shaw 1984) as do their rates of mortality for the embryo and larval stages.

### Eurytopes and stenotopes

Most southern African fish species in estuaries may be described as eurytopes. The words eurytope and stenotope, although they can represent ends of a continuum, are also used as adjectives, indicating which half of the continuum the organism occupies. A eurytopic species has a broader habitat tolerance range relative to a stenotopic species (Vrba 1980) and during its life-history a eurytope may live in a wide range of conditions, often moving readily from one habitat to another. Characteristically, eurytopes are mobile and frequently have a wide geographical distribution (Figure 61). In contrast, a stenotope is usually confined to a single habitat during its life-history and often has a restricted geographical distribution.

Some of the features of eurytopes and stenotopes are compared to the characteristics of



**Figure 61.** The oxeye tarpon *Megalops cyprinoides*, a direct descendant from an ancient, little changed fish lineage, is an excellent example of a highly eurytopic fish species that has a wide geographic distribution, occurs in marine, estuarine and freshwater habitats, is an extremely mobile and versatile predator, and can tolerate hypoxic waters by using an auxiliary air breathing organ (Photo: Olaf Weyl).

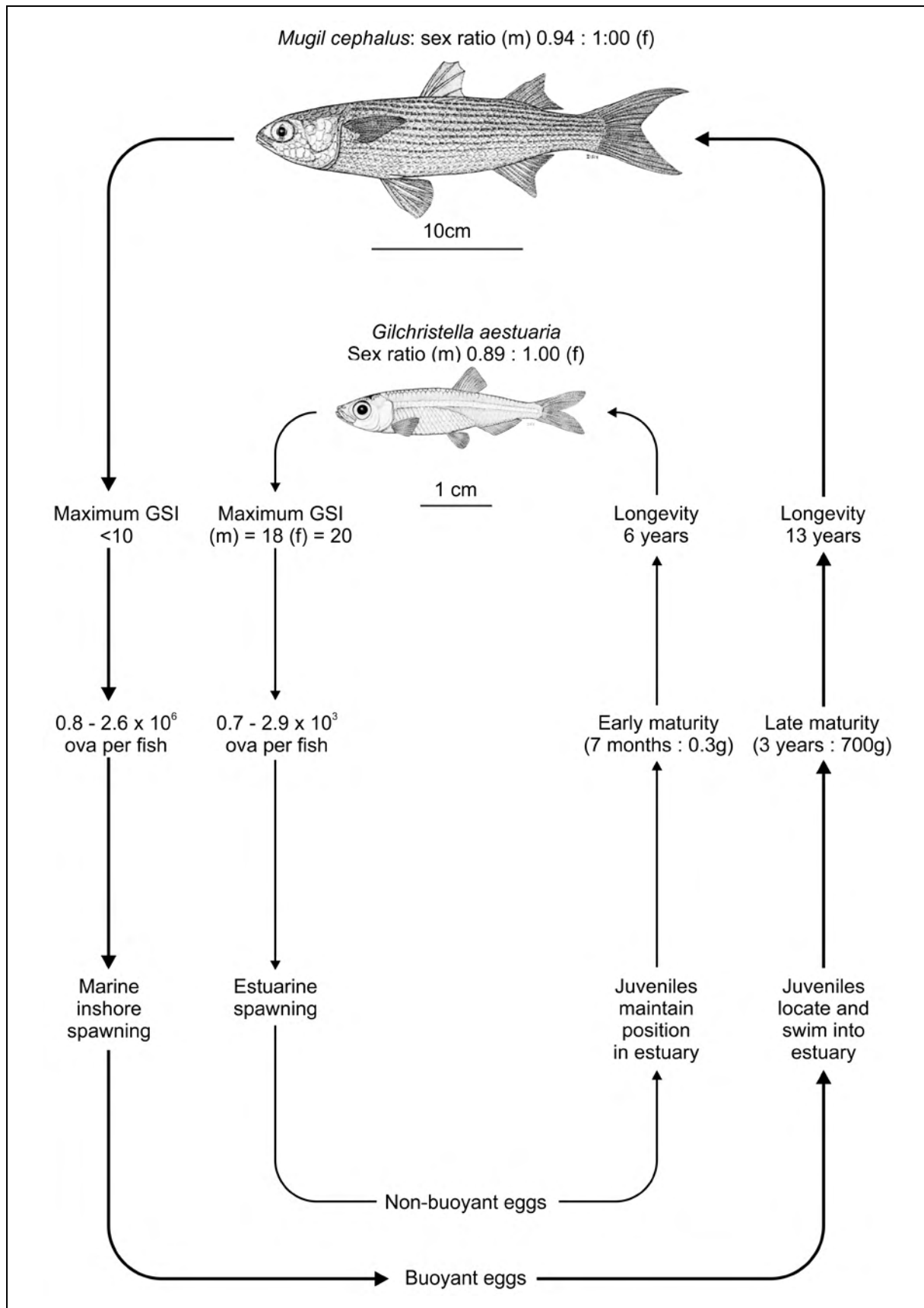
estuarine residents and marine estuarine-opportunistic groups of fishes in southern African estuaries (Figure 62, Table 7). Since marine species dominate estuaries on the subcontinent, it can be concluded that eurytopy is the predominant life form in these systems, and that estuarine fish communities are both resilient and flexible (Whitfield 1980). If one includes the two estuarine spawners (viz. *Atherina breviceps* and *Gilchristella aestuaria*) which have a number of eurytopic characteristics, then the overwhelming number and biomass of fishes in estuaries on the subcontinent are eurytopic.

Attention has been drawn to the relative paucity of freshwater fish species in estuaries. The absence of many freshwater fish species from the upper reaches of estuarine systems where salinities are usually less than 15 is difficult to explain, especially as these species are either hyperosmotic or isosmotic within this salinity range (Whitfield & Blaber 1976).

Perhaps the erratic nature of river inflow into southern African estuaries, which can result in hypersaline conditions developing in the upper

reaches of certain systems (Whitfield & Bruton 1989), effectively prevents freshwater species from establishing themselves in these areas. Also, increased predation within estuaries when compared to the riverine environment may play a role in preventing colonization of these systems by freshwater species. Apart from the anguillid eels, there are no large indigenous piscivorous fish predators in Eastern or Western Cape rivers, whereas both small and large piscivorous fish species are present in the estuaries of these regions (Coetzee 1982b, Smale & Kok 1983).

According to Macfarlane (1923) teleosts originated in freshwater areas, from which colonization of the marine environment occurred. Presumably these fishes would have passed through estuaries on route to the sea and some may have remained in this transitional zone to become the first estuarine residents. An alternative explanation is that estuary-associated fishes are examples of recent recolonization of estuaries by marine species (Panikkar 1960), with few species having adapted their entire life cycle to the fluctuating conditions of the estuarine environment.



**Figure 62.** Contrasting life cycles of the marine estuarine-opportunist *Mugil cephalus* and the estuarine resident *Gilchristella aestuaria* (after Whitfield 1990). Although *M. cephalus* fulfils all the characteristics of a eurytope (Table 7), *G. aestuaria* has both stenotopic and eurytopic traits.



Table 7. Some of the principal characteristics of eurytopes and stenotopes (after Ribbink 1994) compared to those predominating in the estuarine and marine spawning groups of fishes (modified from Whitfield 1990) from southern African estuaries.

Stenotopy	Estuarine spawners	Eurytopy	Marine spawners
Narrow habitat tolerance range	Narrow habitat tolerance range	Broad habitat tolerance range	Broad habitat tolerance range
Narrow distribution	Narrow distribution	Wide distribution	Wide distribution
Sedentary	Relatively sedentary	Mobile	Highly mobile
Small body size	Small body size	Large body size	Large body size
Small populations	Medium populations	Large populations	Large populations
Precocial <sup>1</sup>	Mainly precocial	Altricial <sup>2</sup>	Mainly altricial

<sup>1</sup> A specialist *sensu lato*; usually common in a predictable and competitive environment (Balon 1981).

<sup>2</sup> A generalist *sensu lato*; usually common in an unpredictable and harsh environment (Balon 1981).

This view is supported by the fact that even the most estuarine dependent of the marine species all spawn at sea, where abiotic conditions are more stable and predictable than estuaries.

The importance of salinity and temperature stability on embryo development of the estuary-associated *Mugil cephalus* is indicated by the work of Walsh et al. (1991) which showed that the optimum survival of normal (as opposed to deformed) larvae was at a salinity of 36 and a temperature of 25°C. The lower salinity tolerance limit of *M. cephalus* eggs was approximately 15, a value that is frequently attained during moderate river flow conditions in estuaries on the subcontinent. In addition, Sylvester et al. (1975) found that *Mugil cephalus* eggs were negatively buoyant in salinities below 30, thus accumulating on the bottom and being rendered infertile if aeration was inadequate. This probably helps to explain why southern African estuaries are unsuitable for egg survival of this and other marine fishes that do not have buoyant eggs under low salinity conditions.

In contrast to the physiological sensitivity of *M. cephalus* egg and larval stages, early juveniles of this species in the Eastern Cape are attracted to riverine environments (Bok 1979) where salinities are usually less than 0.5 and water temperatures can show wide fluctuations. The freshwater mullet *Pseudomyxus capensis* is also an obligate marine spawner, with the 0+ juveniles attracted to riverine areas and the upper reaches of estuaries (Bok

1979). However, adults that become trapped in riverine pools or estuaries are unable to spawn within these environments and have to wait for a river flood event to return to the sea.

#### Life-history styles and pipefish success

The evolutionary success of a species within the stenotopic or eurytopic guilds is based on a number of factors. A recent analysis of the life-history traits of two endemic southern African pipefish species that co-occur in estuaries on the southeast coast of South Africa was undertaken (Whitfield et al. 2017a). The larger longsnout pipefish, *Syngnathus temminckii* (Figure 63), is abundant and has a wide range that comprises coastal and estuarine habitats in all three of the region's marine biogeographic provinces. In contrast, the smaller estuarine pipefish *Syngnathus watermeyeri* (Figure 64) is critically endangered, and confined to a few warm-temperate estuaries. Thus, in terms of distribution and habitat, *S. temminckii* is more eurytopic when compared to *S. watermeyeri*. Other attributes of the two species (Table 8) serve to confirm this assessment.

Fecundity is related to fish size, with large live-bearing *S. temminckii* males carrying up to 486 developing eggs/embryos, compared to a maximum of only 44 recorded for *S. watermeyeri* (Mwale et al. 2014). Loss of submerged seagrass habitats in estuaries due to episodic river flooding appears to be correlated with the temporary absence of both

species from such systems. However, in contrast to *S. watermeyeri* which either perishes following such events or has to find a nearby estuary with suitable habitat, *S. temminckii* is capable of switching to a marine existence until such time

as estuarine conditions are favourable.

The greater success of *S. temminckii* when compared to *S. watermeyeri* can be attributed to the former species' wider geographic distribution, fecundity, habitat selection and ability to use both



**Figure 63.** The longsnout pipefish *Syngnathus temminckii* showing the derivation of the common name (Photo: Nicola Goodall)



**Figure 64.** The estuarine pipefish *Syngnathus watermeyeri* with its very short snout: (Photo: Roger Bills).

estuaries and the marine environment as nursery areas (Table 8). Genetic data indicate that this has resulted in a much smaller long-term effective population size of *S. watermeyer* (Whitfield et al. 2017a), a situation that has persisted since

the beginning of the present interglacial period. *Syngnathus watermeyer* is thus naturally more susceptible to anthropogenic disturbances, which have resulted in an alarming reduction in its contemporary population size.

Table 8. Selected life-history traits that, on balance, render an advantage to either the long-snout pipefish *Syngnathus temminckii* or the estuarine pipefish *S. watermeyer*. Traits where both species have similar attributes are not included.

Life-history trait	<i>Syngnathus temminckii</i>	<i>Syngnathus watermeyer</i>	Advantage
Biogeographical distribution	Cool-temperate, warm temperate and subtropical	Warm temperate	<i>S. temminckii</i>
Ecosystem occupation	Estuaries and coasts	Estuaries	<i>S. temminckii</i>
Estuary type occupation	Mainly large permanently open estuaries	Permanently open and temporarily open/closed estuaries	<i>S. watermeyer</i>
Habitat occupation	Submerged macrophyte beds, turbid estuarine littoral and marine reefs	Submerged macrophyte beds	<i>S. temminckii</i>
Reproductive strategy	Estuarine and marine spawning	Estuarine spawning	<i>S. temminckii</i>
Reproductive output	High fecundity and large brood size	Low fecundity and small brood size	<i>S. temminckii</i>
Reproductive timing	Mainly spring and summer but breeding can occur in any month	Spring and summer	<i>S. temminckii</i>
Physiological tolerances	Tolerance of a wide range of both salinities and water temperatures	Tolerance of a wide range of salinities but a moderate range of water temperatures	<i>S. temminckii</i>
Mobility and connectivity	More mobile due to large adult size	Less mobile due to small adult size	<i>S. temminckii</i>
Genetic diversity	High	Low	<i>S. temminckii</i>

## 2.4 FACTORS INFLUENCING ESTUARINE UTILIZATION

Estuaries are characterised by a relatively low ichthyofaunal diversity but high abundance of individual taxa, most of which exhibit wide tolerance limits to the fluctuating conditions found in these systems. Indeed, most southern African estuaries are occupied by fewer than 50 species, with fish population sizes probably totalling several million individuals in some of the larger systems. Even very small estuaries (<1 km<sup>2</sup>) can have single species populations ranging from 10 000-50 000 individuals (Blaber 1973a), and

fish densities in these systems invariably exceed that of the adjacent marine or freshwater environments (Whitfield 1993). This observation leads directly to the question which has been repeatedly asked by both scientists and anglers; why are estuaries so attractive to fishes? Although selected aspects of this question have been directly and indirectly addressed by ichthyologists over the years, it was only during the 1980s that overviews of the situation were presented (Whitfield 1983, Blaber 1985, Marais 1988). During the past few

decades much additional information on the biology and ecology of a number of fish species associated with estuaries has been published, and we are now in a position to examine the issue in more detail (Whitfield 1994d, 1996b).

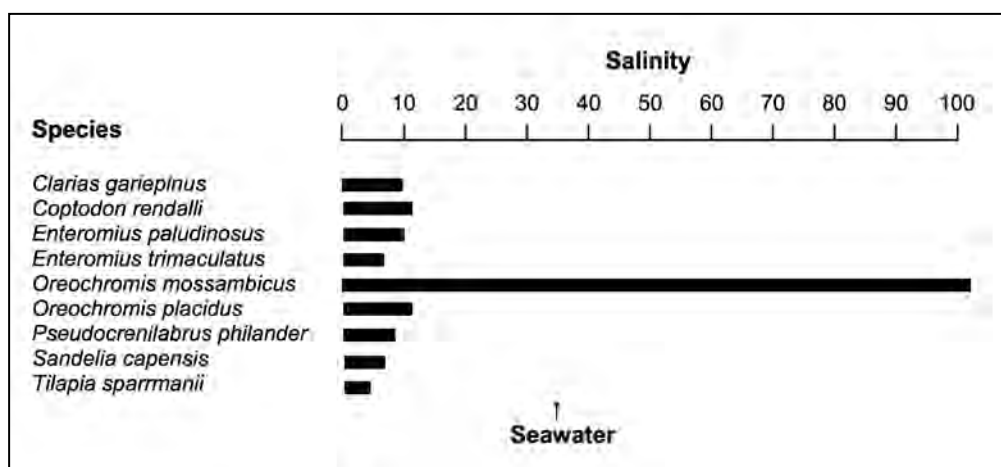
Although most ichthyofaunal studies in southern African estuaries have tended to cover only one or two factors at a time, all scientists acknowledge that multiple variables influence both the abundance and diversity of fishes in these systems. Some of the following factors have been identified as possible or probable determinants of estuarine utilization by fishes, viz. latitude (Wallace 1975a, Blaber 1981a), estuary size (Whitfield 1980d, Begg 1984a), seasonality (Wallace 1975b, Branch & Grindley 1979), catchment size (Marais 1988), habitat type (Hanekom & Baird 1984, Whitfield 1986a), nearshore marine conditions (Whitfield 1989c, Potter et al. 1990), mouth depth and degree of marine influence (Whitfield & Kok 1992, Harrison & Whitfield 1995), estuarine channel dimensions (Hall et al. 1987, Becker et al. 2017), river water quantity and quality (Marais 1988, Plumstead 1990), estuarine productivity (Howard-Williams & Allanson 1981, Heymans & Baird 1995), the occurrence and severity of floods (Marais 1982, Whitfield & Paterson 1995), olfactory cues (Whitfield 1994a, James et al. 2008a), estuary type (Bennett 1989, Kok & Whitfield 1986), timing of the open phase (Wallace & van der Elst 1975, Whitfield & Kok 1992), the ability of species to adjust to salinity and temperature fluctuations (Blaber 1974a, Martin 1988),

dissolved oxygen levels (Russell 1994, Blaber et al. 1984), turbidity (Cyrus & Blaber 1987a, 1987b, 1987c), available food resources (Whitfield 1980e, Whitfield 1988a), predation (Blaber 1973a, Whitfield & Blaber 1978a), competition (Blaber 1976, Whitfield & Blaber 1978b), reproductive condition and proximity to spawning grounds (Wallace 1975b, Lasiak 1984a), juvenile cohort abundance (Blaber 1974c, Wallace & van der Elst 1975), and habitat degradation as a result of pollution (Blaber et al. 1984) or dredging (Cyrus & Blaber 1988). Some of the above factors are expanded upon below.

### Salinity

The most essential adaptation by fish which enter estuarine systems is an ability to adjust to changes in salinity (Panikkar 1960). The change may be gradual, as normally occurs in a temporarily closed estuary, or sudden, as often takes place in tidal estuaries with river inflow.

A characteristic of many fish species entering southern African estuaries is an ability to adapt to both low and high salinity regimes, although it is noteworthy that less than 20 species have their upper recorded limits above 69, whereas more than 60 species can survive in water with a salinity of 1. Fishes are therefore more tolerant of low rather than high salinity conditions (Ter Morshuizen et al. 1996b). This is important since most estuaries are subject to regular periods of freshwater flooding, whereas salinities seldom rise above sea water except in Lake St Lucia and a



**Figure 65.** Recorded salinity ranges of selected indigenous freshwater fishes from southern African estuaries.



few temperate systems to the south. Furthermore, the closure of estuaries is usually associated with declining salinities, and only fishes tolerating these conditions are able to utilize the rich food resources available within these systems.

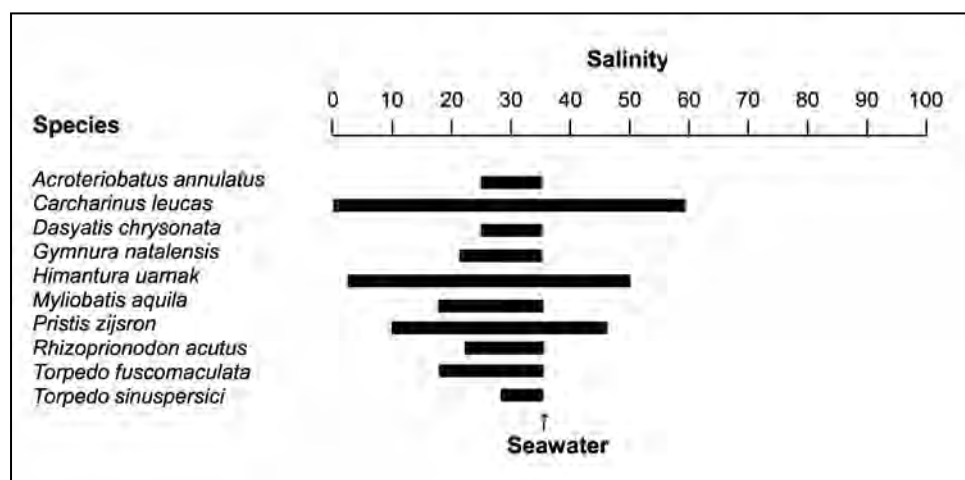
Only a few southern African freshwater teleosts have developed hypotonic regulation but most species are incapable of this adaptation and are therefore excluded from estuaries. Of the nine species shown in Figure 65, only *Oreochromis mossambicus* may be classified as truly euryhaline. Mozambique tilapia were abundant in Lake St Lucia during hypersaline conditions and have been recorded living in areas where the salinity exceeded 110 (Wallace 1975a).

According to Panikkar (1960) only a few species of sharks and rays are known to enter estuarine waters because of their method of osmoregulation. Nevertheless three species of elasmobranchs were recorded from the St Lucia system during 1975 and 1976 (Whitfield et al. 1981). The shark *Carcharinus leucas*, stingray *Himantura leoparda* and sawfish *Pristis zijsron* all occurred in water with a salinity of less than 10 (Figure 66). *Carcharinus leucas* was also regularly netted at Lake St Lucia in salinities up to 47 by Bass et al. (1973), with juveniles <1 m in length adapting well to changing salinities. Significant numbers of the spotted ragged-tooth shark *Carcharias taurus* move into the euhaline Kariega Estuary during coastal upwelling events. In addition, Paterson (1995) recorded juveniles and adults of the blackspotted electric ray *Torpedo fuscomaculata* and blue

stingray *Dasyatis chrysonota* in the lower half of this estuary. None of these species have been recorded in the Kariega system under oligohaline or mesohaline conditions. The lesser guitarfish *Acroteriobatus annulatus* is sometimes recorded in the euhaline lower reaches of permanently open estuaries and is common in estuarine embayments such as Langebaan Lagoon where seawater salinity prevails (Harris et al. 1988).

Most marine fish species associated with estuaries are strong osmoregulators (Figure 67), capable of surviving under both oligohaline and hyperhaline conditions. However, of the approximately 1 200 marine species found in northern KwaZulu-Natal coastal waters (Smith 1980), only 201 (16%) have been recorded entering estuaries (Whitfield 1980d). Fewer than 50 of these species are common in estuaries, with the implication that <5% of marine fishes use estuaries to any great extent. Do salinity fluctuations within estuaries limit the use of these systems by marine fish species? Observations from the Kariega and Bushmans estuaries suggest that some stenohaline marine species do penetrate systems which are euhaline for extended periods. Indeed, estuaries with marine conditions extending into the upper reaches may have higher fish species diversity than estuaries with a more typical salinity gradient.

Several euryhaline marine fish species sometimes penetrate considerable distances up the rivers of southern Africa. For example, Pooley (1975) recorded *Acanthopagrus vagus* on the Phongolo floodplain approximately 100 km from the sea,



**Figure 66.** Recorded salinity ranges of selected marine elasmobranchs found in southern African estuaries.

and Bok (1984) found both *Pseudomyxus capensis* and *Mugil cephalus* 120 km upstream from the head of the Gamtoos Estuary. Similarly, in the Great Fish system, marine species tend to dominate the fish assemblage immediately above the ebb and flow region (Ter Morshuizen et al. 1996b). However, the relatively high conductivity of the Great Fish and some other Eastern Cape river systems suggests that dissolved salts from the catchment geology (ancient marine sediments) may be important in reducing osmoregulatory stress for these temporary riverine residents from the sea and therefore allowing them to occupy more 'freshwater' type habitats above the ebb and flow (Ter Morshuizen et al. 1996a).

Both species composition and abundance seem to respond to salinity changes. There is an inverse relationship between salinity and numbers

of fish species at Lake St Lucia (Whitfield et al. 2006). Fish abundance is also affected, with gill net catch rates when salinities were less than 20 being double those when salinities exceeded 50 (van der Elst et al. 1976). Although the lower catches during the hypersaline period could have been due to osmoregulatory stress, forcing certain fish taxa out of the area, the disappearance of certain food resources, especially many benthic invertebrate species (Bolt 1975), may also have played a role in reducing fish abundance. Wallace (1975a) found that *Pomadasys commersonnii* and *Rhabdosargus sarba* captured in areas where the salinity was in excess of 70 were no longer feeding on normal molluscan and crustacean prey but were consuming filamentous algae.

Prolonged closure of an estuary, in association with dilution of lagoonal waters from inflowing

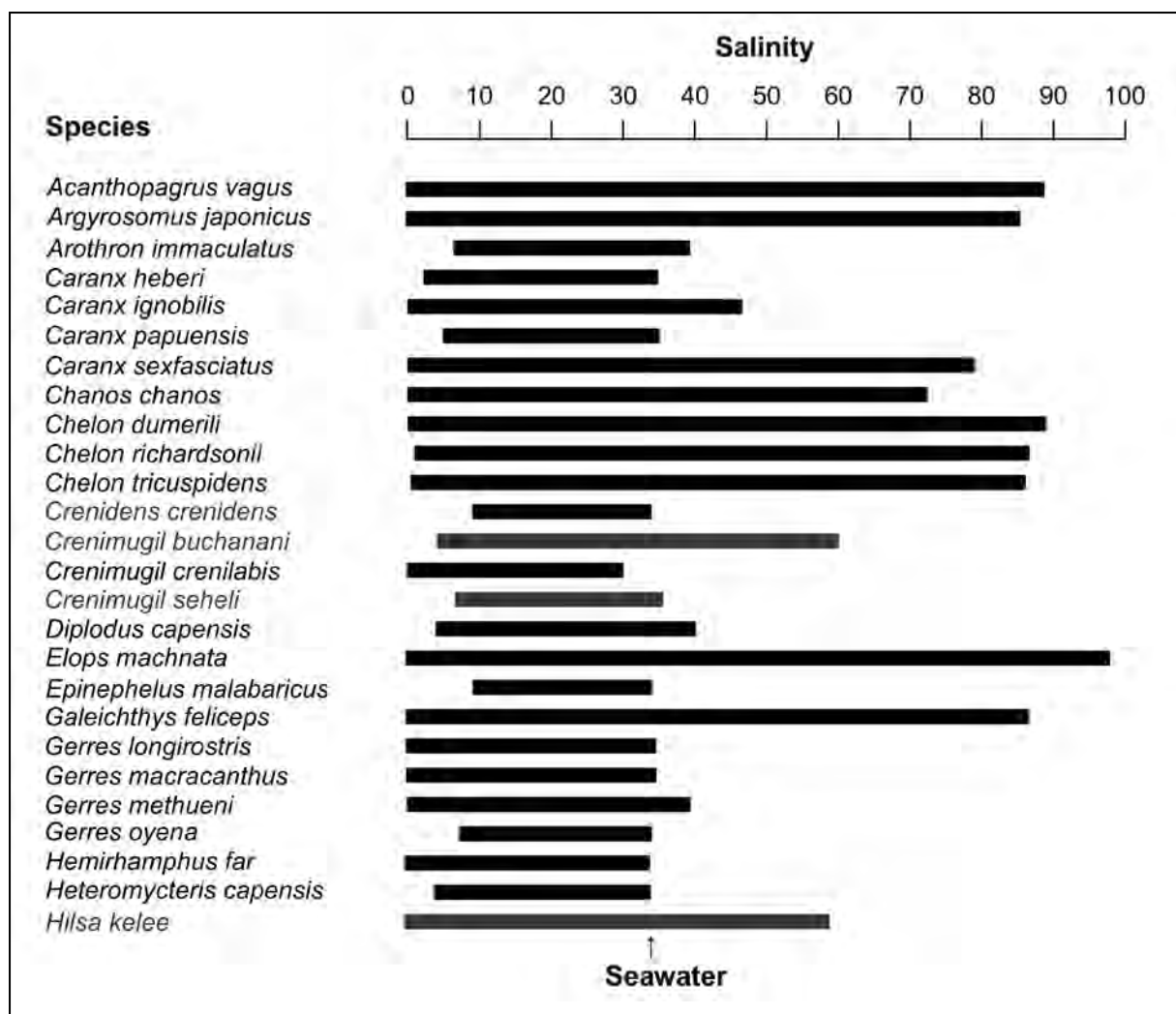


Figure 67. Recorded salinity ranges of selected marine teleosts found in southern African estuaries.



**Figure 67 (continued).** Recorded salinity ranges of selected marine teleosts in southern African estuaries.

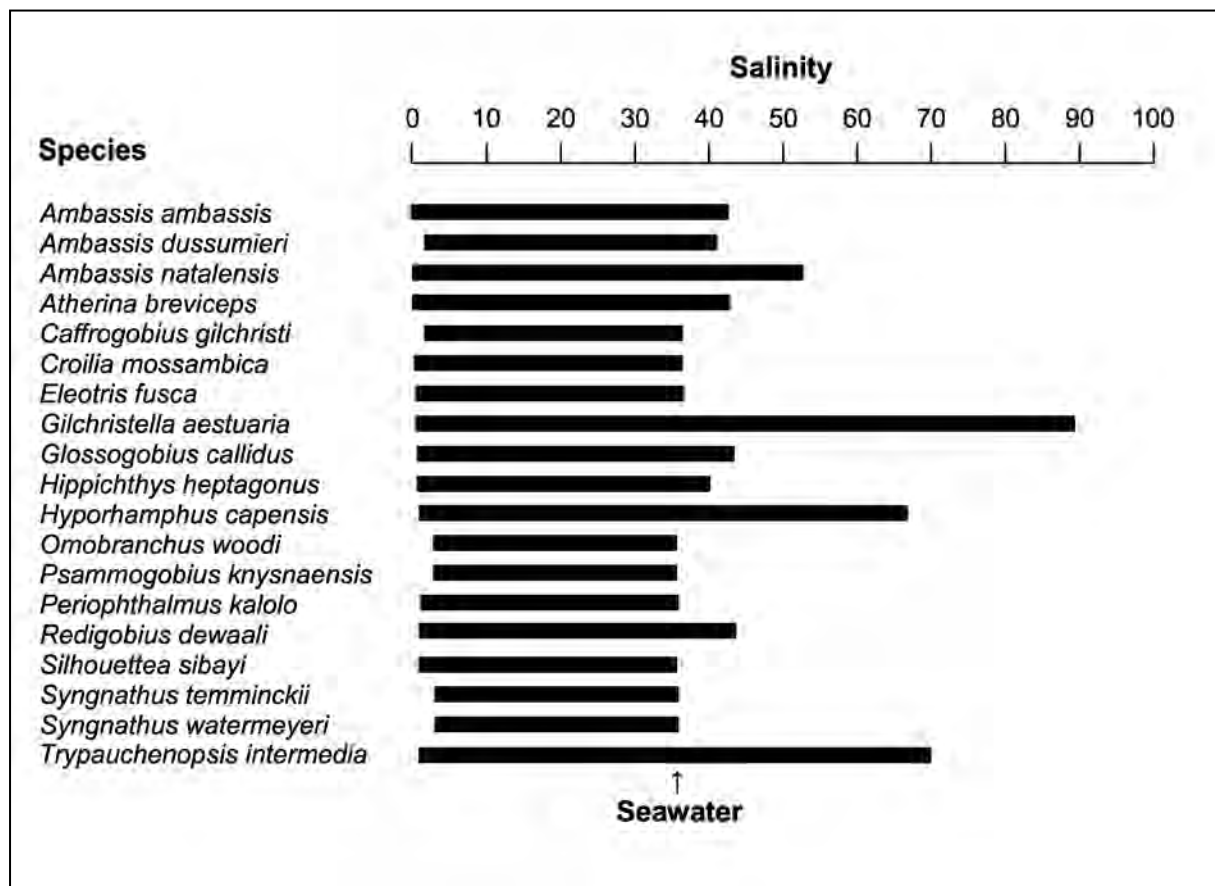
ivers, can cause osmoregulatory stress for some marine fish species trapped inside the closed system. However, estuarine resident taxa appear to be tolerant of prolonged oligohaline conditions, with all species recorded in salinities below 10 and most having also been recorded in fresh water (Figure 68). In contrast to marine taxa, the estuarine group does not appear as well adapted to hypersaline conditions, with only *Gilchristella aestuaria* having been recorded in salinities above 70. Although the eggs and larvae of a number of estuarine species have been recorded under oligohaline, mesohaline, polyhaline and euhaline conditions, it would appear that the eggs of many marine taxa cannot survive decreased salinities (Sylvester et al. 1975) but the fry of these same species are attracted to low salinity or even fresh waters (Mires et al. 1974).

#### River flow

River flow into estuaries influences not only the salinity but also the biochemical properties of

the water body, including the introduction of catchment olfactory cues. Fishes have a highly developed sense of smell and it is possible that olfactory cues guide the larvae of species such as the longfin eel *Anguilla mossambica* up estuaries and into the river catchments. Olfactory cues, which can be of freshwater or estuarine origin, may also guide those marine postlarvae that utilise estuaries as nursery areas (James et al. 2008a).

Permanently open Eastern Cape estuaries with longitudinal salinity differences greater than 19 have considerably higher densities of 0+ juvenile marine fishes than those systems where salinity gradients are small or absent (Whitfield 1994a). Similar findings were arrived at by Martin et al. (1992) who found that the densities of postlarval marine migrants in the St Lucia Estuary increased markedly following an episodic flushing of the system. Nodo et al. (2018) also documented a major increase in benthopelagic fish species in the freshwater deprived Kariega Estuary following episodic river flooding.



**Figure 68.** Recorded salinity ranges of selected estuarine teleosts found in southern African estuaries.



Although the inference from the above studies was that the salinity gradient is the primary attractant for these 0+ juvenile fishes, it is more likely that the increased amount of olfactory cues that are exported to the marine environment on each ebb tide are vital to the recruitment process. Indications are that these juveniles remain within the selected estuary for several years because data presented by Marais (1988) showed that gill net catches in Eastern Cape estuaries were positively correlated with increasing longitudinal salinity gradients.

River pulses also seem important in influencing the abundance of estuarine spawners. Martin et al. (1992) recorded considerably higher abundances of virtually all estuarine resident species following the flushing of the St Lucia Estuary. They found that an order of magnitude increase in the abundance of *Gilchristella aestuaria* could be indirectly linked to the phytoplankton bloom and increased zooplankton stocks which followed the flooding event. Conversely, decimation of the estuarine pipefish *Syngnathus watermeyer* has been attributed to the indirect effect of freshwater deprivation on Eastern Cape estuaries where this endemic species had previously been recorded (Whitfield 1995c).

Despite the positive effects of frequent minor freshwater pulses, river flooding and/or prolonged large freshwater inputs into estuarine systems can result in a depletion of marine and estuarine species (Marais 1983b, Ter Morshuizen et al. 1996a, Nodo et al. 2017). River floods carrying high suspensoid loads can be lethal to both marine migrants and estuarine residents, with extensive mortalities occurring in the Sundays Estuary following a major flash flood (Whitfield & Paterson 1995). Although the suspended silt resulted in a clogging of the fish gill lamellae, it is also plausible that reduced oxygen levels associated with the floodwaters contributed to the asphyxiation of fishes in this estuary.

In the Great Fish system, marine species tend to dominate the fish assemblage immediately above the ebb and flow region (Figure 69). The relatively high conductivity of catchment flows arising from the catchment geology, and presence of marine fishes in the lower portions of the above

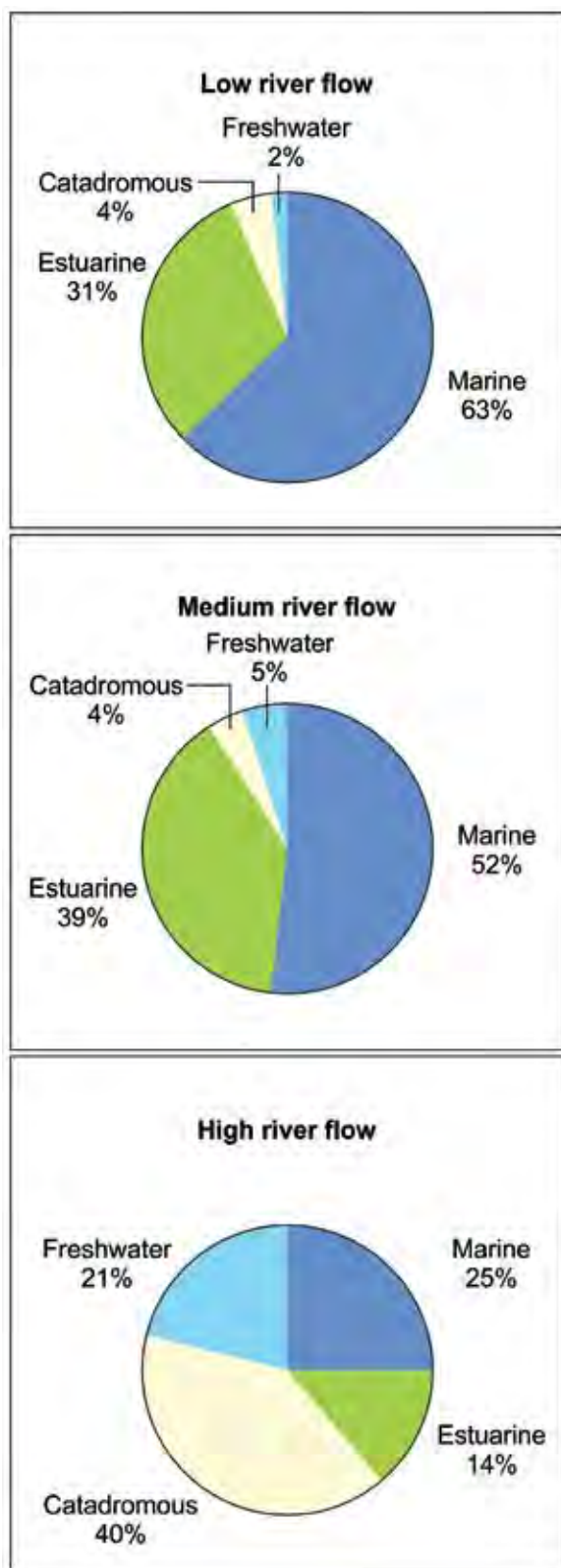
river system, suggests that dissolved salts may be important in reducing osmoregulatory stress for these temporary riverine residents. However, during flooding, the conductivity of the river water declines and both marine and estuarine fish species decrease in diversity and abundance above the head of the estuary (Ter Morshuizen et al. 1996a). Conversely catadromous and freshwater species then dominate the region above the ebb and flow region (Figure 69).

The morphology of an estuary may also influence the response of certain fish taxa to major flooding events. Gill net catches in two Eastern Cape estuaries were studied by Marais (1982) and showed that densities of Mugilidae increased in the broad Swartkops Estuary after river floods but decreased markedly in the channel-like Sundays Estuary. Marais then postulated that the organic rich mud and silt which are deposited in the floodplain-like middle and lower reaches of the Swartkops Estuary act as a food source for the mullet species, whereas the rich epibenthic layer in the Sundays Estuary is washed away by heavy floods.

More recently, a beam trawl study by Nodo et al. (2018) on the demersal fish assemblage in the Kariega Estuary, following a major episodic flood, showed that the reset event resulted in an increase in the abundance of benthopelagic marine migrant species in the the estuary when compared to previous studies when the system was freshwater deprived. In particular, the juveniles of important fishery species benefitted from the re-establishment of typical estuarine conditions within this system. The implication from the above findings is that increased recruitment of juveniles of the above species into the estuary was triggered by the increased river flow to the sea.

### **Turbidity**

Water turbidity influences fishes associated with southern African estuaries, with the juveniles of most estuary-associated marine species being attracted to turbid waters (Cyrus & Blaber 1987c). However, excessively high water turbidities have been shown to negatively affect fish egg survival, hatching success, feeding efficiency, growth rate and population size. In the case of resident species



**Figure 69.** Fish catch composition (grouped according to four primary guilds) above the headwaters of the Great Fish Estuary (i.e. in the river) under conditions of low ( $<10 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ ), medium ( $10 - 20 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ ) and high ( $>20 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ ) catchment flow (after Ter Morshuizen et al. 1996b).

that remain within these systems for their entire life cycle, all life-history stages need to be tolerant of turbid waters arising from flooding of the estuaries.

Few southern African estuaries fall into the clear water category ( $<10 \text{ NTU}$ ) of Cyrus (1988a), with the majority being either semi-turbid ( $10-50 \text{ NTU}$ ) or turbid ( $>50 \text{ NTU}$ ). Closure of an estuary mouth usually leads to decreased water turbidity but when it re-opens at times of high river inflow, turbidities increase rapidly, mainly due to suspensoids carried into the estuary by the floodwaters. This may account for the occurrence of both clear and turbid water species in these systems (Harrison & Whitfield 1995). Wind action can also cause an increase in turbidity in shallow systems with muddy bottom sediments, e.g. Lake St Lucia.

It has been suggested that many southern African estuary-associated fishes are essentially turbid water species that have evolved in turbid oceanic areas of the north-eastern Indian Ocean (Blaber 1981a). Such regions often have reduced salinities and calm waters, conditions that are only available in estuaries of the south-western Indian Ocean.

Research conducted on juvenile marine fishes in KwaZulu-Natal estuaries and in the laboratory (Cyrus & Blaber 1987a, 1987b) has shown that 80% of the species studied were turbid water taxa, whereas only 20% could be classed as truly clear water species. It was suggested that the protective isolation created by turbidity, coupled with other factors, are advantageous to the survival and growth of juvenile fish in estuaries. Supporting this hypothesis, Blaber (1981a) showed that where these conditions exist outside estuaries in the Indo-Pacific region, the same juvenile fish are also present. Shallow, sheltered turbid areas are usually found only within estuaries along the high energy southern African coastline, extending into the sea during river flooding.

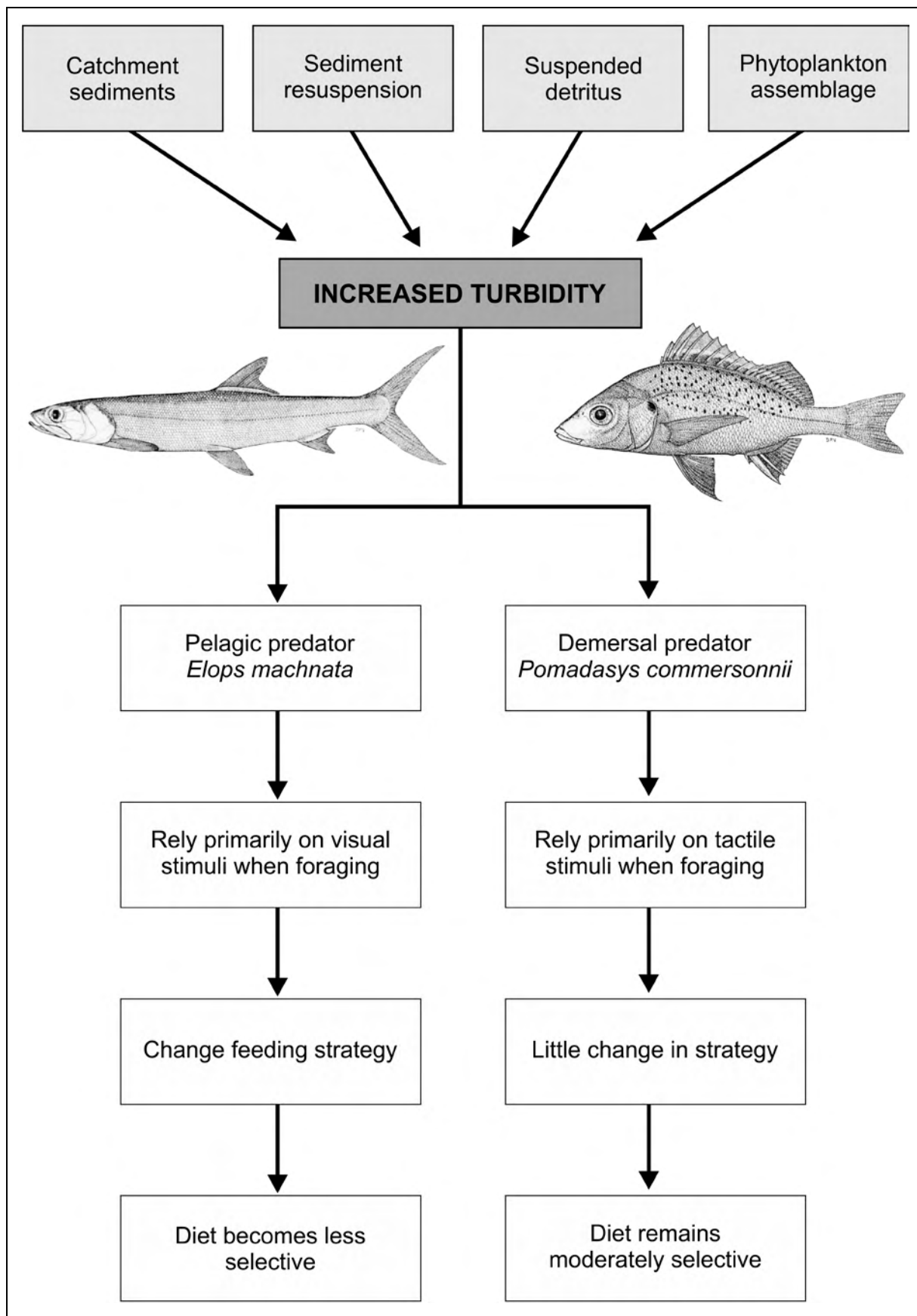
Turbidity gradients usually exist, not only within estuaries, but also from the mouth region into the sea (Figures 70 and 71). Blaber (1987) suggested that postlarval fishes in the marine environment could, by following an increasing turbidity gradient, ultimately reach estuarine



**Figure 70.** Aerial view of turbid water plumes from the Great Fish Estuary (mouth visible in the lower right corner) entering the coastal marine environment on a typical ebb tide (Photo: Alan Whitfield).



**Figure 71.** Turbid river water from the Kowie Estuary entering the sea during a major flood (Photo: Alan Whitfield).



**Figure 72.** Diagram showing the effects of increased turbidity on the foraging strategies of certain fish species in estuaries.



nursery areas. If this hypothesis is true, then the export of estuarine suspensoids could affect fish recruitment into these systems, thereby influencing community structure.

Why is turbidity so important to juvenile fish? Two possible factors include the cover it affords small fishes from predatory teleosts and birds, as well as increased feeding success in suspensoid rich waters. Turbidity preference of juveniles may differ from that of the adults, e.g. Blaber & Cyrus (1983) have shown that *Caranx sexfasciatus* juveniles inhabit estuarine waters which are more turbid than those occupied by the adults, thus avoiding possible intraspecific predation (Cyrus & Blaber 1987a).

Although it is important for fishes to evade predators, the ability to detect food in water where visibility is poor is also important. Species such as *Galeichthys feliceps* have long barbels which perform tactile foraging functions, whereas others (e.g. *Argyrosomus japonicus*) can use olfactory and lateral line sense organs to detect prey.

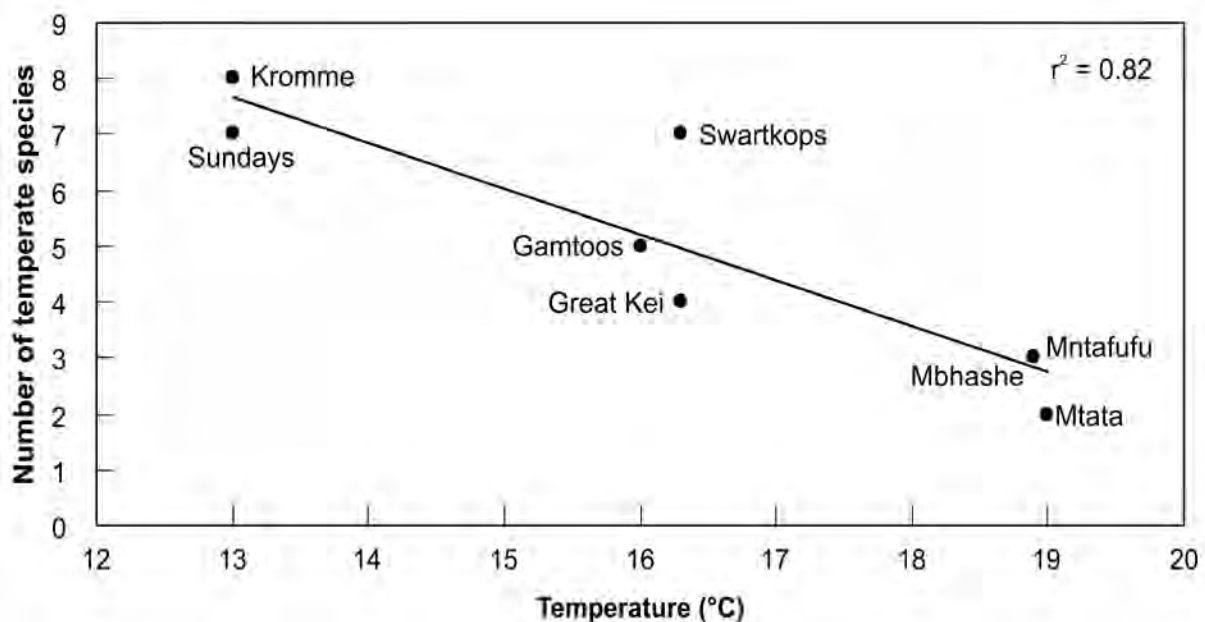
Visual foraging piscivorous fishes in estuaries are adversely affected by high turbidity conditions, whereas non-visual foragers are largely unaffected (Whitfield et al. 1994). This view is supported in a study by Hecht & van der Lingen (1992) who

determined that the feeding rate of visual fish predators was reduced at high turbidity levels. They also confirmed that visual pelagic predators are more affected by increased turbidity than non-visual macrobenthic feeders (Figure 72). However, both fish groups do have the ability to change their foraging strategies in order to optimize the acquisition of food under different turbidity conditions.

Although the zoogeographical affinities of fishes in southeast African estuaries may lie with the turbid waters of the northeast Indian Ocean zone (Blaber 1981a), low turbidity estuaries in southern Africa sometimes have a higher species diversity than more turbid systems, e.g. a much lower fish species richness was recorded in the turbid Great Fish Estuary when compared to the nearby low turbidity Kowie Estuary (Whitfield et al. 1994).

#### Water temperature

Temperature is a key driver influencing the distribution and abundance of fishes in estuaries (Figure 73). Each species has a thermal 'envelope' within which it can survive, with salinity being a major influence on the minimum and maximum temperatures that a particular fish taxon can



**Figure 73.** Relationship between the number of temperate fish species captured by gill nets and the mean of the minimum monthly temperatures in eight permanently open Eastern Cape estuaries (after Maree et al. 2000).

tolerate (Blaber 1973b, Whitfield & Blaber 1976, Kyle 1984). In general, temperature tolerance is greatest when optimum salinities for a particular species prevail. In contrast, very low or very high water temperatures tend to reduce or compromise the fishes' metabolic rate, which therefore impairs its osmoregulatory ability.

As a general rule, tropical fish species have a greater tolerance of high water temperatures whereas temperate species are more tolerant of low water temperatures. Preferred temperature ranges are likely to occur in the central areas of the thermal 'envelope' and these are likely to differ between tropical and temperate taxa, thus reinforcing the differential geographic distribution patterns according to which group a particular species belongs (Figure 74).

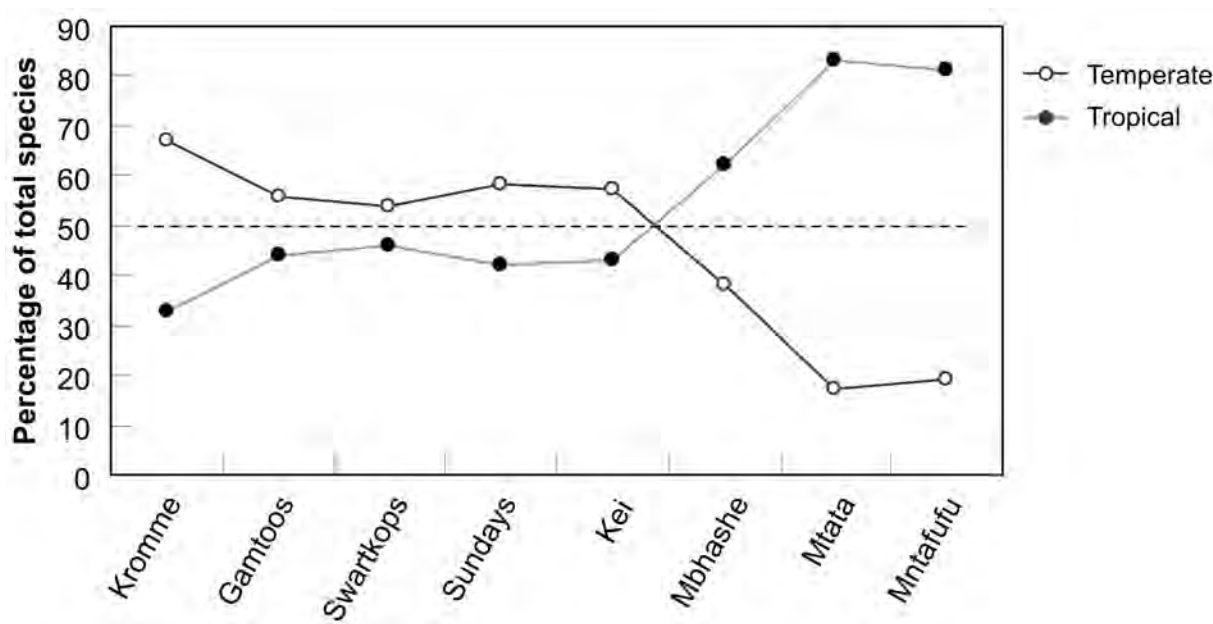
Only a few estuary-associated fish species have very wide thermal tolerance ranges and can occur in both tropical and temperate systems, e.g. the cosmopolitan *Mugil cephalus* occurs in estuaries from 42°N to 42°S (Whitfield et al. 2012) and is one of the few mugilids on the subcontinent that can cross the Benguela upwelling region to new localities.

Fish species in southern African estuaries are strongly influenced by both temperature and

salinity (Harrison & Whitfield 2006). Changes in the distributional patterns of estuary-associated fish species have been recorded along the south-east coast of South Africa associated with climate change, with tropical taxa extending their distribution southwards as coastal marine waters increase in temperature (James et al. 2008c). Similarly, the increase in winter water temperatures in the Mngazana Estuary at the biogeographic transition between the subtropical and warm-temperate zones, has resulted in an increase in the abundance of tropical species in this estuary during winter (Mbande et al. 2005).

Estuaries in South Africa are also known to provide a thermal refuge for coastal species during marine upwelling events (Hanekom et al. 1989). Sudden decreases in coastal temperatures during upwelling will affect both temperate and tropical species, and may prevent the range extensions of tropical species into temperate regions as a result of global warming (James et al. 2013).

Mugilids occur in large numbers in all South African estuaries and are an ideal family to use in terms of acting as an environmental indicator of global warming. Using the relative estuarine abundance of tropical, warm- and cool-water endemic mugilid species, it should be possible to



**Figure 74.** Relative percentages of tropical and temperate species captured by gill nets in eight Eastern Cape estuaries. According to this analysis, the locality of the warm-temperate/subtropical biogeographic boundary occurs as a subtraction zone between the Kei and Mbhashe estuaries (after Maree et al. 2000).

monitor future climate (temperature) change in estuaries and the adjacent coastal waters (James et al. 2016).

### Mouth phase

Although the degree of isolation of an estuary from the sea (Figures 75 and 76) has long been recognized as a major factor influencing southern African estuarine ichthyofaunal diversity, it was only comparatively recently that various studies have quantified this perception (e.g. Vorwerk et al. 2003, Harrison & Whitfield 2006c).

Formation of a sand bar across the mouth of an estuary effectively blocks any further recruitment of marine juveniles into a system, or emigration of subadults/adults back to the sea, thereby directly influencing the composition of the estuarine fish assemblage. Bennett (1989), working in the temporarily closed Bot Estuary, calculated that marine migrants numerically comprised only 1% and residents 99% of the fish fauna, whereas the two groups occurred in approximately equal abundance in the nearby permanently open Palmiet Estuary. In contrast to the prolonged (several years) closed phase of the Bot Estuary, the Swartvlei system usually opens annually, so the marine migrants are well represented in this estuarine lake when compared to the Bot (Kok & Whitfield 1986, Bennett 1989, Russell 1996).

Comparisons between the nearby Swartvlei and Knysna estuaries indicated that the CPUE of most marine migrants were higher in the latter system (Whitfield & Kok 1992). Apart from mouth condition, most of the factors influencing fish abundance in the two estuaries were similar, so it appears that the higher densities of most species in the Knysna system may be attributed to the deep, permanently open mouth and strong marine influence. Overall, the species richness (R) of fishes associated with *Zostera capensis* beds in the Knysna Estuary was more than twice that of Swartvlei Estuary *Z. capensis* beds, a result that can be directly linked to connectivity (Whitfield et al. 1989).

In KwaZulu-Natal, Begg (1984a) found that species rich estuaries were normally open and dominated by a wide variety of marine teleosts, especially mugilids and sparids. In contrast, systems

that were normally closed had relatively few species and commonly dominated by a few estuarine and freshwater taxa. Harrison & Whitfield (1995) found that the species diversity in three temporarily open /closed KwaZulu-Natal estuaries was also related to the duration of the open mouth phase. The Damba Estuary remained closed for much of the study period and had the lowest diversity, whereas the Zotsha Estuary remained open for most of the study period and had the highest diversity. In addition, in both the Zotsha and Mhlanga estuaries, there was a significant positive correlation ( $r > 0.80$ ,  $p < 0.05$ ) between the numbers of species recorded within each system and the time that the mouth remained open during a particular season.

The fact that estuarine ichthyofaunal diversity is positively linked to the duration of the open mouth phase can result in an overemphasis of the importance of permanently open estuaries as nursery areas for juvenile marine fish. However, there are distinct benefits to those juvenile fish which enter estuaries that subsequently close, e.g. the nursery area available to foraging fishes in the Mhlanga, Bot and Swartvlei estuaries increases considerably during the lagoonal phase due to elevated water levels inundating intertidal and supratidal habitats (Whitfield 1980b, Bennett et al. 1985, Kok & Whitfield 1986). These vegetated shallow areas are often structurally complex and less accessible to large predatory fishes, thereby enhancing their nursery function for small fishes (Leslie et al. 2017).

Breaching of closed estuaries results in a decline in the volume and area of the aquatic environment, together with a slump in aquatic plant and invertebrate food resources (Whitfield 1980b, et al. 1985, Ortega-Cisneros et al. 2014). In contrast, permanently open systems such as the Knysna Estuary offer a more predictable nursery area, which fluctuates in depth and area according to the tidal regime. However, low tide conditions usually result in the intertidal flats being made unavailable for occupation by juvenile fishes, often forcing them into channel areas where they are more vulnerable to predation by large piscivorous fishes (Whitfield 2017). In addition, spring tides usually inundate high parts of the intertidal zone



**Figure 75.** The sand bar at the mouth of the Mpekweni Estuary, representing a formidable barrier to fish recruitment or emigration from this system (Photo: Alan Whitfield).



**Figure 76.** The absence of a sand bar at the mouth of the Mbhashe Estuary showing a large deep channel that allows for the free movement of fish between the sea and estuary (Photo: Alan Whitfield).



that have very limited populations of amphipods, isopods, tanaids, polychaetes and small bivalves that are the favoured prey of zoobenthivorous fish species.

Immigration of juvenile fishes into estuaries may be either active or passive when the mouth is open (Beckley 1985a, Harrison & Cooper 1991, Strydom & Wooldridge 2005, Patrick & Strydom 2014). However, marine fish postlarvae may also gain access into temporarily closed estuaries by being washed into them during storm events when waves overtop the bar, a process that has been documented in both KwaZulu-Natal (Vivier & Cyrus 2001) and Eastern Cape closed estuaries (Bell et al. 2001).

Adult fish have also been reported migrating over Eastern Cape estuary sand bars during major marine overwash events. Dundas (1994) describes how large *Argyrosomus japonicus* and *Lithognathus lithognathus* were observed entering the Kabeljous Estuary in association with exceptionally high seas and adult *Mugil cephalus* became stranded on the West Kleinemonde Estuary sand bar whilst attempting to exit the system during an overtopping event (Whitfield 2016a). Based on the above evidence, large-scale overwash or overtopping events may have a profound effect on the ichthyofaunal structure of temporarily closed estuaries, particularly those systems where the sand berm remains intact for several years in succession.

Estuary mouth state has a major influence on the water level and therefore also water connections within segmented coastal lakes and lagoons. In the Wilderness system, movement of fishes between the lakes can only take place along narrow channels linking each compartment (Hall et al. 1987). When the estuary mouth is open, some interconnecting channels are too shallow to permit the movements or migration of even juvenile fish. Only when the mouth closes and water levels rise do these connections become viable migration routes for fishes. Ultimately, however, the natural progression for segmented estuarine lake systems is towards the isolation of sections which then become brackish or freshwater coastal lakes. This has already happened to Groenvlei, which was previously linked to the Swartvlei Estuary.

Although relic estuarine fish species are still found in Groenvlei, all the marine migrants have disappeared from that system (Whitfield et al. 2017b).

### Dissolved oxygen

Oxygen depletion within the water column has the potential to restrict the distribution and movement of fishes within estuaries. In subtropical estuaries this may be more pronounced because of the generally higher water temperatures. Additional oxygen-demanding substances added to the water in the form of pollution may further limit the distribution of fishes in an estuary, or result in fish mortalities. Begg (1984a) noted that organic pollution played a role in suppressing species diversity in some degraded KwaZulu-Natal estuaries such as the Sipingo, Sezela and Mbokodweni.

Blaber et al. (1984) suggested that low dissolved oxygen values contributed to an impoverished fish fauna in the Tongati Estuary, and Russell (1994) has shown how depleted oxygen levels resulted in fish mortalities within the Wilderness Lakes. Under natural conditions it is probable that only a few southern African estuaries would experience exceptionally low dissolved oxygen levels ( $<1 \text{ mg l}^{-1}$ ). Examples of such systems include the meromictic lakes Mpungwini and Swartvlei where the bottom waters are usually anoxic and rich in hydrogen sulphide (Allanson & Howard-Williams 1984). Periodic dissolved oxygen depletion can also occur during episodic river flooding which may cause mass fish mortalities in estuaries (Whitfield & Paterson 1995).

### Habitat variability and complexity

A major factor frequently overlooked in the assessment of ichthyofaunal diversity is habitat variation (Edworthy & Strydom 2016), with littoral macrophytes playing a critical role in influencing species richness (Whitfield 2017). Estuaries with a wide range of substrata and littoral plant growth normally have a higher species diversity and richness than more uniform systems (Whitfield 1983).

Day et al. (1981) reviewed the ichthyofaunal richness of certain very turbid estuaries such as the Mzimvubu and Kei, and concluded that the relatively low biodiversity was due to the consistent heavy silt loads carried by these rivers. Suspended

silt reduces light penetration and, when large quantities are deposited in estuaries, it smothers submerged vegetation and reduces habitat diversity. The low species richness of very turbid estuaries may therefore be linked to the indirect effect of the loss of submerged aquatic macrophytes and the associated invertebrate prey. In addition, those fish species attracted to low turbidity systems (e.g. Kosi) are likely to be absent from such estuaries.

In the Mhlanga and Swartvlei estuarine systems, the ichthyofaunal diversity did not decline when water transparency decreased as a result of river flooding (Whitfield 1983), thus supporting Blaber's (1981a) postulate that most marine teleosts occurring in Indo-Pacific estuaries are tolerant of turbid water. However, Marais (1982, 1983b) determined that river floods in the Swartkops, Sundays and Gamtoos estuaries have a considerable impact on the fish populations, depending on the severity of the river flow, the configuration of the estuary and the extent to which food sources are affected by the floodwaters.

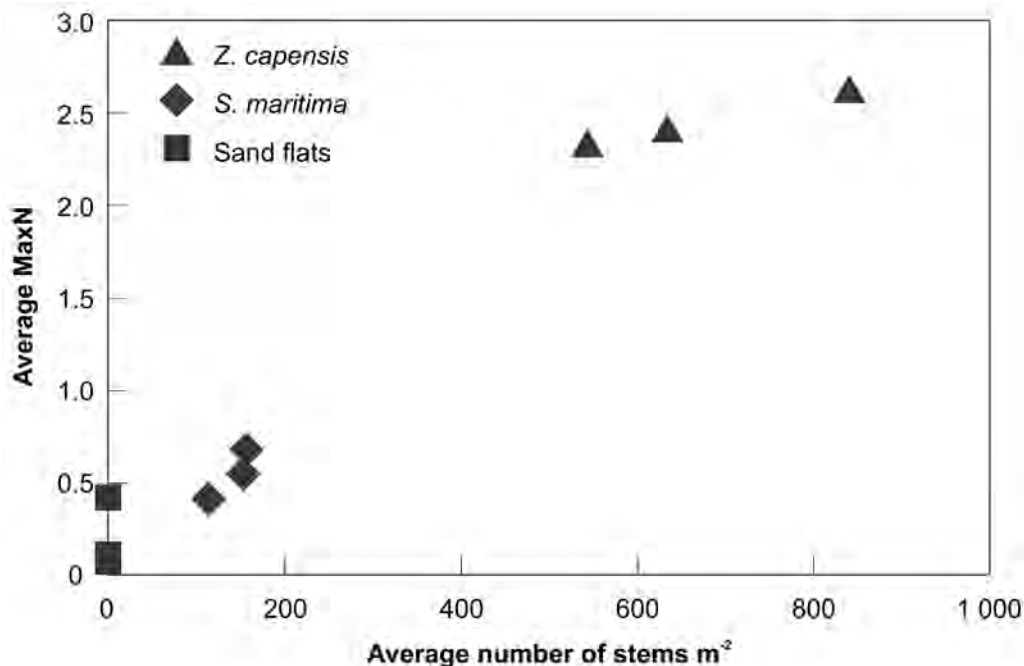
Prolonged droughts can increase habitat diversity in permanently open estuaries where eelgrass (*Zostera capensis*) beds expand in systems where freshwater inflow is minimal or has ceased altogether (Adams & Talbot 1992). Fish that are

usually closely associated with aquatic macrophyte beds in estuaries include the clinid *Clinus superciliosus*, syngnathid *Syngnathus temminckii*, and sparid *Sarpa salpa*. Both *Rhabdosargus holubi* and *Monodactylus falciformis* occurred in significantly higher numbers in *Zostera* than in non-*Zostera* regions of the Kromme Estuary (Hanekom & Baird 1984), thus emphasizing the importance of suitable aquatic macrophyte habitats to certain fish species.

A more detailed analysis of the influence of vegetation complexity on *R. holubi* was conducted by Leslie et al. (2017). These authors found that the relative abundance of this fish species was significantly higher in *Zostera* than *Spartina* and sand flat habitats (Figure 77), whilst the behaviour of *R. holubi* as determined from underwater video cameras indicated a higher degree of habitat use in structured plant habitats when compared to unstructured sand flat habitats.

### Biogeography

Latitude (water temperature characteristics) affects both fish richness (number of species) and equitability (relative abundance of the different taxa) in estuaries around the world. In general, there is a decline in estuarine fish diversity from



**Figure 77.** The relationship between plant stem density and average MaxN of *Rhabdosargus holubi* in each habitat type within the Bushmans Estuary (after Leslie et al. 2017).

KwaZulu-Natal, along the Eastern Cape coast, around the Western Cape and up the Atlantic west coast (Figure 78). The decline in diversity towards the south-west seems due to the attenuation in the distribution of tropical and subtropical marine species which comprise the bulk of the southern African ichthyofauna (Harrison 2005). The influence of latitude can be illustrated by comparing the species diversity of the Kosi system to that of the Swartvlei system. Both estuarine lake systems are clear and have a wide variety of available habitats. The rocky reef inside the mouth of the Kosi estuary has a much higher species diversity than the rocky reef inside the mouth of the Swartvlei Estuary, primarily because the Maputland region supports an abundance of tropical Indo-Pacific reef-dwelling fishes, some of which utilize the Kosi rocky outcrop (Blaber & Cyrus 1981).

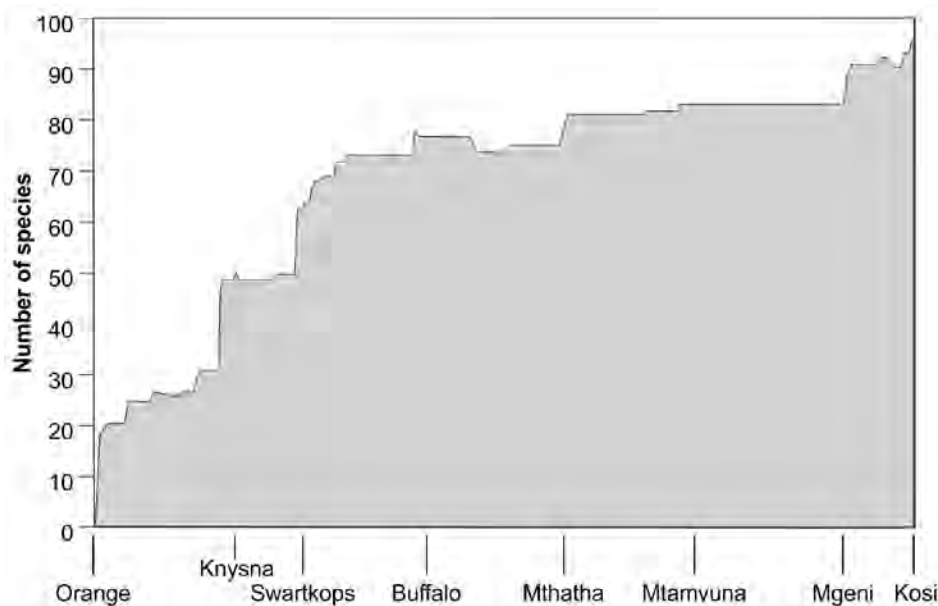
Species diversity in estuaries along the Atlantic west coast are much lower than estuaries on the Indian Ocean east coast. There are almost 30 commonly occurring fish species in estuaries near Port St Johns, compared to less than 10 in estuaries on a similar latitude along the Western Cape coast (Day et al. 1981). This fact alone emphasizes that latitude on its own is not a valid measure of the

potential species richness in a particular estuary and that biogeography needs to be included in any species diversity or richness analysis.

According to Smith (1980), 80% of all marine fishes of shallow waters known from southern Africa occur in northern KwaZulu-Natal seas. Consequently it is not surprising that KwaZulu-Natal estuaries have the highest species diversity in South Africa. The cool upwelled waters of the west coast are the obvious reason for the scarcity of tropical and subtropical fishes in this region. Even in summer, water temperatures along the Atlantic coast seldom rise above 15°C (Christensen 1980). These low marine water temperatures probably act as a barrier that prevents estuary-associated tropical West African fish species from reaching the Northern and Western Cape Provinces.

#### Catchment and estuary size

These two factors are difficult to examine in isolation since both have an influence on other parameters such as hydrodynamics and mouth state. How do estuary size and catchment characteristics (Figure 79) influence fish abundance? Clearly large estuaries will invariably have greater fish populations than small estuaries, due primarily to increased food and habitat availability.



**Figure 78.** Distribution patterns of 109 estuary-associated fish species in 251 South African estuaries between the Orange Estuary in the south-west and Kosi Estuary in the north-east (after Maree et al. 2000). Notice the high species richness north of the Mthatha Estuary, strong declines west of the Swartkops Estuary (Algoa Bay) and again west of the Knysna Estuary.

As far as catchment characteristics are concerned, Marais (1988) determined that in the Eastern Cape Province there was a highly significant positive correlation ( $r=0.46$ ,  $p<0.001$ ) between estuarine fish abundance and catchment size, as well as between fish biomass and catchment area ( $r=0.59$ ,  $p<0.001$ ). He suggested that it was not the actual catchment size that influenced fish stocks, but rather the hydrological consequences of increasing river inflow with increasing catchment area. Higher run-off almost invariably leads to greater nutrient inputs, positive estuarine salinity gradients, and increased water turbidity, all of which have been shown to be associated with increased fish abundance (Whitfield et al. 1994).

The higher nutrient and organic matter loading of estuaries with larger catchments invariably

leads to elevated primary and secondary production. This is particularly the case for those systems where water residence time is enhanced due to estuary length and volume (Hilmer & Bate 1991). Another potential factor accounting for the positive correlation between fish abundance and catchment size is the magnitude of olfactory cues entering the marine environment. Large perennial rivers are going to transmit greater volumes of land based cues to potential marine fish recruits when compared to small intermittent river systems.

The number of species found in an estuary appears to be related to estuary size, with larger systems generally having a higher ichthyofaunal diversity (Blaber 1985). This is probably related to two major factors; marine interaction and habitat diversity. Firstly, small estuaries are often closed



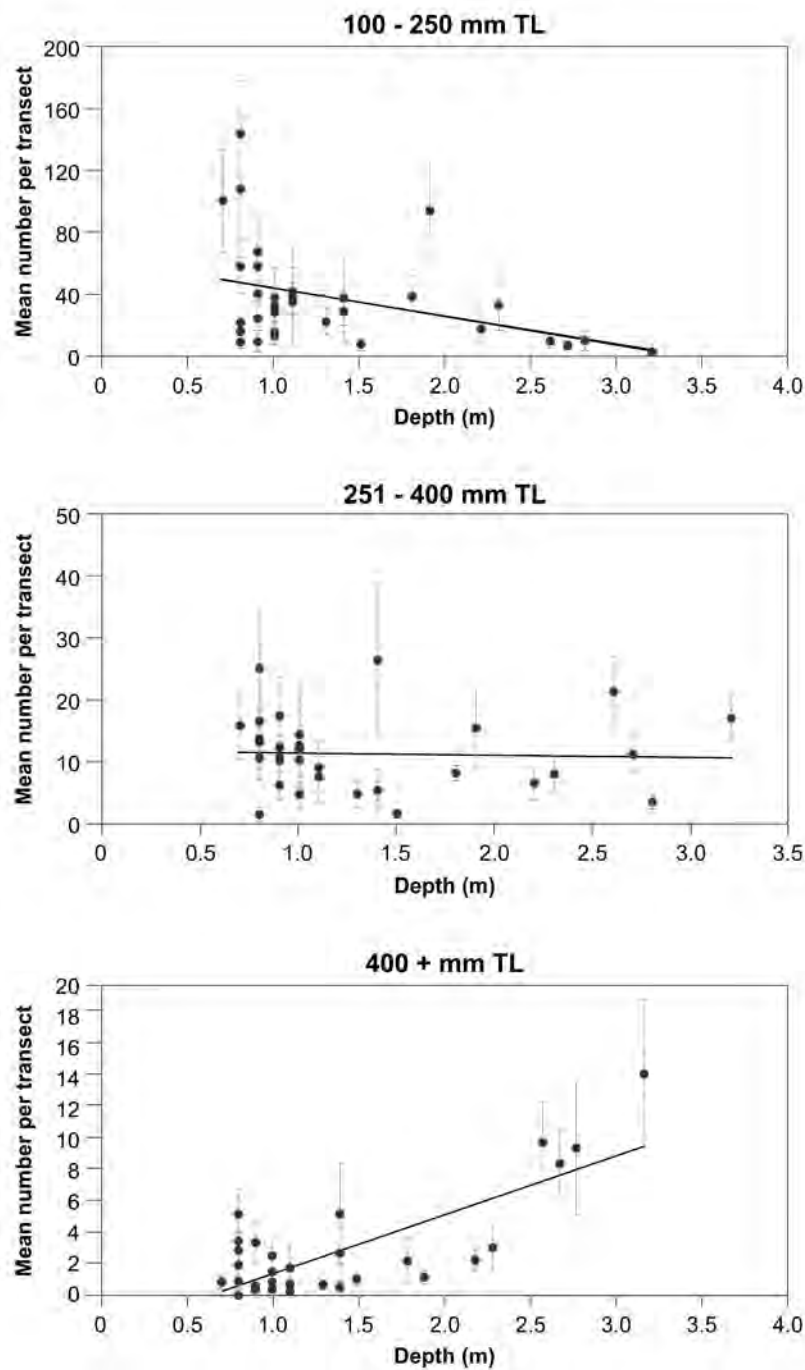
**Figure 79.** East Kleinemonde Estuary functional zone (grey) and catchment boundary delineations (white line) (after Masfield et al. 2014).



to the sea for prolonged periods, with a concomitant reduction in the number of marine species that can recruit into these systems (Vorwerk et al. 2003). Secondly, the range of habitats is generally reduced in smaller systems which tend to have a greater degree of uniformity in biophysical characteristics.

### Water depth

Maximum water depths are often related to estuary size, with large estuaries usually having a wider range in water depths than small estuaries. Juvenile fish in estuaries tend to prefer littoral areas, especially where habitats such as submerged or emergent macrophytes are present (Whitfield



**Figure 80.** Trends in fish abundance (mean number per 100m section) for 100-250 mm, 251-400 mm and > 401 mm TL size classes relative to estuary water depth in the small East Kleinemonde system (after Becker et al. 2017).

2017). Shallow waters provide these smaller fishes with a refuge from larger piscivorous teleosts (Paterson & Whitfield 2000a) that are usually restricted to deeper channel areas.

In temporarily closed estuaries piscivorous species such as *Argyrosomus japonicus* were present in the deeper Mhlanga and Zotsha systems (channels 1.5-3 m depth), while in the relatively shallow Damba Estuary (channel <1.5 m depth) these predators were usually absent (Harrison & Whitfield 1995). A similar trend pertains to other types of estuaries, where large piscivorous species are abundant only in those systems which have channel depths >1.5 m (Marais 1984).

More recently, acoustic camera transects along the entire length of the East Kleinemonde Estuary indicated that different size-cohorts of fishes were distributed heterogeneously along the estuary (Becker et al. 2017). By comparing the abundance of fish to the bathymetry, it was found that correlations existed between depth and abundance for two of three size classes (Figure 80). Large fish (>401 mm) were more abundant

in deeper areas (>1.5 m) whereas there were more small fish (100-250 mm) in the shallower parts (<1.5 m) of the estuary.

#### Estuarine productivity

Estuaries are highly productive ecosystems, ranking with coral reefs and mangals in terms of organic matter produced. Some systems in the Eastern Cape Province have large inputs of nutrient rich river water (Emmerson 1989), often leading to elevated phytoplankton levels (Snow et al. 2000). The abundant fish stocks associated with estuaries such as the Great Fish are probably linked to the perennial input of nutrient rich river water and the resulting exceptional primary productivity of this system (Allanson & Read 1995).

Although the high primary productivity of estuaries is widely accepted, the considerable autochthonous production (Adams et al. 1999) would be of little benefit to the biota if entirely exported to the sea. The key to the attractiveness of estuarine systems to fishes therefore lies in the fact that they act as detritus traps for both



**Figure 81.** Wind blown terrestrial leaf material, as well as intertidal saltmarsh and subtidal primary production, is retained and utilised within the estuarine food web (Photo: Alan Whitfield).

autochthonous and allochthonous production (Figure 81), thus providing abundant food resources for filter and deposit-feeding invertebrate prey, as well as detritivorous fish species. Visual evidence of this process can be seen in estuaries where marine macroalgal debris accumulates in the lower reaches, and littoral plants such as mangroves, saltmarsh grasses and reeds accumulate mats of decomposing riverine and estuarine plant material around their stems and roots. Wind-blown leaves from trees and bushes are also deposited and retained within estuaries.

How do the different types of estuaries act as detritus traps? Temporarily closed systems automatically accumulate all detritus that enters them during the closed phase. Estuarine coastal lakes usually have only narrow channels linking them to the sea, which effectively reduces the loss of organic products from these systems. Indeed, it could be argued that because of the narrow exit channels and the limited scouring action within the lakes, only a relatively small proportion of the accumulated detrital material within these

systems is exported to the sea, thus promoting secondary productivity in systems such as Lake St Lucia.

In permanently open estuaries, however, river floods cause large-scale exports of both macrodetritus and finer particulate organic matter into the sea where it boosts food availability to consumers. Nevertheless, during the non-flood phase, which is the dominant condition in permanently open estuaries, seawater wedges and tidal action aid in the retention, redistribution and accumulation of detrital material (Whitfield 1988b).

### **Resource utilization**

Does the efficient utilization of estuarine food resources depend on the species diversity of the fish community? There were fewer than 10 fish taxa found to be abundant in the Mhlanga Estuary, yet the study by Whitfield (1980e) indicated that all potential food categories, with the possible exception of phytoplankton, were utilized. Furthermore, the composition of the ichthyofaunal community was related to the proportions, based on the



**Figure 82.** Detritus, a major component of all estuarine food webs in southern Africa (Photo: Alan Whitfield).





**Figure 83.** An example of seven species of mullet from a single gill net catch in the Msikaba Estuary. From top to bottom these species are *Planiliza alata*, *Crenimugil buehneri*, *Chelon tricuspis*, *Mugil cephalus*, *Pseudomyxus capensis*, *Planiliza macrolepis* and *Osteomugil robustus*. Despite feeding on similar foods, the mean size of sand granules in the stomach contents of these mugilids is different (Photo: Alan Whitfield).



estimated standing stock energy values of the different food types.

In the Swartvlei Estuary, there were also fewer than 10 abundant fish species, with the available food resources being exploited but not always in proportion to their availability (Whitfield 1988a). Using Ivlev's electivity index, which compares the availability of a particular food resource to its utilization by the fish community, it was shown that there was a strong positive selection for epifaunal invertebrates but poor utilization of the infauna and submerged aquatic macrophytes. Plant consumption by herbivorous fishes in the Swartvlei Estuary indicated poor utilization of macrophytes, and mainly centred around filamentous algae and diatoms growing on *Zostera capensis*, rather than eelgrass leaf material (Whitfield 1988a).

Both *Rhabdosargus holubi* and *Sarpa salpa* digest microalgae but appear unable to assimilate aquatic macrophyte material (Blaber 1974b, Gerking 1984). Low abundance of predominantly herbivorous fish species in southern African estuaries is not simply a reflection of the absence of a cellulase in the digestive tract of teleosts (Kapoor et al. 1975) but is more likely due to the fluctuating nature of submerged plant communities within most estuaries. Indeed there are many systems that possess only small or no submerged plant beds.

Detritus in estuaries consists of a mixture of plant debris and amorphous organic matter (Figure 82), together with associated heterotrophic and autotrophic micro-organisms (Bowen 1976). Detritus is an important food source for many estuarine invertebrates (Whitfield 1989d) which are in turn consumed by carnivorous fishes (Bennett & Branch 1990). Detritivorous fish taxa are well represented in southern African estuaries (Whitfield & Blaber 1978b) and, despite the often higher species diversity of carnivorous fishes, the former group, mainly represented by the family Mugilidae (Blaber 1977) (Figure 83), are often dominant in terms of biomass (Branch & Grindley 1979, Harrison & Whitfield 1995).

In North American estuaries the supply of energy to fishes depends primarily on the detrital food web (Odum 1971, Yanez-Arancibia 1985) and studies in southern African systems reinforce

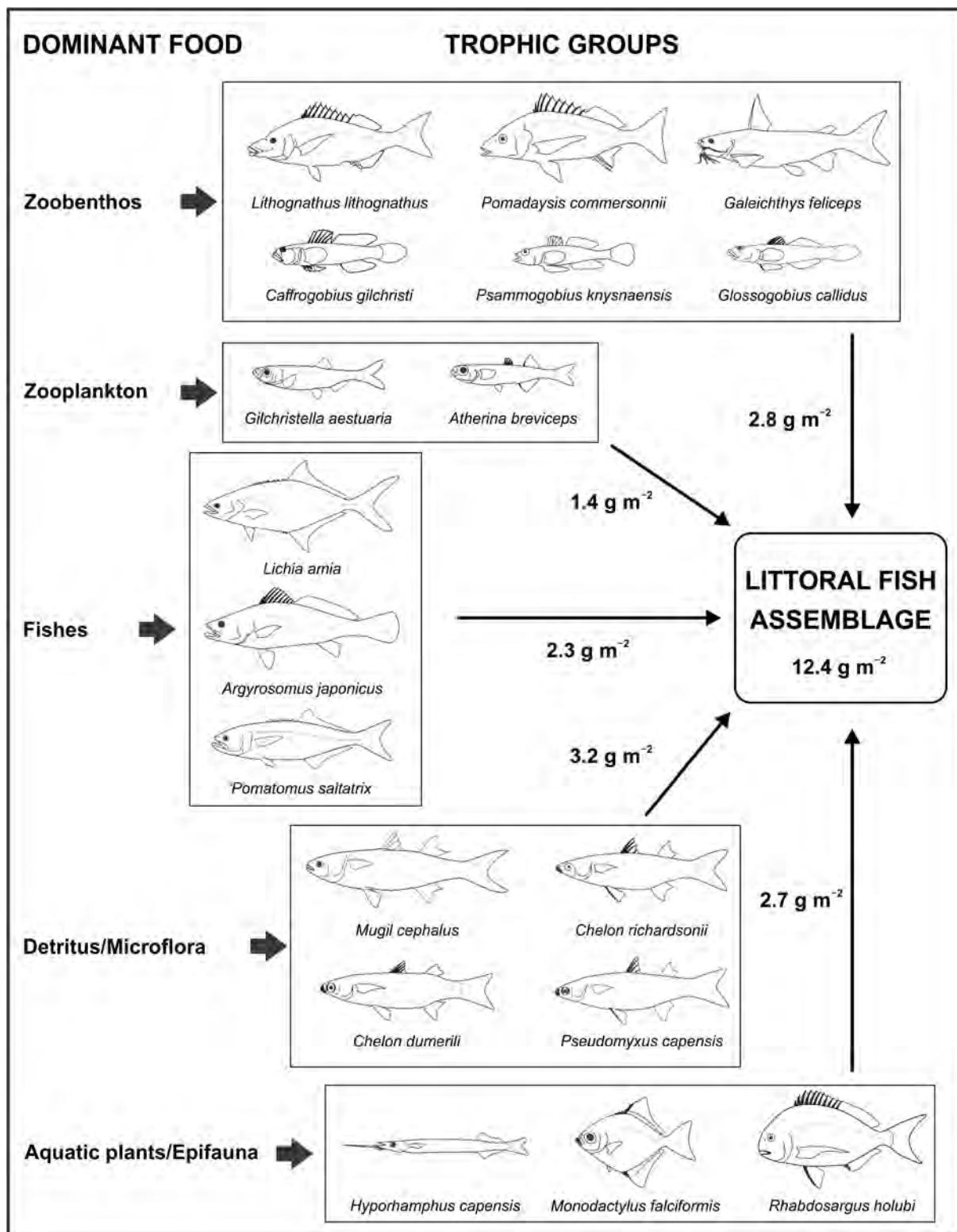
this concept (Blaber 1985, Whitfield 1988a). Indeed, food webs in estuaries on the subcontinent seem to show a surprisingly small number of energy pathways and therefore a high energy flow per pathway (Whitfield 1980e, Heymans & Baird 1995). This is reflected in Swartvlei (Figure 84) where only five trophic compartments could be recognised, four of which were linked to the detrital food chain, and no single compartment was less than 11% of the total fish biomass (Whitfield 1993).

Zooplanktonic invertebrates, which feed extensively on phytoplankton and suspended particulate organic material, are sometimes present in large numbers in estuaries and are an important food source for planktivorous fishes (Blaber 1979). However, phytoplankton biomass varies both spatially and seasonally (Campbell et al. 1991), whereas an abundance of detritus is always available to estuarine consumers, including planktivorous and detritivorous fish species, throughout the year (Whitfield 1980b). It would appear, therefore, that detritus confers stability to estuarine ecosystems by extending the availability of seasonally fixed energy into a resource that is always present.

Microphytobenthos is an important component in the detrital food web. Most invertebrate and fish detritivores ingest diatoms and other benthic algae along with particulate organic material. The high incidence of unicellular algae in the diet of mugilids from the Eastern Cape (Masson & Marais 1975) and KwaZulu-Natal (Blaber 1976) suggests that microphytobenthos (especially diatoms) are a favoured food item.

Clearly the balance between energy supply sources in an estuary varies on a temporal basis, as well as from one system to another. An illustration of the major carbon (detrital) pathways within the Kariega Estuary is shown in Figure 85, with the macrophytes *Spartina maritima* and *Zostera capensis* being of prime importance in supplying energy to the littoral ichthyofauna, and the channel species being more closely linked to the pelagic food web.

The importance of different fish species influencing the populations of different prey species has been highlighted using mesocosm

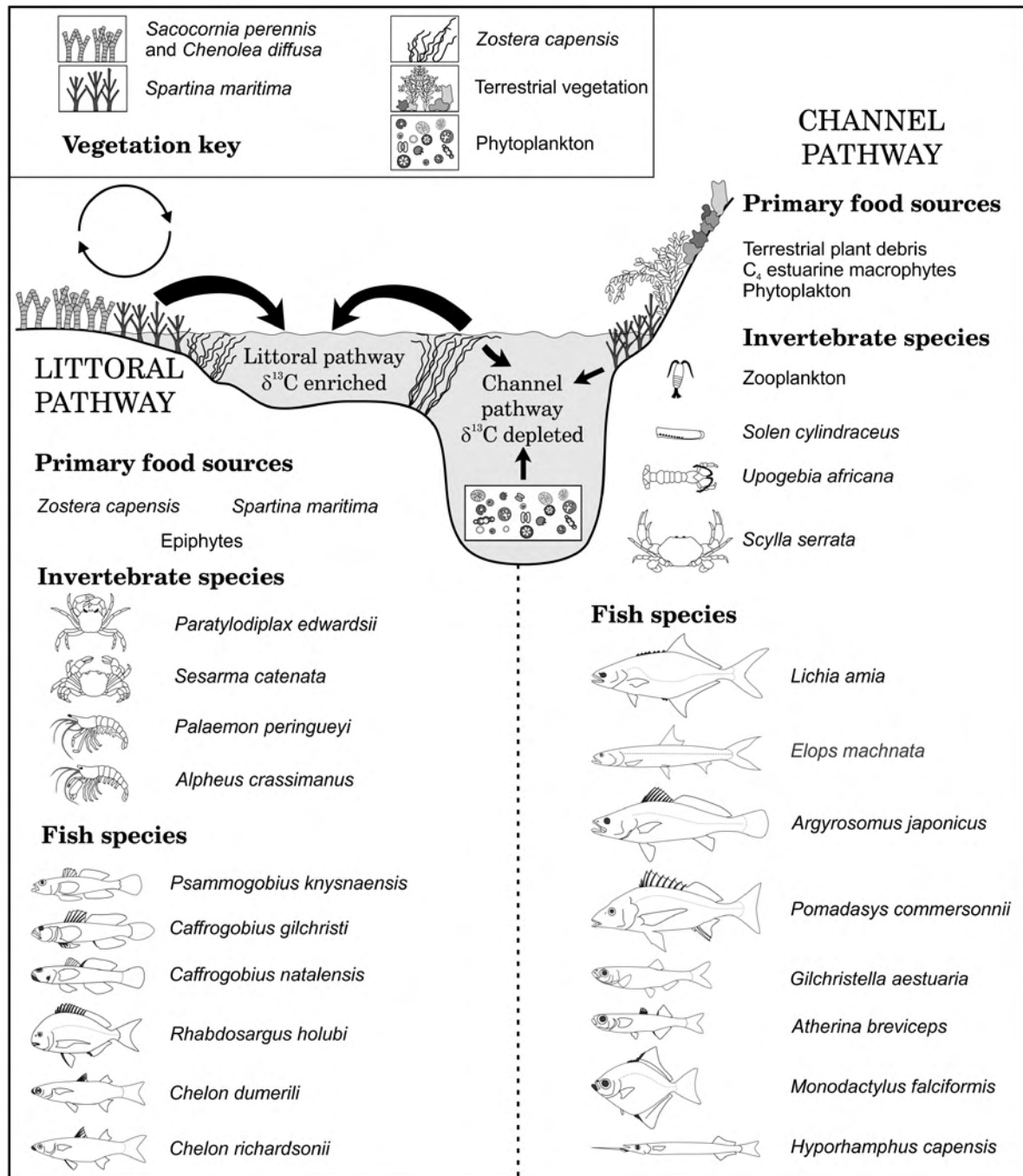


**Figure 84.** Diagrammatic representation of the 1980 biomass (wet) contributions by various trophic groupings to the Swartvlei littoral fish assemblage. It should be emphasized that this study was conducted during the *Stuckenia pectinata* senescent phase and the contribution by macrophyte associated fish species (e.g. *Monodactylus falciformis* and *Rhabdosargus holubi*) to the littoral fish biomass was therefore much lower during this period when compared to the *S. pectinata* canopy phase (after Whitfield 1993).

experiments (Wasserman et al. 2014). In these experiments the pelagic feeding *Monodactylus falciformis* was found to prey mainly on the mid-water copepod species *Paracartia longipatella* whereas the hyperbenthic *Glossogobius callidus* had a greater impact on the calanoid copepod *Pseudodiaptomus hessei* that undergoes strong diel vertical migrations. Predation by these two fish species may even influence benthic microalgal

biomass through the trophic cascade created by the fishes (Wasserman et al. 2015a).

Very little quantitative information is available on competition for food resources by fishes within southern African estuaries. Most carnivorous species feed on a wide range of prey and can adjust their diet according to environmental conditions and food availability (Marais 1984). In the Bot Estuary, resident fish consumed only



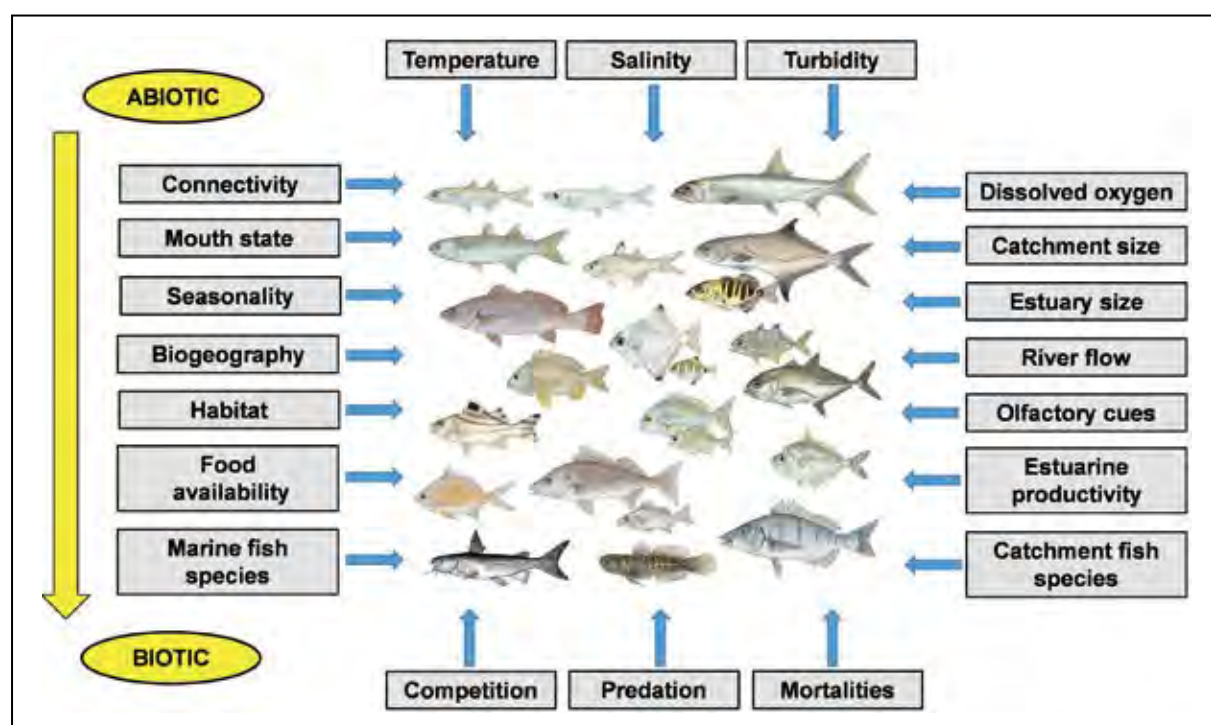
**Figure 85.** Diagrammatic representation, based upon stable carbon isotope analyses, of major energy pathways within the Kariega Estuary food web (after Paterson & Whitfield 1997).

30% of the secondary production by prey species (Bennett & Branch 1990), suggesting that food was not in short supply. Dietary overlap was common, with the most successful fish species in this estuary being those with the broadest niche.

There appears to be an even greater overlap in the diets of detritivorous fish species in estuaries, with competition being reduced by different feeding mechanisms which result in the available food items being consumed in differing quantities (Whitfield & Blaber 1978b). However, among mugilids there appears to be little feeding segregation between species (Blaber 1976, 1977), with the large biomass, abundance and diversity of this family indicating a possible superabundance of detritus within estuaries.

### Some preliminary conclusions

The biotic and abiotic factors which determine the distribution and abundance of fishes in southern African estuaries are shown in Figure 86. These factors are not independent but interact directly and indirectly with the fishes that inhabit estuaries. For example, river floods directly influence estuarine water temperature, salinity, turbidity, olfactory cues and dissolved oxygen concentrations, and indirectly affect mouth condition, habitat diversity, productivity, fish recruitment, food availability and competition. Future research therefore needs to be broadened to include multiple drivers in order to fully understand species interactions with both abiotic and biotic influences on the lives of fishes in estuaries.



**Figure 86.** Biotic and abiotic factors influencing fish species in southern African estuaries. The scale on the left-hand side illustrates the trend from predominantly abiotic variables in the top of the diagram to mainly biotic variables at the bottom.



## 2.5 HOW DEPENDENT ARE FISHES ON ESTUARIES?

The reliance of juveniles of migrant marine species on estuarine nursery grounds varies considerably, and ranges from marine stragglers which are seldom found in estuaries, to those species that are dependent on estuaries during the juvenile phase of their life cycle (Wallace et al. 1984a). Some species such as *Chelon richardsonii* and *Pomatomus saltatrix* appear to use favourable estuarine conditions opportunistically, with the juveniles also being very abundant in the sea. Other taxa such as *Rhabdosargus holubi* and *Monodactylus falciformis* are considered to be dependent on estuaries, and Bennett et al. (1985) have gone so far as to suggest that certain species might even become extinct if denied access to these nursery areas.

Adult marine fish also show considerable variability in their association with estuaries, with some species making extensive use of this environment and others never returning to their natal habitat. For example, large post-spawning shoals of *Pomadasys commersonnii* regularly enter estuaries during early spring, whereas *Rhabdosargus holubi* adults are seldom recorded in these systems, despite the overwhelming dependence of their juveniles on this environment. A number of piscivorous fish species (e.g. *Argyrosomus japonicus*, *Elops machnata* and *Lichia amia*) use estuaries as both juveniles and adults, primarily because of the large number of juvenile fishes and small pelagic species that occur within these systems (Whitfield & Blaber 1978a).

In addition, a number of species breed in southern African estuaries, some of which are totally dependent upon these habitats for their survival (e.g. *Syngnathus watermeyerii*). A few fishes (e.g. *Anguilla mossambica*) use estuaries as transit routes in their migrations between rivers and sea, and others make only sporadic use of these productive systems. From the above observations it becomes apparent that the degree of estuarine dependence varies from one species to another. There is clearly a need to develop a rational estuary-association classification for fishes according to the importance these systems represent in the life cycles of individual species.

The association by particular fish species with

estuaries along certain sections of the coast is likely to change over time. Increasing sea surface temperatures may have a range of implications for estuary-associated fish species, such as shifts in the distribution and abundance of individual species or species assemblages, e.g. the fishes of the warm-temperate East Kleinemonde Estuary have been sampled since 1995 and six new species of tropical fishes were recorded from 1999 onwards (James et al. 2008c). Mean annual sea surface temperatures recorded along the adjacent coast also increased and may have facilitated the southward extension of tropical marine fishes into the warm-temperate biogeographic zone. Similarly, the diversity and dominance of tropical species in the Mngazana Estuary during 2001-2002 (Mbande et al. 2005) increased when compared with a similar study conducted 25 years earlier.

Ichthyologists working in southern Cape estuaries have noticed increasing numbers of more tropical species such as *Pomadasys commersonnii* which may even have established breeding populations within the area (Lamberth pers. comm.). Thus the dependence of fish species on an estuary is not a constant, particularly under the present rapid climate change scenario.

### Categorization of fishes in estuaries

Estuary-dependent fish species are defined as those taxa whose southern African populations would be adversely affected by the loss of estuarine habitats on the subcontinent. Wallace et al. (1984a) divided South Africa's estuary-associated ichthyofauna into six categories according to their use of these systems and identified 81 species which were wholly or partially dependent on these systems. Research over the past few decades has provided much additional information on many fish species, and identified life-history styles of taxa previously excluded from the 1984 analysis.

A new estuary-association classification system for southern African fishes, based on a version developed by Whitfield (1994c), is described in Table 9. It comprises five major categories with three divisions in Category II. Category IIa comprises species that are highly dependent

on estuaries, whereas Category IIb and IIc species are at least partially dependent on estuarine systems, with a large proportion of these fishes being regarded as marine / estuarine opportunists. Category III comprises mainly stenohaline marine species which occur in low numbers in estuaries and have been sampled in at least three systems in a particular region. Category IV consists of a few freshwater fish species for which the degree of penetration into estuaries is determined primarily by salinity tolerance. Finally, Category V includes obligate catadromous species which use estuaries as transit routes between marine and freshwater environments.

### Biogeographical considerations

Wallace et al. (1984a) were the first scientists to examine southern African estuaries and their associated fish fauna as a single entity. However, very few species occur in all systems, with some taxa confined to a particular biogeographical region, or even to a few estuaries within that region. Those species that straddle estuaries across transition zones (Figure 89) are usually more successful than those taxa that are restricted to a particular zoogeographic region.

The following three sections provide an insight into the ichthyofaunal changes that occur between subtropical estuaries in the northeast and cool-temperate systems in the southwest. Tropical estuaries (i.e. north of 26°S on the east coast) are not dealt with in this monograph because of a paucity of estuarine ichthyofaunal information from Mozambique.

### Cool-temperate estuaries

Cool-temperate estuaries of the Northern and Western Cape Province have a relatively low ichthyofaunal diversity and are dominated by only a few species (Millard & Scott 1954). Several authors (e.g. Wallace & van der Elst 1975, Day et al. 1981, Whitfield et al. 1989) have highlighted the southward decline in estuarine fish diversity from KwaZulu-Natal around the Cape to the Atlantic west coast. The reason for this decline is linked to the subtraction of tropical and subtropical species (Blaber 1981a), which together comprise the bulk of the southern African estuarine ichthyofauna.

Only 11 of the 34 species associated with cool-temperate estuaries have distributions which extend into tropical waters, the remainder being confined to areas south of 26°S. As many as 18

Table 9. The five major categories of fishes which utilize southern African estuaries (modified from Whitfield 1994c).

Categories	Description of categories
I	Estuarine species which breed in southern African estuaries. This category includes resident species that spawn only in estuaries, as well as species that also have marine or freshwater breeding populations.
II	Euryhaline marine species which usually breed at sea, with the juveniles showing varying degrees of association with southern African estuaries. Further subdivided into: IIa. Juveniles dependant on estuaries as nursery areas. IIb. Juveniles occur mainly in estuaries, but are also common at sea. IIc. Juveniles sometimes occur in estuaries but are more abundant at sea
III	Marine stragglers which occur in estuaries in very small numbers and are not dependent on these systems.
IV	Freshwater species, whose penetration into estuaries is determined primarily by salinity tolerance. This category includes a few species which may breed in both freshwater and estuarine systems (Figure 87). It also includes some freshwater stragglers that are seldom recorded in estuaries.
V	Obligate catadromous species which use estuaries as transit routes between the marine and freshwater environments (Figure 88).



**Figure 87.** Mozambique tilapia *Oreochromis mossambicus*, the only freshwater fish species that makes extensive use of estuarine lakes and lagoons on the subcontinent, including the ability to breed within these systems (Photo: Trevor Harrison).



**Figure 88.** The catadromous longfin eel *Anguilla mossambica* in its natural Eastern Cape riverine environment. This species uses crevices in rocky pools for protection and also as an ideal habitat from which to launch predatory forays (Photo: Bruce Ellender).

(53%) of the 34 taxa are endemic to southern Africa and this group includes all the dominant species found in these systems. The overwhelming dominance of *Chelon richardsonii* and relative scarcity of most other marine species from west coast estuaries is noteworthy.

Marine water temperatures probably play a major role in the low fish species representation described above (Figure 90). There is a marked decline in the average winter and summer sea temperatures between Maputo Bay in the north-east and False Bay in the south west. As expected, lower temperatures are also found in estuaries as one moves in a south-westerly direction along the coast (Day 1981b). The minimum winter water temperatures of 10-12°C recorded in cool-temperate estuaries would probably be lethal for many of the warm water species found in subtropical and warm-temperate systems.

In addition, low winter temperatures in combination with low salinities can result in severe physiological stress, even to estuarine fish species (Whitfield et al. 1981). Since low temperatures and salinities are frequently recorded in cool-temperate estuaries, this combination probably limits the colonization of these systems by certain species; e.g. *Rhabdosargus holubi*, which is abundant in both warm-temperate and subtropical estuaries, is represented by only a few 'stragglers' in cool-temperate systems.

### Warm-temperate estuaries

The warm-temperate region represents a transition zone between subtropical estuaries to the north-east and cool-temperate systems to the west. Most warm-temperate estuaries contain species which are representative of all three biogeographic regions discussed in this chapter, as well as the tropical region. Of the 88 estuary-associated species occurring in warm-temperate systems, 31 (35%) are endemic to southern African waters, with the remainder mainly having a distribution which extends into tropical areas north of the equator on the African east coast. A total of 43 fish species (48%) may be regarded as having a strong association with estuaries in the warm-temperate region.

Many of the tropical and subtropical species found in warm-temperate estuaries are more

common in the northern part of the Eastern Cape during the summer months, and are usually rare or absent from estuaries west of Algoa Bay (e.g. *Acanthopagrus vagus*). In addition, a number of endemic fish species which are particularly abundant in some Western Cape estuaries reach the north-eastern limits of their distribution in the Eastern Cape (e.g. *Rhabdosargus globiceps*). The north-eastern portion of the warm-temperate region therefore represents an important subtraction zone in the distribution of both tropical and temperate fish species.

*Anguilla mossambica* is the only anguillid eel which occurs in large numbers in the riverine and estuarine systems of the subtropical and warm-temperate regions of southern Africa. However, numerous specimens of *Anguilla marmorata* and *A. bicolor* have also been recorded in rivers on the subcontinent (Bruton et al. 1987).

During or shortly after strong easterly winds have been blowing along the Eastern and Western Cape coast during summer, some unusual marine fish species may make an appearance in estuaries, e.g. large shoals of *Sparodon durbanensis*, *Cheimarius nufar*, *Coracinus capensis* and *Pachymetopon grande* have been recorded sheltering in the Storms River Estuary during upwelling events on the Tsitsikamma coast (Hanekom et al. 1989). These easterly winds set up water movements which result in the upwelling of cool (10-15°C) waters into the nearshore area (Figure 91, Schumann et al. 1988) and are therefore indirectly responsible for essentially marine fishes sometimes seeking refuge in the warmer waters of adjacent estuaries. Such species are not regarded as being part of the typical estuarine ichthyofauna and are therefore not included in any of the analyses of estuary-associated fish taxa. It should also be noted that the more warm water estuary-associated species tend to retreat upstream during these upwelling events.

### Subtropical estuaries

The highest ichthyofaunal diversity on the subcontinent occurs in the subtropical region. Altogether, 157 species are associated with these systems, of which 25 (16%) are endemic to southern Africa. Approximately half of the 157 species may be





**Figure 89.** Turbid upper reaches of the Mbashe Estuary which is situated in the biogeographic transition zone between the subtropical and warm-temperate regions (Photo: Alan Whitfield).



**Figure 90.** Humate stained outflow from the cool-temperate Bot/Klein estuarine system in the Western Cape. These dissolved humic substances precipitate out in the sea and the water then clears (Photo: Alan Whitfield).

regarded as having a strong association with estuaries in this region. More than 100 of the above species have a distribution that extends into the tropics, thus illustrating the dominance of subtropical estuaries by fish taxa with tropical zoogeographical affinities (Blaber 1981a).

Maximum summer temperatures in the estuaries of southern Africa do not differ greatly and usually range from 24-28°C. This suggests that current maximum temperatures are not an important factor in limiting fish distribution, since temperate, subtropical and tropical species all live in estuaries which attain these levels. For

example, the maximum recorded channel temperatures in the Berg Estuary (Western Cape Province) is 27°C and that in the Morrumbene Estuary (Mozambique) is 28°C (Day 1981b).

Minimum winter water temperatures in Kwa-Zulu-Natal estuaries are usually above 14°C (Begg 1978) and are an important factor, together with the general absence of cool upwelled marine waters along the coast, in accounting for the high tropical fish species representation in this region. Nevertheless sequential cold fronts in winter, in association with oligohaline estuarine conditions, can result in fish kills (Blaber & Whitfield 1976).



**Figure 91.** Fog in the mouth region of the Birha Estuary (Eastern Cape Province) created by mixing of the air above cool upwelled marine water and warm air from the land (Photo: Alan Whitfield).

## Estuary-association analysis

An analysis of the degree of estuarine dependence by the various categories of indigenous fishes in southern African estuaries is given in Table 10. Estuarine species that breed within these systems comprise 25% (43 species) of the total ichthyofaunal diversity in estuaries on the subcontinent (172 species).

The dominant component is derived from marine taxa that use estuarine systems as nurseries and/or foraging areas (73 species = 42% of total) but only 21% (36 species) of this group are strongly associated with estuaries (Table 10). If one combines these 36 species with the 43 estuarine resident taxa, then 79 species (46% of the total ichthyofaunal richness) can be described as either completely or partially dependent on estuaries for their existence.

Although marine stragglers make up 22% (37 species) of all estuary-associated fish taxa (Table 10), this group does not make much use of estuaries and is generally present in the lower reaches of only a few estuaries and in very limited numbers. If measured on a numerical or biomass basis, marine stragglers would comprise only a very small percentage of the total estuarine ichthyofauna.

As expected, most fish species (157) are associated with subtropical estuaries, fewer are linked

with warm-temperate systems (88), and the lowest number (34) occur in cool-temperate estuaries (Table 11). The reason for this south-westerly decline in numbers of species can be attributed to the higher diversity of tropical taxa finding their way into subtropical waters. Conversely the species richness of cool water taxa is very low but some of these fish can be abundant, e.g. *Liza richardsonii*.

Altogether 58 families of fishes are associated with southern African estuaries (Table 11), of which 54 have a primarily marine origin, three are derived from freshwater environments, and one is represented by catadromous species. In terms of species number, the Gobiidae (25 species), Mugilidae (14 species) and Sparidae (13 species) are the most diverse.

Within the above families, 62% (8 species) of the Sparidae, 36% (9 species) of the Gobiidae, and 21% (3 species) of the Mugilidae are endemic to estuaries of the region. Altogether 38 fish species (22% of all estuary-associated taxa) are endemic to southern African waters. This high degree of endemism elevates the level of responsibility imposed on estuarine environmental managers to conserve these valuable ecosystems for the future existence of a diverse and unique ichthyofauna.

Table 10. Categories of fishes (for details see Table 9) which utilize southern African estuaries to varying degrees. The total number of estuary-associated species = 172. Solid circles (●) show strong dependence on a particular habitat, squares (■) indicate that some species use the particular habitat facultatively, and a triangle (▲) indicates that estuaries represent transit corridors for obligate catadromous species. Abbreviations: Fre. = Freshwater, Est. = Estuary, Mar. = Marine, No. = Number of species.

Category	Spawning sites			Juvenile habitat			Analysis	
	Fre.	Est.	Mar.	Fre.	Est.	Mar.	No.	%
1. Estuarine species	■	●	■	■	●	■	43	25
2. Marine species, some of whose juveniles are:								
a. Wholly estuary dependent			●		●		19	11
b. Mainly estuary dependent			●		●	■	17	10
c. Weakly estuary dependent			●			●	43	25
3. Marine stragglers			●			●	37	22
4. Freshwater species	●	■		●			9	5
5. Catadromous species			●	●	▲		4	2

Table 11. Ichthyofauna associated with southern African estuaries, indicating their geographical range, geographical occurrence in estuaries and the estuary-association category for each species. An asterisk (\*) after a species name indicates a southern African endemic. Common names and the international guild association for each of these species are given in the Appendix (pages 490-494).

<sup>1</sup>Range: T = Tropical; S = Subtropical; W = Warm-temperate; C = Cool-temperate.

<sup>2</sup>Geographical distribution in estuaries: S = Subtropical; W = Warm-temperate; C = Cool-temperate.

<sup>3</sup>Estuarine dependence categories (for a description of the codes used, please see Table 9).

Family	Scientific name	Geographical range <sup>1</sup>	Southern African estuaries <sup>2</sup>	Estuary-association category <sup>3</sup>
Ambassidae	<i>Ambassis ambassis</i>	T-S	S	I
	<i>Ambassis dussumieri</i>	T-W	S/W	I
	<i>Ambassis natalensis</i>	T-S	S	I
Anguillidae	<i>Anguilla bengalensis</i>	T-S	S	V
	<i>Anguilla bicolor</i>	T-W	S	V
	<i>Anguilla marmorata</i>	T-W	S/W	V
	<i>Anguilla mossambica</i>	T-C	S/W/C	V
Antennariidae	<i>Antennarius striatus</i>	T-S	S	III
Ariidae	<i>Galeichthys feliceps</i> *	S-C	S/W/C	IIb
Atherinidae	<i>Atherina breviceps</i> *	S-C	S/W/C	I
	<i>Atherinomorus duodecimalis</i>	T-S	S	III
	<i>Atherinomorus lacunosus</i>	T-S	S	III
Belonidae	<i>Strongylura leiura</i>	T-S	S	IIc
Blenniidae	<i>Omobranchus woodi</i> *	W-S	W	I
	<i>Parablennius pilicornis</i>	T-W	S/W	III
Bothidae	<i>Bothus pantherinus</i>	T-W	S/W	IIc
Carangidae	<i>Caranx heberi</i>	T-W	S/W	III
	<i>Caranx ignobilis</i>	T-W	S/W	IIb
	<i>Caranx melampygus</i>	T-S	S	IIc
	<i>Caranx papuensis</i>	T-W	S/W	IIc
	<i>Caranx sexfasciatus</i>	T-W	S/W	IIb
	<i>Lichia amia</i>	T-C	S/W/C	IIa
	<i>Scomberoides commersonnianus</i>	T-W	S	III
	<i>Scomberoides lysan</i>	T-S	S	IIc
	<i>Scomberoides tol</i>	T-S	S	IIc
	<i>Trachinotus africanus</i>	T-S	S	III
	<i>Trachurus delagoa</i> *	S-W	W	III
Carcharhinidae	<i>Carcharhinus leucas</i>	T-W	S	IIb
Chanidae	<i>Chanos chanos</i>	T-W	S/W	IIc
Cichlidae	<i>Coptodon rendalli</i>	T-S	S	IV
	<i>Oreochromis mossambicus</i>	T-W	S/W/C	IV
	<i>Pseudocrenilabrus philander</i>	T-S	S	IV



Family	Scientific name	Geographical range <sup>1</sup>	Southern African estuaries <sup>2</sup>	Estuary-association category <sup>3</sup>
Cichlidae (cont.)	<i>Tilapia sparrmanii</i>	T-S	S	IV
Clariidae	<i>Clarias gariepinus</i>	T-W	S	IV
Clinidae	<i>Clinus spatulatus</i> *	C	C	I
	<i>Clinus superciliosus</i> *	W-C	W/C	I
Clupeidae	<i>Etrumeus whiteheadi</i> *	S-C	W	III
	<i>Gilchristella aestuaria</i> *	S-C	S/W/C	I
	<i>Herklotsichthys quadrimaculatus</i>	T-S	S	III
	<i>Hilsa kelee</i>	T-S	S	IIb
	<i>Sardinops ocellatus</i>	S-C	W	III
Dasyatidae	<i>Dasyatis chrysonota</i>	T-C	W	III
	<i>Gymnura natalensis</i> *	S-W	W	III
	<i>Himantura leoparda</i>	T-W	S	IIc
Drepanidae	<i>Drepane longimanus</i>	T-W	S	III
Eleotridae	<i>Butis butis</i>	T-S	S	I
	<i>Eleotris fusca</i>	T-S	S	I
	<i>Eleotris mauritianus</i>	T-S	S	I
	<i>Eleotris melanosoma</i>	T-S	S	I
	<i>Hypseleotris cyprinoides</i> *	S	S	IV
Elopidae	<i>Elops machnata</i>	T-C	S/W/C	IIa
Engraulidae	<i>Engraulis capensis</i> *	W-C	W	III
	<i>Stolephorus holodon</i>	T-W	S/W	IIc
	<i>Thryssa setirostris</i>	T-S	S	III
	<i>Thryssa vitrirostris</i>	T-W	S	IIb
Fistulariidae	<i>Fistularia commersonii</i>	T-W	S/W	III
Galaxiidae	<i>Galaxias zebratus</i>	C	C	IV
Gerreidae	<i>Gerres filamentosus</i>	T-S	S	IIb
	<i>Gerres longirostris</i>	T-W	S/W	IIb
	<i>Gerres methueni</i> *	T-W	S/W	IIb
	<i>Gerres oblongus</i>	T-S	S	III
	<i>Gerres oyena</i>	T-S	S	IIc
Gobiidae	<i>Awaous aeneofuscus</i>	T-W	S	IV
	<i>Caffrogobius gilchristi</i> *	S-C	S/W/C	I
	<i>Caffrogobius natalensis</i> *	S-W	S/W	I
	<i>Caffrogobius nudiceps</i> *	W-C	W/C	I
	<i>Croilia mossambica</i> *	T-S	S	I
	<i>Favonigobius melanobranchus</i>	T-S	S	I
	<i>Favonigobius reichei</i>	T-S	S	I
	<i>Glossogobius biocellatus</i>	T-S	S	I
	<i>Glossogobius callidus</i> *	T-W	S/W	I

Table 11 (cont.). Ichthyofauna associated with southern African estuaries, indicating their geographical range, geographical occurrence in estuaries and the estuary-association category for each species. An asterisk (\*) after a species name indicates a southern African endemic. Common names and the international guild association for each of these species are given in the Appendix (pages 490-494).

<sup>1</sup>Range: T = Tropical; S = Subtropical; W = Warm-temperate; C = Cool-temperate.

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<sup>3</sup>Estuarine dependence categories (for a description of the codes used, please see Table 9).

Family	Scientific name	Geographical range <sup>1</sup>	Southern African estuaries <sup>2</sup>	Estuary-association category <sup>3</sup>
Gobiidae (cont.)	<i>Glossogobius giuris</i>	T-S	S	IV
	<i>Mugilogobius mertonii</i>	T-S	S	I
	<i>Oligolepis acutipennis</i>	T-W	S	I
	<i>Oxyurichthys keiensis</i>	T-W	S/W	I
	<i>Oxyurichthys ophthalmonema</i>	T-S	S	I
	<i>Pandaka silvana</i>	T-W	S/W	I
	<i>Paratrypauchen microcephalus</i>	T-S	S	I
	<i>Periophthalmus argentilineatus</i>	T-S	S	I
	<i>Psammogobius knysnaensis</i> *	S-C	S/W/C	I
	<i>Redigobius bikolanus</i>	T-S	S	I
	<i>Redigobius dewaali</i> *	S-W	S/W	I
	<i>Silhouettea sibayi</i> *	S	S	I
	<i>Stenogobius polyzona</i>	T-S	S	I
	<i>Taenioides esquivel</i> *	S	S	I
	<i>Trypauchenopsis intermedia</i>	T-S	S	I
	<i>Yongeichthys nebulosus</i>	T-S	S	I
Haemulidae	<i>Plectorhinchus gibbosus</i>	T-S	S	III
	<i>Pomadasys commersonnii</i>	T-C	S/W/C	IIa
	<i>Pomadasys kaakan</i>	T-W	S	IIc
	<i>Pomadasys multimaculatus</i>	T-W	S	IIc
	<i>Pomadasys olivaceus</i>	T-C	S/W/C	IIc
Hemiramphidae	<i>Hemiramphus far</i>	S-W	S/W	IIc
	<i>Hyporhamphus capensis</i> *	S-C	S/W/C	I
Kuhliidae	<i>Kuhlia mugil</i>	T-W	S/W	IIc
	<i>Kuhlia rupestris</i>	T-S	S	III
Leiognathidae	<i>Leiognathus equula</i>	T-S	S	IIb
Lethrinidae	<i>Lethrinus nebulosus</i>	T-S	S	III
Lobotidae	<i>Lobotes surinamensis</i>	T-W	S	IIc
Lutjanidae	<i>Lutjanus argentimaculatus</i>	T-W	S/W	IIc
	<i>Lutjanus fulvivflamma</i>	T-W	S/W	IIc
Megalopidae	<i>Megalops cyprinoides</i>	T-W	S	IIa
Monacanthidae	<i>Stephanolepis auratus</i>	T-W	S/W	III

Family	Scientific name	Geographical range <sup>1</sup>	Southern African estuaries <sup>2</sup>	Estuary-association category <sup>3</sup>
Monodactylidae	<i>Monodactylus argenteus</i>	T-W	S/W	IIb
	<i>Monodactylus falciformis</i>	T-C	S/W/C	IIa
Mugilidae	<i>Chelon dumerili</i>	S-C	S/W/C	IIa
	<i>Chelon melinopterus</i>	T-S	S	IIb
	<i>Chelon richardsonii</i> *	S-C	S/W/C	IIb
	<i>Chelon tricuspidens</i> *	S-C	S/W/C	IIb
	<i>Crenimugil buchanani</i>	T-W	S/W	III
	<i>Crenimugil crenilabis</i>	T-W	S/W	III
	<i>Crenimugil seбели</i>	T-S	S	III
	<i>Moolgarda cunnesius</i>	T-S	S	IIa
	<i>Mugil cephalus</i>	T-C	S/W/C	IIa
	<i>Osteomugil robustus</i>	T-S	S	IIa
	<i>Planiliza alata</i>	T-S	S	IIa
	<i>Planiliza macrolepis</i>	T-S	S	IIa
	<i>Planiliza subviridis</i>	T-S	S	IIb
	<i>Pseudomyxus capensis</i> *	S-C	S/W/C	IIa
Muraenesocidae	<i>Muraenesox bagio</i>	T-W	S	IIc
Muraenidae	<i>Strophidon sathete</i>	T-S	S	IIc
Myliobatidae	<i>Myliobatis aquila</i>	S-C	S/W	IIc
Ophichthidae	<i>Ophisurus serpens</i>	T-C	S/W/C	IIc
	<i>Pisodonophis boro</i>	T-S	S	IIc
Paralichthyidae	<i>Pseudorhombus arsius</i>	T-W	S/W	III
Platycephalidae	<i>Platycephalus indicus</i>	T-W	S/W	IIc
Polynemidae	<i>Polydactylus plebeius</i>	T-S	S	III
	<i>Polydactylus sextarius</i>	T-W	S	III
Pomatomidae	<i>Pomatomus saltatrix</i>	T-C	S/W/C	IIc
Pristidae	<i>Pristis zijsron</i>	T-S	S	IIb
Rhinobatidae	<i>Acroteriobatus annulatus</i> *	S-C	S/W/C	III
Sciaenidae	<i>Argyrosomus japonicus</i>	T-C	S/W/C	IIa
	<i>Johnius dorsalis</i>	T-W	S	IIc
	<i>Otolithes ruber</i>	T-S	S	IIc
Scorpaenidae	<i>Pterois miles</i>	T-W	S/W	III
Serranidae	<i>Epinephelus andersoni</i>	T-W	S/W	III
	<i>Epinephelus malabaricus</i>	T-S	S	III
	<i>Epinephelus marginatus</i>	T-S	S	III
Siganidae	<i>Siganus sutor</i>	T-W	S/W	III
Sillaginidae	<i>Sillago sihama</i>	T-W	S	IIc
Soleidae	<i>Heteromycteris capensis</i> *	S-C	S/W/C	IIa
	<i>Solea turbynei</i> *	S-C	S/W/C	IIa
Sparidae	<i>Acanthopagrus vagus</i>	T-W	S/W	IIa

Table 11 (cont.). Ichthyofauna associated with southern African estuaries, indicating their geographical range, geographical occurrence in estuaries and the estuary-association category for each species. An asterisk (\*) after a species name indicates a southern African endemic. Common names and the international guild association for each of these species are given in the Appendix (pages 490-494).

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<sup>2</sup>Geographical distribution in estuaries: S = Subtropical; W = Warm-temperate; C = Cool-temperate.

<sup>3</sup>Estuarine dependence categories (for a description of the codes used, please see Table 9).

Family	Scientific name	Geographical range <sup>1</sup>	Southern African estuaries <sup>2</sup>	Estuary-association category <sup>3</sup>
Sparidae (cont.)	<i>Crenidens crenidens</i>	T-S	S	III
	<i>Diplodus hottentotus</i> *	S-C	S/W	IIc
	<i>Diplodus capensis</i> *	T-C	S/W/C	IIc
	<i>Lithognathus lithognathus</i> *	S-C	S/W/C	IIa
	<i>Lithognathus mormyrus</i>	S-C	S/W/C	IIc
	<i>Rhabdosargus globiceps</i> *	W-C	W/C	IIIc
	<i>Rhabdosargus holubi</i> *	S-C	S/W/C	IIa
	<i>Rhabdosargus sarba</i>	T-W	S/W	IIb
	<i>Rhabdosargus thorpei</i> *	S	S	IIc
	<i>Sarpa salpa</i>	S-C	S/W/C	IIc
	<i>Sparodon durbanensis</i> *	S-C	W	IIc
	<i>Spondyllosoma emarginatum</i> *	S-C	W/C	III
Sphyraenidae	<i>Sphyraena barracuda</i>	T-S	S	IIb
	<i>Sphyraena jello</i>	T-W	S/W	IIc
Syngnathidae	<i>Hippichthys heptagonus</i>	T-S	S	I
	<i>Hippichthys spicifer</i>	T-W	S/W	I
	<i>Hippocampus capensis</i> *	W	W	I
	<i>Microphis brachyurus</i>	T-S	S	I
	<i>Microphis fluviatilis</i>	T-S	S	I
	<i>Syngnathus temminckii</i>	S-C	S/W/C	I
	<i>Syngnathus watermeyerii</i> *	W	W	I
Terapontidae	<i>Pelates quadrilineatus</i>	T-S	S	IIc
	<i>Terapon jarbua</i>	T-W	S/W	IIa
Tetraodontidae	<i>Arothron hispidus</i>	T-W	S/W	IIc
	<i>Arothron immaculatus</i>	T-W	S/W	IIc
	<i>Geneion honckenii</i>	T-C	S/W/C	IIc
	<i>Leiodon laticeps</i>	T-S	S	III
Torpedinidae	<i>Torpedo fuscumaculata</i>	T-W	S/W	IIc
	<i>Torpedo sinuspersici</i>	T-W	S/W	IIc
Trichiuridae	<i>Trichiurus lepturus</i>	T-W	S/W	III



## Why so few freshwater fish species?

Estuarine fish assemblage studies around the world have shown that freshwater fish species are generally poorly represented or absent from systems where a typical salinity gradient from seawater at the mouth to brackish water at the head of the estuary exists. There are at least six possible reasons why freshwater fish species appear to be under-represented in estuaries, including an inability to;

- cope physiologically with the large salinity ranges that occur in most estuaries.
- adapt to the altered food resources in estuaries when compared to freshwater systems.
- compete with estuarine and marine fish species in estuaries.
- withstand higher piscivorous predation rates associated with predatory fishes and birds in estuaries.
- match the more diverse marine fish assemblage entering estuaries from the sea.
- overcome connectivity issues between estuaries and upstream river systems.

Before examining these possible reasons in more detail, it is necessary to summarize the physiological changes that occur when fishes are exposed to different external salinities. Freshwater fish species are required to maintain the  $\text{Na}^+$  and  $\text{Cl}^-$  levels in their body at a higher concentration than that of the external freshwater medium. Diffusive losses of salts need to be balanced by active uptake and the gills are the primary site for both processes, with the kidney and gastrointestinal tract playing secondary roles (Figure 92). At the same time large volumes of very dilute urine are produced by the kidneys of these fishes in order to get rid of the excess water that continually diffuses across permeable membranes (e.g. the gills) into the body (Figure 92).

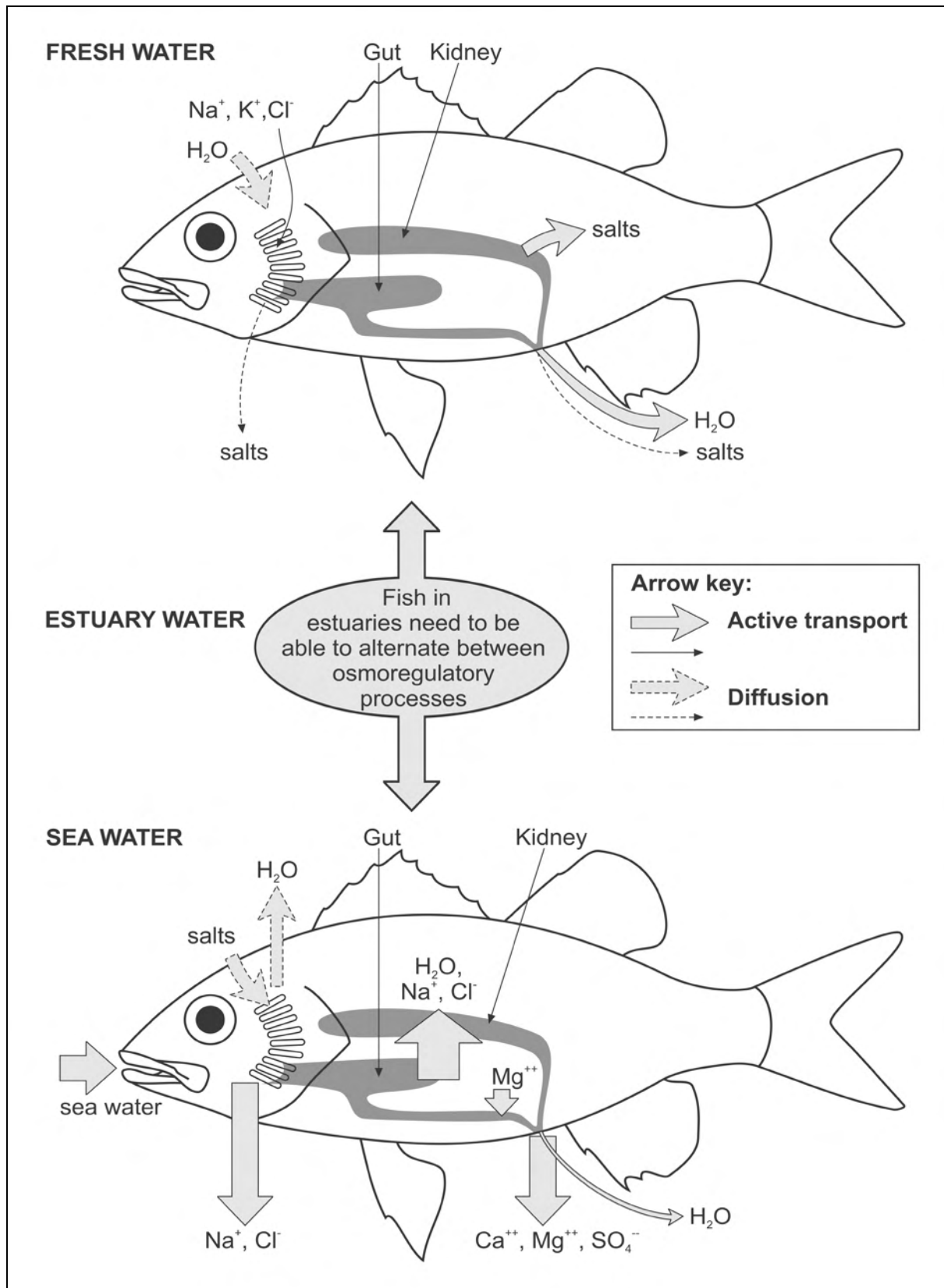
In an almost complete reversal of the above pattern, marine fish species lose water across the gills and must therefore drink from the external medium in order to balance these losses. Although water is absorbed into the body across the gut, salts (mainly  $\text{Na}^+$  and  $\text{Cl}^-$ ) are also transferred into the body of the fish and then have to be actively secreted across the gills and skin epithelia

where possible. At the same time, the marine fish kidney produces a minimal volume of urine that contains an abundance of divalent cation salts (Figure 92). In addition, the bladders of marine, euryhaline and freshwater fish species also differ in some fundamental ways, e.g. the bladders of stenohaline and euryhaline freshwater fishes were found to be nearly impermeable to water irrespective of environmental salinity, whereas euryhaline marine fishes appear to be able to modify the permeability of their bladders from permeable in seawater to impermeable in freshwater.

When a fish crosses the isosmotic line for that species, there is a change from active salt excretion via the gills under higher salinity conditions, to active  $\text{Na}^+$  and  $\text{Cl}^-$  uptake under lower salinity conditions, with the former condition being termed hypo-osmoregulation and the latter hyper-osmoregulation. These changes in osmoregulatory response can occur within minutes of a fish moving from one salinity to another but obviously come with physiological and energetic costs to the fish. In addition, it would appear that only those freshwater fish species that have the ability to develop chloride cells in gill filament epithelia are able to tolerate the wide range of salinities present in estuaries. The above factors are likely to be major contributors to the lack of freshwater fish species in most estuaries.

### Salinity

Panikkar (1960) suggested that the most essential adaptation required by fishes to enter estuaries is an ability to adjust to changing salinity regimes. The changes may be gradual or sudden, depending mainly upon the balance between freshwater inputs and the tidal regime, with evaporation playing a major role in estuarine lake systems with a high surface area to volume ratio. In estuaries with a so-called 'normal' salinity gradient, the composition of the fish assemblages along the gradient tends to change in response to this driver. However, even in those estuaries and bays that have relatively large freshwater inputs and low salinities in the upper reaches, freshwater fish taxa



**Figure 92.** Generalised models showing the pattern of salt and water movement during osmoregulation in freshwater and marine teleosts. The key to whether the transport is active or due to diffusion is shown on each fish and the sizes of the arrows provide a rough indication of quantity. Dotted lines and arrows = diffusion and solid lines and arrows = active transport (modified from Smith 1982).

are often poorly represented. In addition, those few freshwater species that do venture into the upper reaches of estuaries with perennial rivers, are often forced to retreat into the catchments during drought years when salinities in these systems increase.

A characteristic of most fish species entering southern African estuaries is an ability to tolerate both low and high salinity regimes, although it is of interest to note that <25 species have their upper recorded limits above 65, whereas >85 species can survive in waters with a salinity of <5 (Whitfield 1998). Research at St Lucia has shown that as salinities increase between 10 and 80 there are declining numbers of fish species recorded in the system (Whitfield et al. 2006). Estuarine ichthyofauna therefore appear to be more tolerant of low, rather than high salinities (Whitfield et al. 1981), and this adaptability to oligohaline conditions is important since most estuaries are subject to frequent periods of river flooding but seldom experience hyperhaline states.

There is considerable evidence to suggest that the optimum salinity for estuary-associated fishes,

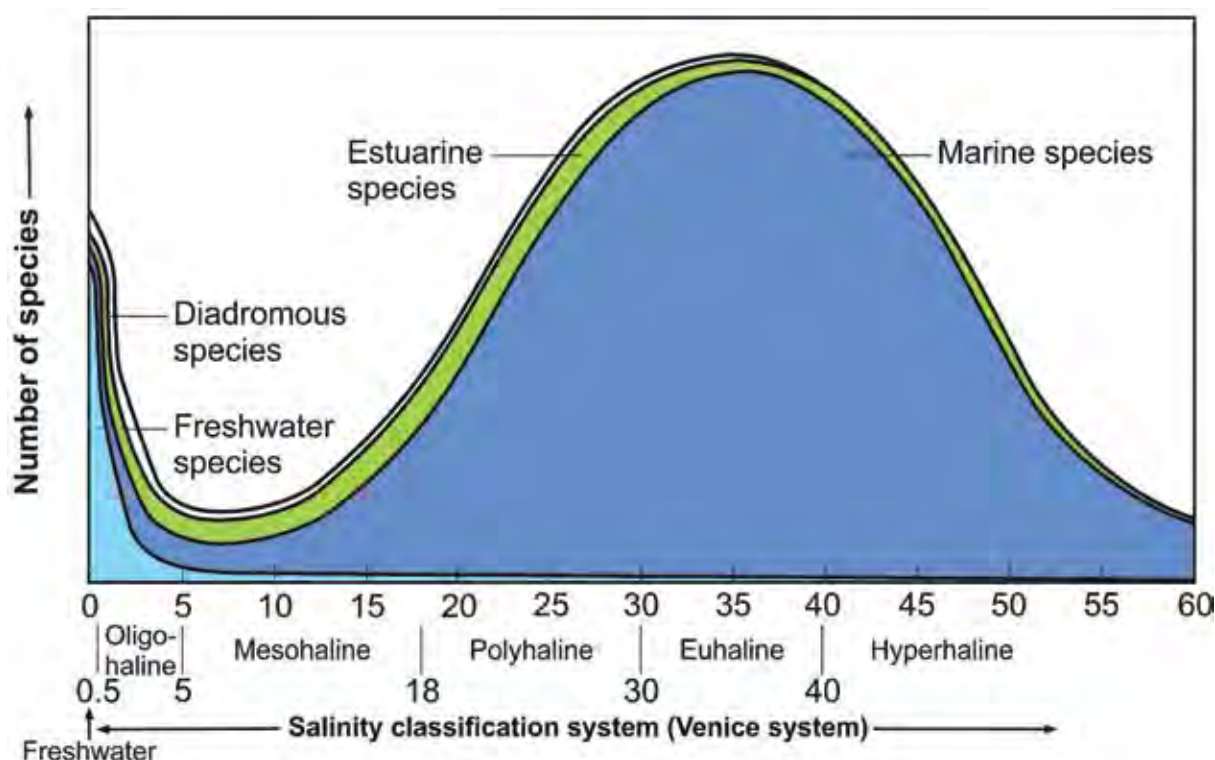
including freshwater taxa, is in within the range 8-14 because this encompasses the isosmotic state for many species (e.g. Blaber 1974a; Whitfield & Blaber 1976; Martin 1990; Deacon & Hecht 1999). Stenohaline marine species are unable to switch their osmoregulation to cope with changes driven by a hyper- to a hypo-osmotic external medium (Figure 92) and are therefore restricted to salinities above isosmotic values.

Some freshwater fish species appear to be very susceptible to even slight increases in salinity above the oligohaline range. For example, mass mortalities of the sharptooth catfish *Clarias gariepinus* (Figure 93) have been recorded in Lake St Lucia when salinities increased above 10 (Blaber 1981b). The reason why such species cannot tolerate mesohaline waters closer to their isosmotic state remains difficult to explain.

The Remane model depicts a rapid decline in freshwater fish species diversity as the salinity begins to rise (Figure 94). This decline is offset by an increase in estuarine and marine fish species diversity as salinities increase above oligohaline levels (Whitfield et al. 2012a). However, what the



**Figure 93.** A sharptooth catfish *Clarias gariepinus* in the St Lucia littoral during oligohaline conditions caused by freshwater seepage along the eastern shore of South Lake (Photo: Caroline Fox).



**Figure 94.** Conceptual model for estuarine fish species diversity covering the salinity continuum from fresh water to hyperhaline conditions (after Whitfield et al. 2012a).

Table 12. Fish osmoregulatory abilities and some representative examples from the different guilds found in African estuaries (modified from Whitfield 2015).

Osmoregulatory category	Presence in estuaries	Examples of fish from each category	
Stenohaline /slightly euryhaline freshwater fish species	A moderate number of species that rarely occur in estuaries except under oligohaline or low mesohaline conditions	<i>Clarias gariepinus</i>	<i>Sandelia capensis</i>
Highly euryhaline freshwater fish species	A few taxa that can be abundant in some estuaries under an extremely wide range of salinities	<i>Sarotherodon melanotheron</i>	<i>Oreochromis mossambicus</i>
Highly euryhaline estuarine and marine fish species	A diverse assemblage of fishes occurring in large numbers in the lower, middle and upper reaches of estuaries, and tolerating a wide range of salinities from oligohaline to hyperhaline	<i>Elops machnata</i> <i>Megalops cyprinoides</i>	<i>Gilchristella aestuaria</i> <i>Mugil cephalus</i>
Stenohaline /slightly euryhaline marine fish species	A large number of species usually recorded in small numbers in the lower and sometimes middle reaches of certain estuaries where oligohaline conditions are absent	<i>Crenidens crenidens</i>	<i>Epinephelus malabaricus</i>



decline shows very clearly is that freshwater fish species are not well adapted to a life in estuaries.

Examples of fish species from the different osmoregulatory categories in estuaries are shown in Table 12 which clusters the words stenohaline and slightly euryhaline into a single category. The reason for this is that most published papers on so-called stenohaline fishes show that these species have a slight tolerance to a limited salinity range. Since the primary aim of this section is to assess the reasons for the apparent lack of colonization of estuaries by freshwater fish species from the catchment in comparison to marine species from the sea, catadromous and estuarine resident taxa have not been the focus of attention. It is accepted that catadromous and estuarine resident species are all euryhaline, with members of the diadromous group switching their osmoregulatory mechanisms as they pass from freshwater to the sea or vice versa.

### Food

It has been estimated that approximately 10% of the total energy budget of fishes can be attributed to osmotic costs and that salinity has a strong influence on fish metabolism, growth and development. Therefore movements of fishes into higher or lower than optimum salinities for a particular species should have significant implications for energy expenditure that would require adjustments to food intake if a more sub-optimal salinity habitat was occupied for a prolonged period of time. This would apply to both marine and freshwater fishes entering estuaries but perhaps for euryhaline species the elevated food resources, especially the rich diversity and abundance of invertebrates in estuarine environments (Figures 95-100), compensates for the additional osmoregulatory costs.

In the same way that salinity is an important driving force that can influence the structuring of estuarine fish assemblages, so too does salinity have an influence on food availability in estuaries (Forbes & Cyrus 1993). The types and amount of food will vary both spatially and temporarily within each estuary and is likely to differ considerably from the prey species available to fishes in an adjacent freshwater ecosystem. These differences

may influence the ability of freshwater fish species to find suitable food in estuaries but the invasion of estuaries from adjacent rivers when salinities decline to oligohaline levels (Whitfield et al. 2006) suggest that this is not a major limitation.

Despite the overall positive effects of frequent minor freshwater pulses into estuaries, river flooding can result in a temporary depletion of marine fish species in these systems (Marais 1983). In both the Thukela and Great Fish estuaries there was a decline in ichthyofaunal abundance under high riverine inputs (Ter Morshuizen et al. 1996a, Whitfield & Harrison 2003). This decline can be attributed to both direct physiological stresses imposed upon the estuarine biota (Hill 1981) and a temporary reduction in available food resources, mostly linked to the negative impacts of river flooding on benthic invertebrate stocks (Hanekom 1989). This loss in food resources may also partially explain the lack of colonisation of these estuaries by freshwater fish species after flooding, despite the virtual absence of potential marine competitors under a river dominated estuarine scenario.

During hyperhaline periods in Lake St Lucia, fish catch rates decline and this has been attributed mainly to osmoregulatory stress forcing fish taxa out of the high salinity areas (Wallace 1975a, Whitfield et al. 2006). In addition, the decline or disappearance of certain invertebrate food resources during hyperhaline periods (Bolt 1975) may have played a role in reducing fish abundance under such conditions. Piscivores, zoobenthivores, zooplanktivores and detritivores are all represented in the lake under both low and high salinity conditions (Forbes & Cyrus 1993). However, *Pomadasys commersonnii* and *Rhabdosargus sarba* that were captured in areas where the salinity was >70 were no longer feeding on typical invertebrate prey but were consuming mainly filamentous algae (Wallace 1975a), thus indicating dramatic changes in the St Lucia benthic food web.

### Competition

Fish species trends in most estuaries indicate that overall diversity declines from the euhaline, polyhaline and mesohaline sections of an estuary towards the oligohaline headwater region.



**Figure 95.** The infaunal mudprawn *Upogebia africana* crawling on the sediment surface (Photo: Alan Whitfield).



**Figure 96.** The infaunal sandprawn *Kraussillichirus kraussi* exposed on the sediment surface (Photo: George Branch).

However, even in this latter region, marine taxa are often dominant in terms of species richness and biomass, provided salinities remain  $>3$ . The euryhaline marine fish species that do penetrate oligohaline waters are likely to be related to the osmoregulatory abilities of each species, a large number of which are capable of surviving in these waters for prolonged periods (Whitfield et al. 2006).

The juveniles of some estuary-associated marine species are more abundant in the upper reaches than the middle or lower reaches (e.g. *Pseudomyxus capensis*) and this will tend to increase competition for food with potential freshwater recruits in the headwaters of such estuaries. It would appear that, particularly in the subtropics and tropics, many euryhaline marine species can tolerate oligohaline waters and that these species even dominate the ebb and flow region of some systems (Ter Morshuizen et al. 1996b). The relative scarcity of freshwater fish taxa in estuarine headwaters where marine species are abundant suggests some form of competitive exclusion, since salinities are often oligohaline in such areas and should therefore not be a limiting factor influencing occupation by the former group.

Conversely, the ability of euryhaline cichlids such as *Oreochromis mossambicus* to avoid direct competition with marine detritivorous fishes in estuaries (Whitfield & Blaber 1978b) under a range of salinity conditions suggests that competition is not such an important factor. Similarly, there was widespread occurrence of the sharp-tooth catfish *Clarias gariepinus* in oligohaline Lake St Lucia when estuary-associated marine predators were also abundant within the system (Whitfield & Blaber 1978a) and this attests to the ability of certain predatory freshwater fish species to compete for food resources under low salinity estuarine conditions.

Marine fish mortalities at either end of the salinity spectrum would also reduce competition for freshwater species capable of living in such environments. Mass mortalities under hypersaline conditions usually occur when fish are trapped in an estuary that lacks freshwater inflow for prolonged periods. For example, during October and November 2003 there were extensive mortalities

of marine fish species in the St Lucia system when drought conditions resulted in lake compartments experiencing salinities in excess of 70 (Whitfield 2005b, Cyrus et al. 2010a). The fish fauna was unable to avoid extreme hypersaline conditions because evaporative declines in lake water level had resulted in compartmentalisation of the system, effectively cutting off any escape routes.

Mass mortalities of marine fish species under oligohaline conditions are a much more frequent happening than under hyperhaline conditions (Whitfield 1995), probably linked to the more widespread occurrence of the former state. Most of these mortalities are associated with very low salinities ( $<3$ ) and simultaneous low water temperatures ( $<13^{\circ}\text{C}$  in subtropical estuaries), e.g. at least 11 species were recorded dying in subtropical Lake St Lucia during June 1976, when the salinity declined to  $<3$  and the water temperature suddenly dropped to  $12^{\circ}\text{C}$  (Blaber & Whitfield 1976). A similar mortality of marine fishes was recorded in the Kosi lakes system where low salinity conditions occurred in combination with abnormally low temperatures (Kyle 1989).

In conclusion, those few euryhaline freshwater fish species that can tolerate either extreme low or high salinities are at a distinct advantage due to the departure of potential competitors, particularly in the upper parts of certain estuarine systems where these salinity extremes are most prevalent (Wallace 1975a). From the above it is also apparent that extreme hypersalinity may affect fish food resources to such an extent that relatively few fish taxa remain within the ecosystem and thus enable euryhaline freshwater fish species to gain a competitive advantage. This is especially the case for those freshwater fish taxa that feed low down in the food web, since detritus and associated microbiota are always present, even under hypersaline conditions. However, it should be emphasized that only a few species within the Cichlidae are both detritivorous and capable of tolerating hypersaline conditions.

### Predation

Although estuarine fish assemblages tend to be numerically dominated by small estuarine resident species and the juveniles of marine species





**Figure 97.** The surface dwelling crown crab *Hymenosoma orbiculare* (Photo: George Branch).



**Figure 98:** A favoured fish food item, the amphipod *Americorophium triaenonyx* (Photo: Charles Griffiths).





**Figure 99.** The epibenthic estuarine shrimp *Palaemon peringueyi* (Photo: George Branch).



**Figure 100.** The small epifaunal bivalve *Brachidontes virgiliae* (Photo: George Branch).



**Figure 101.** The swift and very effective piscivore *Lichia amia*, one of several marine predatory fishes in southern African estuaries (Photo: Alan Whitfield).



**Figure 102.** The darter *Anhinga rufa*, one of many piscivorous bird species associated with southern African estuaries (Photo: Tris Wooldridge).

that use these systems as nursery areas (Harrison & Whitfield 2008), there are also considerable numbers of small and large piscivorous fishes that are attracted to estuaries (Figure 101, Whitfield & Blaber 1978a). Some of these piscivores may even extend their range into the low salinity upper reaches of these systems. Nevertheless, oligohaline conditions in the headwaters of estuaries, where freshwater fish species are likely to occur, would tend to have reduced numbers and diversity of marine piscivorous fishes when compared to the lower and middle reaches.

Marine fish species richness is usually higher in the lower reaches of estuaries, particularly those systems with a wide entrance and the prevalence of polyhaline or euhaline waters within this reach. Consequently the complete absence of freshwater fish species from the lower reaches of such estuaries is to be expected based on both salinity and predation factors, but their limited presence in the oligohaline and mesohaline upper reaches of estuaries where physiochemical conditions and predator risks are more favourable, is more difficult to explain.

One of the suggestions as to why euryhaline freshwater cichlids are so successful in the hyperhaline upper reaches of some estuarine systems is that most marine piscivorous fishes are absent from these areas during such times. However, the piscivorous West African ladyfish *Elops lacerta* is present in the hyperhaline upper reaches of the Casamance Estuary (Kantoussan et al. 2012) and *Elops machnata* in the hyperhaline upper lakes of the St Lucia system (Wallace 1975a). At the same time the 'freshwater' *Sarotherodon melanotheron* and *Oreochromis mossambicus* are abundant in the Casamance and St Lucia systems respectively. Perhaps the reduced piscivorous fish abundance and diversity, together with the lack of marine detritivorous competitors, is sufficient to attract these cichlids into the above areas.

Piscivorous birds are a diverse and abundant predatory component of estuaries when compared to adjacent river systems. This avifaunal cluster includes aerial hunters (e.g. kingfishers, terns and fish eagles), wading birds (e.g. egrets and herons) as well as swimming/diving species (e.g. pelicans, cormorants and darters)

(Whitfield & Blaber 1978d, 1979a, 1979b). An example of one of these bird species is shown in Figure 102.

### Diversity

Fish species richness in estuaries is strongly driven by the potential recruits from both the marine and estuarine environments. As a generalization, the species richness is higher in the coastal marine environment when compared to the freshwater environment upstream of an estuary (Whitfield et al. 2012a). This is brought about by the vast Indo-Pacific fish fauna that has access to southern African coastal areas when compared to the much more limited range of African freshwater species that penetrate the subcontinent in decreasing numbers in a southerly direction (Skelton 2001)

Clearly the taxonomic composition of the freshwater ichthyofauna will also influence the number of species that can enter an estuary. Those catchments where species belonging to the Cichlidae and Cyprinidae are diverse and abundant would have a greater potential to occupy the downstream estuaries than those systems where these families are absent (Table 13). Thus Verlorenvlei has only five freshwater fish species recorded whereas Mgobozeleni has ten taxa belonging to the freshwater guild (Table 13).

The types of estuarine systems present in a particular region will also play a role, with low salinity estuarine lakes and lagoons being especially favoured for colonisation by freshwater fish species (Hill et al. 1975, Whitfield 2005b). Conversely more saline estuarine lakes (e.g. St Lucia) have very poor freshwater guild representation (Cyrus et al. 2011), with the exception of *Oreochromis mossambicus*.

The extent to which the loss of marine fish species from estuaries with high river flows creates a vacant niche for freshwater species to enter these systems has not been quantified. There are, however, a number of examples of how river flooding can impact negatively on marine fish recruitment into estuaries. Although high river flow events in the Thukela and Great Fish estuaries do appear to temporarily flush many marine fishes into the sea, there is no evidence to suggest that these temporarily vacated ecosystems

Table 13. Indigenous fish species occurrence in five southern African estuarine lakes and lagoons in various stages of isolation from the sea (modified from Whitfield et al. 2017b). Ve = Velorenvlei, LR = Langvlei and Rondevlei, Mz = Mzingazi, Cu = Cubhu and Mg = Mgobezeleni.

Fish family	Fish species	Ve	LR	Mz	Cu	Mg
<b>Freshwater guild</b>						
Anabantidae	<i>Sandelia capensis</i>	×				
Cichlidae	<i>Coptodon rendalli</i>			×	×	×
	<i>Oreochromis mossambicus</i>	×	×	×	×	×
	<i>Oreochromis placidus</i>					×
	<i>Pseudocrenilabrus philander</i>			×	×	×
	<i>Serranochromis meridianus</i>					×
	<i>Tilapia sparrmanii</i>	×		×	×	×
Clariidae	<i>Clarias gariepinus</i>			×	×	×
	<i>Clarias theodora</i>				×	
Cyprinidae	<i>Enteromius paludinosus</i>			×		×
	<i>Enteromius radiates</i>					×
	<i>Enteromius viviparus</i>			×	×	
	<i>Pseudobarbus verlore</i>	×				
Galaxiidae	<i>Galaxias zebratus</i>	×				
Mormyridae	<i>Marcusenius macrolepidotus</i>			×	×	
Poeciliidae	<i>Aplocheilichthys katangae</i>			×		×
	<i>Aplocheilichthys johnstonii</i>			×		
<b>Catadromous guild</b>						
Anguillidae	<i>Anguilla bengalensis</i>					×
	<i>Anguilla bicolor</i>				×	×
	<i>Anguilla mossambica</i>		×		×	×
	<i>Anguilla marmorata</i>				×	
<b>Estuarine guild</b>						
Atherinidae	<i>Atherina breviceps</i>		×			
Clinidae	<i>Clinus superciliosus</i>		×			
Clupeidae	<i>Gilchristella aestuaria</i>	×	×	×	×	
Eleotridae	<i>Eleotris melanosoma</i>					×
	<i>Eleotris fuscus</i>				×	
Gobiidae	<i>Awaous aenofuscus</i>					×
	<i>Glossogobius callidus</i>			×		
	<i>Glossogobius giuris</i>			×	×	×
	<i>Croilia mossambicus</i>			×	×	
	<i>Psammogobius knysnaensis</i>		×			
Hyporhamphidae	<i>Hyporhamphus capensis</i>		×	×		
Syngnathidae	<i>Microphis brachyurus</i>		×			



Fish family (cont.)	Fish species	Ve	LR	Mz	Cu	Mg
<b>Marine guild</b>						
Carangidae	<i>Caranx sexfasciatus</i>			×		
	<i>Lichia amia</i>		×			
Haemulidae	<i>Pomadasys commersonnii</i>		×			
Megalopidae	<i>Megalops cyprinoides</i>			×	×	×
	<i>Elops machnata</i>				×	
Monodactylidae	<i>Monodactylus falciformis</i>		×		×	
Mugilidae	<i>Chelon dumerili</i>		×			
	<i>Chelon richardsonii</i>	×	×			
	<i>Chelon tricuspidens</i>		×			
	<i>Mugil cephalus</i>	×	×			
	<i>Pseudomyxus capensis</i>		×	×	×	
	<i>Planiliza macrolepis</i>					×
Sparidae	<i>Acanthopagrus vagus</i>				×	
	<i>Rhabdosargus holubi</i>		×			
	<i>Lithognathus lithognathus</i>	×	×			

are then occupied by freshwater fish species (Ter Morshuizen et al. 1996a; Whitfield & Harrison 2003). There is also the possibility that major river flooding temporarily removes most of the zooplankton and surface dwelling zoobenthos from the estuary, thus making it an unattractive environment for freshwater fish colonization. In addition, physiological challenges would arise as soon as tidal conditions were re-established within the affected estuary.

Whilst it is widely accepted that estuaries are ideal nursery areas for juvenile marine fishes, these same systems should provide ideal nursery areas for freshwater species as well. For example, diversity and abundance of freshwater fish taxa in the St Lucia system increases following river flooding and lowering of lake salinities into the oligohaline range (Whitfield et al. 2006). However, if salinities within an estuary remain within the mesohaline range following increased river flow, large-scale colonization of the system by freshwater species from the river is unlikely (Vorwerk et al., 2008b).

Further evidence of fish responses to oligohaline waters can be found in the Kosi lake system where marine fish species richness exhibits a

decline between the northern, more saline compartments, and the southern oligohaline Lake Nhlangwe (Blaber 1978). During the late 1970s, increased rainfall and run-off into Lake Nhlangwe resulted in further salinity declines to <1, with concomitant increases in the abundance of freshwater species and the departure of some marine fish taxa away from this compartment to the more saline northern lakes (Blaber & Cyrus 1981). Unfortunately, the small size of the freshwater catchment entering the Kosi system meant that the number of potential new freshwater species to recruit into Lake Nhlangwe was very limited when compared to large catchments to the west, e.g. Phongolo.

The absence of freshwater fish species from most estuarine ichthyoplankton assemblages in southern Africa (e.g. Harrison & Whitfield 1990, Montoya-Maya & Strydom 2009a) is further evidence of the lack of occupation of estuaries by this group. The inability of the eggs and larvae of many freshwater fish species to survive in saline waters may also be one of the reasons for their absence from estuaries but it could be significant that those few cichlids which occupy hyperhaline waters in estuaries are also able to

successfully breed within these systems (Cyrus & Vivier 2006a). However, it is important to note that most euryhaline marine fish species also do not breed in estuaries and these taxa often have a larval phase in the sea before recruiting into estuaries as late larvae or early juveniles (Wallace 1975a).

Laguna Madre has widely fluctuating salinities, ranging from more than 100 in some years to almost fresh following major rainfall events. Almost double the number of fish species are found in this system during low salinities (<10) when compared to high salinity (>60) regimes (Hedgpeth 1967), a situation that is very similar to fish species richness responses to major salinity swings in Lake St Lucia (Whitfield et al. 2006).

### Connectivity

River base flows drive connectivity between the catchment and the estuary (Figures 103 and 104), with these flows being particularly important for freshwater fish to be able to access the downstream estuary. When large dams are built in

river catchments, these impoundments sometimes have the capacity to capture the entire mean annual runoff of the river system. Since freshwater abstraction under the above circumstances is often very high, the downstream river then flows only very intermittently. This 'segmentation' of rivers due to the temporary loss of base flow has major deleterious consequences for the potential colonisation of estuaries by freshwater fishes, as well as the migrations of anguillid eels between estuaries and their associated catchment (Bruton et al. 1987).

In addition to river segmentation caused by the reduction in base flows, there are also the physical barriers created by impoundments in the catchment. The impact of such barriers is major, and results in very different fish communities above and below dam walls. The positioning of these barriers has differential effects on diadromous and migratory freshwater species, with dams or weirs near an estuary having a greater impact on diadromous taxa than those further inland. An example of the impact of weirs is provided



**Figure 103.** Catchment connectivity for freshwater fish species entering estuaries is facilitated by perennial river systems with shaded river banks (Photo: Alan Whitfield).

by the Mhlathuze complex of lakes in KwaZulu-Natal, where the movement of estuary-associated fish species has been severely curtailed by weirs above the estuary and at the entrances of some of the lakes (Weerts & Cyrus 1998, 2001). A similar situation pertains to the siting of the Mpofu Dam on the Kromme River, severely restricting fish access to the catchment.

The size of the river-estuary interface (REI) zone in estuaries is directly related to the volume of freshwater entering the estuary (Whitfield & Wood 2003). Any major reduction in river flow as a result of excessive abstraction has major implications for those freshwater fish species that require oligohaline conditions in the upper estuary. Indeed, in some estuarine systems the REI zone has been replaced by a hyperhaline zone due to lack of river base flow as a result of numerous dams in the catchment (Allanson & Read 1995), thereby eliminating potential habitat for freshwater fish species in the estuary (Whitfield & Paterson 2003). In reality, however, the

oligohaline zone of most estuaries is usually dominated by estuarine resident or estuary-associated marine species, with the balance between these two guilds being determined by the magnitude of the river flow and the size of the REI zone.

The relationship between salinity and the abundance of marine fish species in estuarine lakes can also be driven by the segmented nature of certain systems, e.g. Hill et al. (1975) found that the fish community in Lagoa Poelela was dominated by freshwater species, mainly *Oreochromis mossambicus* and *Coptodon rendalli*, despite the fact that the average salinity in the lake was 8. The low representation of marine fish taxa in Lagoa Poelela, which would have been expected to dominate the system at this salinity, was attributed to the 75 km long natural channel and segmented lagoonal systems connecting the lake to the sea. Marine species that were not recorded in Lagoa Poelela were found in Lagoa Quissico and Massava, which were nearer to the sea than Lagoa Poelela (Hill et al. 1975).



**Figure 104.** Intermittently flowing rivers and thick vegetation within the river bed are barriers to freshwater fish interactions with estuaries. However, fish colonization of such estuaries is possible during river flooding (Photo: Alan Whitfield).



### Some preliminary conclusions

There are five broad conclusions, all of which require further investigation to fully understand why the freshwater fish component is not better represented in estuarine systems.

- Freshwater fish assemblages in estuaries on the subcontinent are not as species rich as marine taxa in the same systems, with estuarine ichthyoplankton generally lacking any freshwater fish species eggs or larvae.
- The majority of freshwater fish species do not penetrate waters where the salinities are mesohaline, polyhaline or euhaline. The reason why mesohaline waters (5-18) are avoided is very difficult to explain since many freshwater fish species would be isosmotic within this salinity range.
- In order to become euryhaline, a fish species needs to be able to develop chloride cells in gill filament epithelia to get rid of excessive salts. Only a few freshwater fish species, mostly cichlids, seem to have developed this capacity and they have successfully occupied estuaries.
- Factors such as increased competition for food and higher predation rates by piscivorous fish and birds in estuaries may play a role in the low species richness and abundance of freshwater taxa in these systems.
- The relatively low diversity of freshwater fish species in a river catchment when compared to marine fish species in the adjacent coastal zone may be partially responsible for the lower freshwater species richness in the associated estuary.

## 2.6 DISTRIBUTION, MOVEMENTS AND MIGRATIONS

Numerous acoustic telemetry and other more conventional tagging studies have been conducted over the past two decades on some of the dominant and larger fish species in Eastern and Western Cape estuaries. The focus of attention has been on those species that are important to either recreational and /or subsistence level fishers. The following taxa have been well studied and we are now able to quantify aspects such as area use, home range dynamics and movement patterns of several estuary-associated marine taxa.

### Cape stumpnose *Rhabdosargus holubi*

This keystone species in estuaries has only recently received the acoustic telemetry attention that it deserves. Juvenile *R. holubi* were tagged with internal acoustic transmitters in the lower, middle and upper reaches of the 21 km long Kowie Estuary (Grant et al. 2017a). The movements of the fish were continually monitored using stationary data-logging acoustic receivers. Results indicated that *R. holubi* spent the highest proportion of time within the estuarine environment (83%), with the sea (16%) and riverine (1%) environments being used to a much lesser extent (Figure 105).

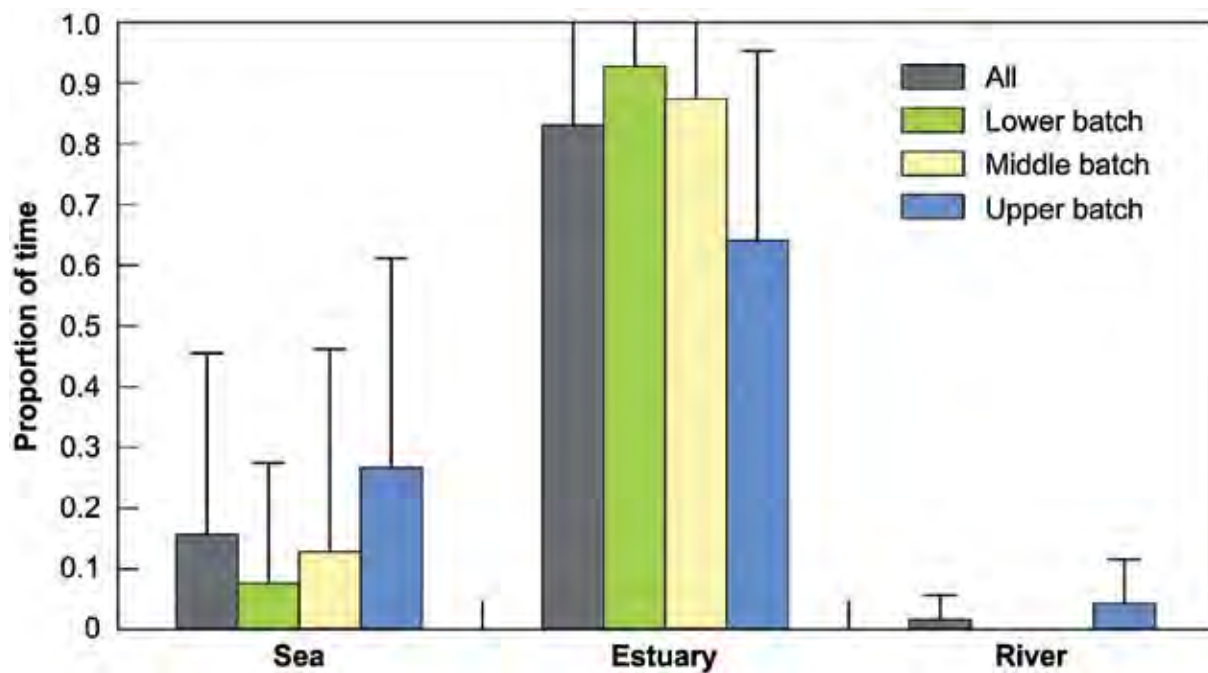
The above study confirmed the importance of estuaries as nursery areas for juvenile *R. holubi*,

with tagged individuals showing high levels of residency and fidelity to their capture and release sites. When the larger juvenile *R. holubi* migrated back to the sea for the next phase of their life cycle, they generally did not return to the estuarine environment, thus indicating a permanent ontogenetic shift in habitat use with the onset of sexual maturity (Grant et al. 2017a).

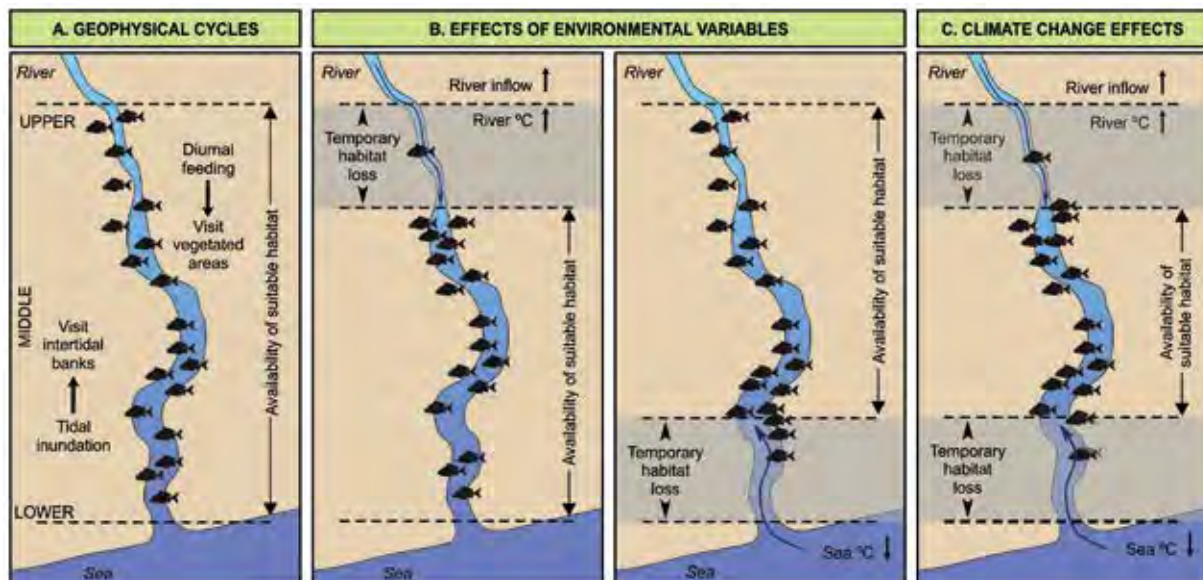
Another study using early 0+ juvenile *R. holubi* showed that movements between two nearby mangrove habitats in the Mngazana Estuary indicated that residency based on short-term (days) and long-term (weeks) data was high (Muller & Strydom 2017). In addition, stable isotope (carbon and nitrogen) analyses of the Cape stumpnose associated with the white and red mangrove habitats in this estuary indicated strong subpopulation residency by this species for the respective mangroves, despite apparent differences in habitat quality and food availability between the two sites.

The high degree of residency exhibited by *R. holubi* in the Eastern Cape estuaries is also reflected in the closely related *Rhabdosargus globiceps* from Langebaan Lagoon in the Western Cape. In this particular study, a high proportion of the 30 transmitter-tagged fish spent 50% of





**Figure 105.** Mean ( $\pm$  SD) proportions of time spent in the marine, estuarine and riverine environments for all tagged juvenile *Rhabdosargus holubi*, and for each batch separately (after Grant et al. 2017a).



**Figure 106.** Schematic representation of the effects of (A) geophysical cycles and 'normal' estuarine conditions, (B) changes in estuarine environmental variables (elevated river inflow, increased river temperature and lowered sea temperature), and (C) predicted impacts of future climate change (increased river temperature affecting the estuarine upper reaches and more frequent ocean upwelling influencing the lower reaches), on the distribution of *Rhabdosargus holubi* within Kowie Estuary habitats (after Grant et al. 2017b).

their time in a small protected area (4% of total habitat area) during summer, thus minimizing the negative impact of recreational fishing on this species (Kerwath et al. 2009).

Diel and tidal cycles were identified in the movements of several individual *R. holubi* in the Kowie Estuary (Grant et al. 2017b). However, the lack of extensive movements for most individuals emphasized the high residency by the species to particular sections of the estuary. It was also found that river inflow and water temperature significantly affected the movement behaviour of most tagged *R. holubi*. Periods of increased freshwater inflow and rising riverine temperatures prompted certain individuals to shift their position downstream, while reduced sea temperatures in the lower reaches prompted certain individuals to shift their position further upstream from the mouth (Figure 106).

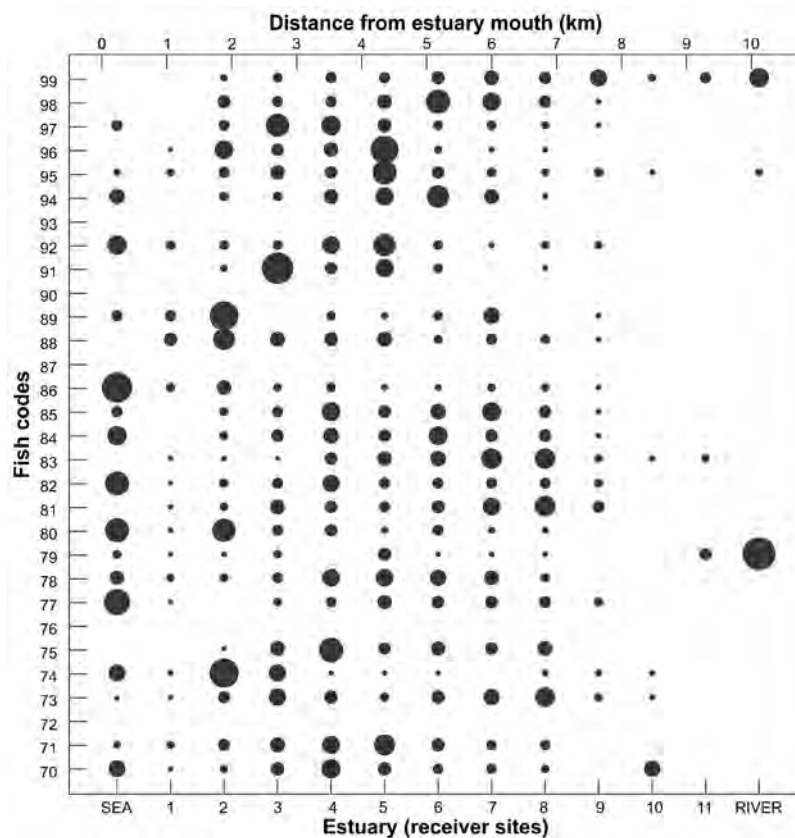
Given the predicted effects of climate change in the study region, which include increased river

inflow due to catchment rainfall and decreased sea temperatures due to ocean upwelling, the above results suggest that *R. holubi* may be sensitive to the environmental effects of global warming and that the distribution and movement behaviour of this species in southern African estuaries is likely to be affected as climate change proceeds.

#### Dusky kob *Argyrosomus japonicus*

Juvenile *A. japonicus* in the Great Fish Estuary spend most time in the estuary (84%), compared with 13% in the sea and only 4% in the adjacent river (Figure 107). Tagged fish made use of the estuary from the mouth to 10 km upstream, with most time being spent between 0.5 km and 6.5 km from the mouth (Cowley et al. 2008). Although there was broad conformity in terms of estuarine use, Figure 107 shows that no two fish had the identical spatial distribution pattern.

Indications were that the *A. japonicus* in the Great Fish Estuary alternated between moving



**Figure 107.** Bubble-plot representation of the proportion of time (% frequency, March - September 2004) each tagged *Argyrosomus japonicus* (n = 25) spent at sea, in the Great Fish Estuary (given as time spent in the vicinity of each receiver) and the river (after Cowley et al. 2008).

and stationary behaviour (Næsje et al. 2012). Up-estuary movements ( $0.29 \text{ m s}^{-1}$ ), usually at night, were slightly faster than down-estuary movements ( $0.22 \text{ m s}^{-1}$ ), mainly at dawn and dusk. This ‘riding the tide’ was suggested as a successful foraging strategy when targeting prey that follows the tidal current (Næsje et al. 2012).

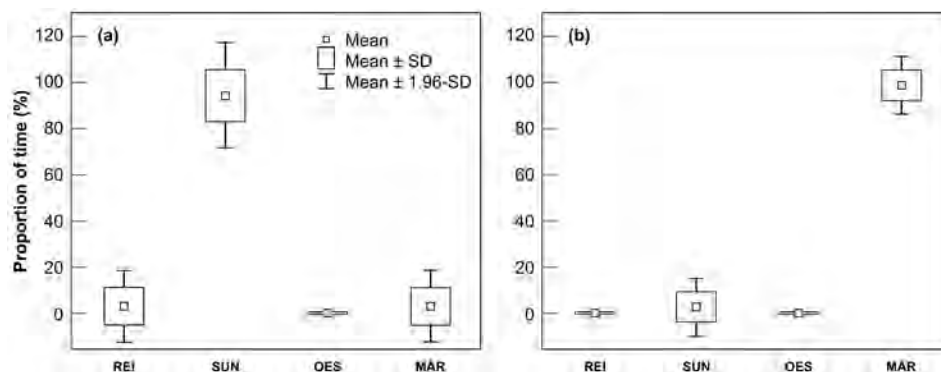
A total of 18 of the 29 acoustically tagged fish undertook sea trips (mean duration = 3.5 days), whereas three individuals made riverine excursions (mean duration = 7.3 days). Altogether 12 (41%) of the tagged fishes were captured by fishermen in the estuary during the monitoring period (up to 195 days), thus highlighting the

high mortality of this species during its nursery phase (Cowley et al. 2008).

Additional acoustic tracking of juvenile *A. japonicus* in the Sundays Estuary and adjacent marine habitat has provided new insights into the intra-population structure of this estuary-dependent species (Childs 2013). The movements of 85 juvenile *A. japonicus*, tagged with acoustic transmitters in the estuarine and marine environments, was monitored. While one-third of the tagged fish visited adjacent marine or estuarine habitats, the majority exhibited high levels of residency to their respective estuarine or coastal tagging sites (Figure 109). This high level of residency suggests that



**Figure 108.** An acoustically tagged adult *Argyrosomus japonicus* about to be released by JD Filmlater (Photo: Paul Cowley).



**Figure 109.** Mean proportions (%) of time spent by (a) estuarine-tagged *Argyrosomus japonicus* and (b) marine-tagged *A. japonicus* in the Sundays River-Estuary Interface (REI) zone, Sundays Estuary (SUN), other estuaries (OES) and the marine environment (MAR) (after Childs et al. 2015).

juvenile *A. japonicus* exist as a metapopulation, with several non-dispersing subpopulations, each with distinct estuarine and marine contingents (Childs et al. 2015).

The estuarine contingent had a higher fishing recapture (mortality) rate (35%) than the marine contingent (20%) and, within the estuarine contingent, the recapture rate was higher for resident individuals (41%) than migratory individuals (23%). Species with different contingents, each exhibiting retentive and migratory/exploratory behaviours (i.e. partial migration) are likely to be more resilient to fishing pressure. However, certain behavioural strategies, particularly estuarine residency by *A. japonicus*, make this species vulnerable to exploitation (Childs et al. 2015).

An ontogenetic shift in habitat use was observed in estuarine-tagged individuals by Childs (2013), with larger *A. japonicus* spending significantly less time in the estuary and undertaking significantly more sea trips than smaller individuals. The tidal and diel behavioural patterns displayed by these dusky kob when undertaking major habitat change movements suggest that this species may maintain endogenous circatidal and circadian rhythms that facilitate their estuarine-coastal and estuarine-riverine connectivity. All major excursions by *A. japonicus* occurred at night, with movements into the estuary occurring on the incoming (75%) and high (11%) tide, and movements out of the estuary on the ebbing (54%) and high (18%) tide. Circatidal rhythms also facilitated estuarine-riverine movements, but a crepuscular activity pattern was observed by Childs (2013) in the use of the river-estuary-interface (REI) region by this species.

While several environmental factors influenced estuarine use by *A. japonicus*, the circannual rhythm and season had the most significant effect on estuarine-coastal and estuarine-riverine connectivity (Childs 2013). Almost all excursions undertaken by estuarine- and marine-tagged juveniles occurred during summer and by tagged adults in spring. Furthermore, almost all visits by *A. japonicus* to the REI region occurred in spring and early summer (Figure 110).

River inflow and rough sea events (both indicators of climate change) also played a minor, yet

significant role in estuarine-coastal connectivity for dusky kob in the Eastern Cape. According to Childs (2013) this suggests that *A. japonicus* could be a good indicator species to test the long-term effects of climate change on both estuarine and coastal zone ecology in the region.

### **Leervis *Lichia amia***

Data from the ORI national fish tagging study were analysed by Dunlop et al. (2015) and results indicated that out of a total of 10 762 *L. amia* dart tagged over many years, 744 (7%) were recaptured. Movements by juvenile leervis were largely restricted to individual estuaries that were used as nursery areas, primarily on the south-eastern and southern parts of the subcontinent. Results from the study also showed that there was a significant effect of fish size on the distance moved (Figure 111), with adults undertaking a longshore migration up the south-eastern coast towards KwaZulu-Natal. These findings, and those of Murray et al. (2017), support the contention that juvenile *L. amia* are largely resident in estuaries with the adults undertaking a winter migration into the subtropics to spawn.

A detailed study of *L. amia* in selected permanently open Eastern and Western Cape estuaries using conventional dart tagging and passive acoustic telemetry methods provided detailed movement behaviour of juvenile leervis within and between estuaries (Murray 2016). The results identified substantial small-scale intra-population variability among different individuals, as well as between the tagging estuaries. For example, 75% of all *L. amia* recaptures (87% of which were juveniles) using conventional dart tagging in the Swartkops Estuary were tagged in the same estuary (Murray et al. 2017).

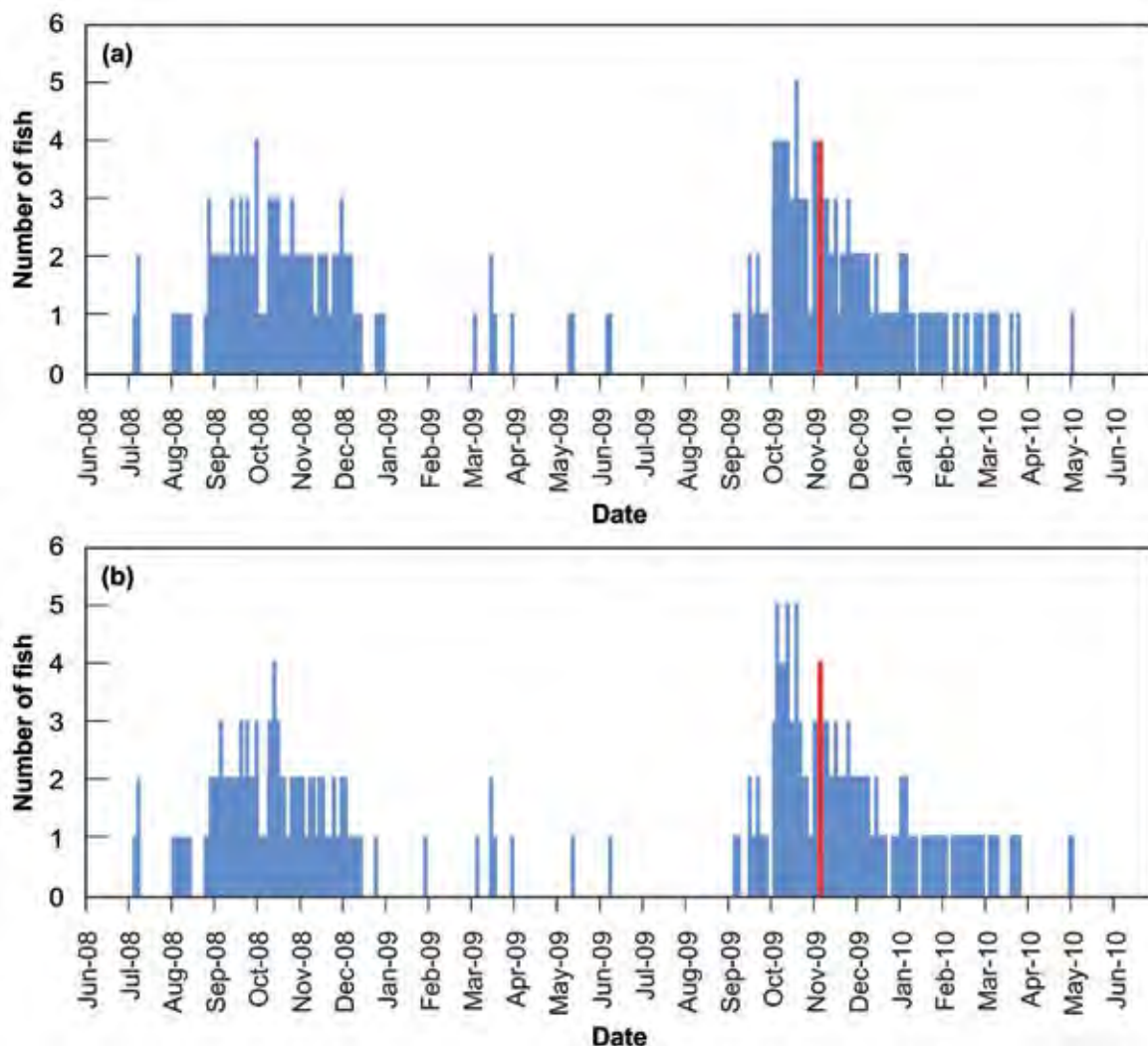
Acoustic telemetry methods on mainly juvenile leervis in the Kowie and Goukou estuaries revealed 56% of the time being spent in the former and 38% in the latter estuary. Goukou fish spent a large proportion of time during the monitoring period in the sheltered bay adjacent to the Goukou Estuary mouth. This bay may have served as an interim nursery habitat when estuarine conditions became unfavourable due to cool river inflow and the resultant decrease in estuarine



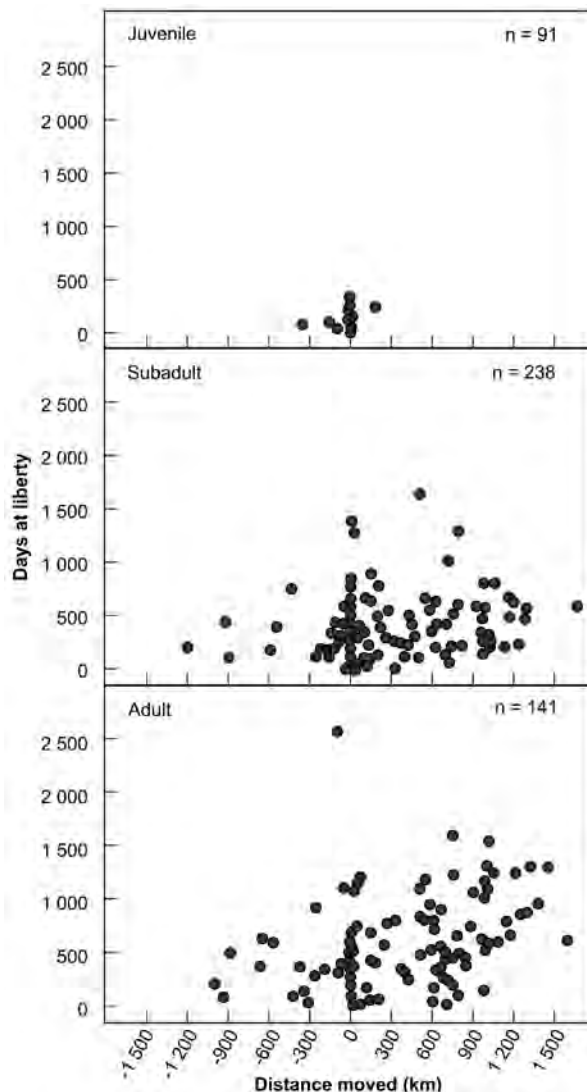
water temperature (Murray 2016). In the Kowie Estuary, leervis moved downstream during winter but did not leave the estuary as occurred in the Goukou system during winter.

In general, the juvenile *L. amia* spent the majority of time in the lower reaches of warm-temperate estuaries, with both tides and diel periodicity influencing their movements in an estuary-specific manner. Marine excursions by leervis often coincided with an early morning outgoing tide, with a reverse habitat shift from the sea to an estuary being linked to late afternoon incoming tides (Murray 2016).

Where juveniles were recorded visiting adjacent estuaries, very few returned to their natal system, e.g. only two of 21 Kowie *L. amia* were recorded returning to their natal system after having visited an adjacent estuary. Thus even though dependence on their primary estuary had diminished, juvenile tagged fish were still dependent on estuaries (Figure 112). It was also noted that juvenile leervis that estuary ‘hopped’ were recorded moving fairly rapidly between systems, reinforcing the view that estuaries are the prime habitat for this life-history stage (Murray 2016). It should also be mentioned that the ability



**Figure 110.** Number of estuarine-tagged juvenile *Argyrosomus japonicus* recorded on the acoustic receiver situated in the River-Estuary Interface (REI) region of the Sundays Estuary. Vertical bars represent synchronous visits to the REI receiver (a) and synchronous departures from the REI receiver (b). The two red lines in each figure represent the synchronous arrival (a) and departure (b) from the REI receiver by the only marine-tagged juvenile *A. japonicus* to visit the area, and which occurred at the same time as a visit by three estuarine-tagged juveniles to the REI (after Childs 2013).

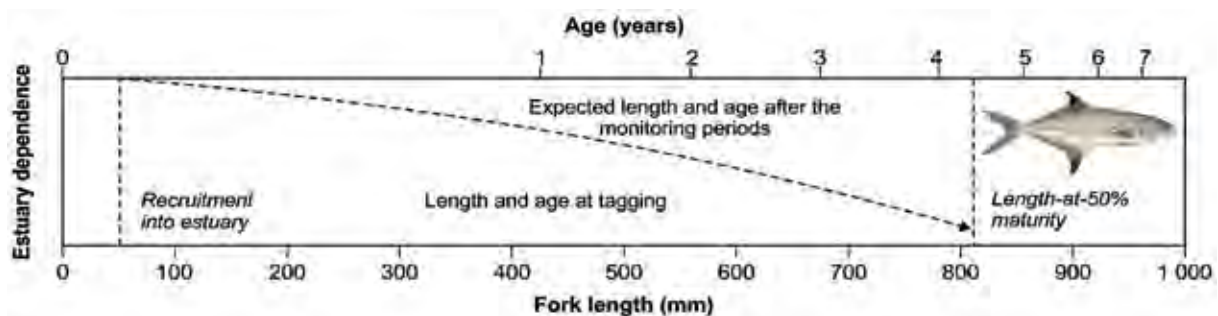


**Figure 111.** Relationship between distance moved (kilometres) and time at liberty for *Lichia amia* recaptured along the South African coastline (January 1984 - December 2012). Data were assigned to three size classes (juveniles = <500 mm FL, subadult = >500-800 mm FL, adult = >800 mm FL). Positive and negative values represent movement in an easterly and westerly direction respectively (after Dunlop et al. 2015).

of juvenile *L. amia* to estuary 'hop' is dependent on the availability of nearby estuaries for occupation, since there are long stretches of the southern African coastline where permanently open estuaries are scarce.

In general, the above study showed that smaller individuals displayed higher levels of residency than larger individuals (Figure 112), with most remaining in the tagging estuaries for the entire duration of the monitoring period. Other *L. amia* moved repeatedly into adjacent marine and estuarine environments and did not show the same degree of residency to a particular estuarine system. It has been suggested by Murray (2016) that these movements to other estuaries may be indicative of exploratory behaviour and, based on food availability, competition and the suitability of the new estuary to occupation, these particular individuals then take up residency in the new system.

Additionally, all *L. amia* responded to changing environmental fluctuations in the study estuaries. Underlying behavioural mechanisms in the form of rhythmic cycles confirmed that leervis change their position within an estuary as a result of the highly variable characteristics of southern African systems, e.g. periods of increased rainfall resulted in increases in river flow, decreases in salinity and temperature, and increases in turbidity. The combination of the above physico-chemical changes invariably induced a downstream shift in the mean position of *L. amia* within the study estuaries (Murray 2016). In some cases this may even result in the leervis temporarily leaving the estuary and preferentially occupying the nearshore marine environment.



**Figure 112.** Graphical representation of the varying levels of dependence by *Lichia amia* on estuaries with an increase in length (mm FL, primary x-axis) and age (years, secondary x-axis) (after Murray 2016).

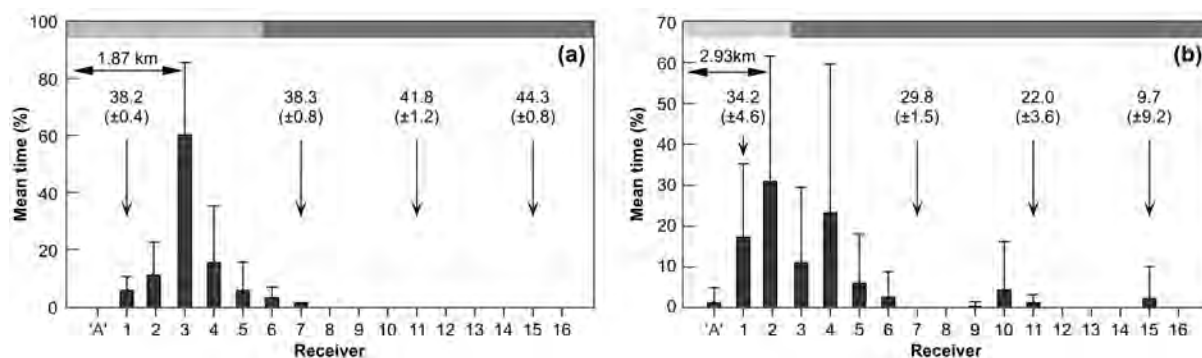


Figure 113. Mean ( $\pm$  SD) proportion of time (%) spent by white steenbras *Lithognathus lithognathus* in the vicinity of each of 16 receivers in (a) Kariega and (b) Sundays estuaries. The dominant substratum types (light grey = sandy, dark grey = muddy) and mean salinities ( $\pm$  SD) at receivers 1, 7, 11 and 15 are also shown. Absence periods of certain fish due to 'sea trips' are indicated by Receiver 'A' (after Bennett et al. 2015).

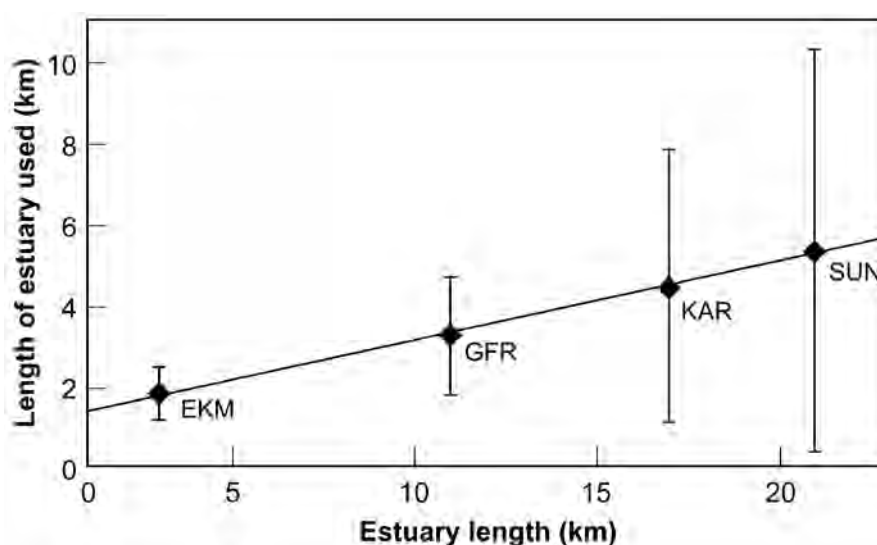


Figure 114. Regression plot of the mean length ( $\pm$  SD) of estuary used (km) by tagged *Lithognathus lithognathus*, against total estuary length (km) in the East Kleinemonde (EKM), Great Fish (GFR), Kariega (KAR) and Sundays (SUN) estuaries ( $p = 0.0007$ ,  $r^2 = 0.98$ ) (after Bennett et al. 2015).

### White steenbras *Lithognathus lithognathus*

One of the earliest space use studies by an estuary-associated marine fish species was conducted in 2003 on juvenile *L. lithognathus* in the Great Fish Estuary (Bennett et al. 2011). Seven individuals were tagged with acoustic transmitters and spent the majority of their time 5-7 km from the mouth in mesohaline and oligohaline reaches of the estuary where sandy sediments predominated. Similar studies in the Kariega and Sundays estuaries revealed that the distribution of juvenile *L. lithognathus* was closer to mouth (Figure 113) where euhaline conditions were present but sediments in these localities were also predominantly sandy (Bennett et al. 2015).

Fifteen years of bi-annual seine-netting in the

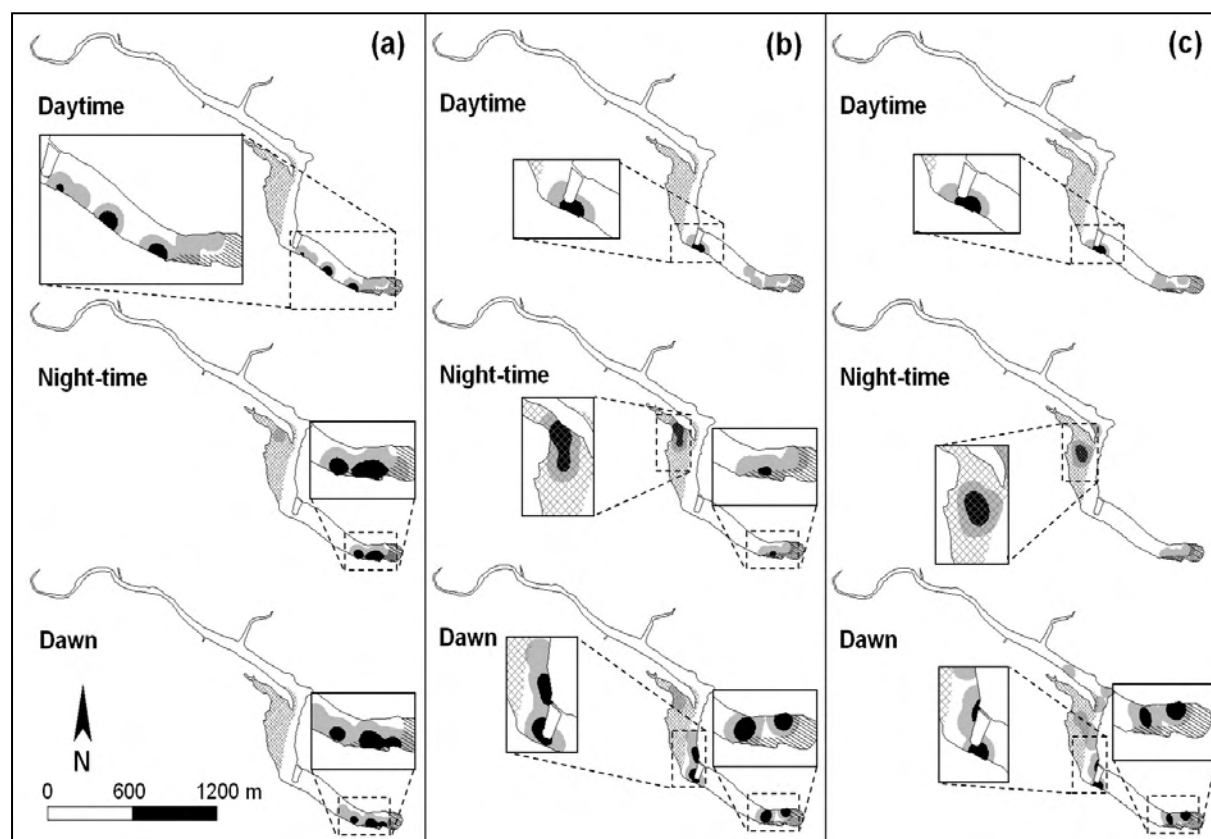
East Kleinemonde Estuary showed that white steenbras abundance was highest in the mouth region and decreased with distance upstream. Fifteen fish equipped with acoustic transmitters were monitored for eight months using an array of stationary acoustic receivers, while five of these fish were also manually tracked for two months (Bennett et al. 2012). Results from both telemetry methods indicated that activity was greatest in the mouth region and lower reaches of the estuary where sandy habitats predominated.

All individuals in the East Kleinemonde Estuary exhibited site fidelity and remained resident near their sites of capture. The mean length of estuary used per individual was 1.9 km (Bennett et al. 2012). Similarly, in the Great Fish Estuary,

the mean length of estuary used per individual was 1.7 km using manual tracking and the fish were highly resident, showing fidelity towards their site of capture (Bennett et al. 2011). However a later and more comprehensive dataset using stationary receiver distances (Bennett et al. 2015) showed that mean lengths of estuary used by juvenile *L. lithognathus* showed a strong and significant correlation with estuary length (Figure 114).

Long-term residency by juvenile white steenbras was also confirmed by Bennett et al. (2015), with only 24% of the tagged fish undertaking brief 'sea trips'. In addition, the estuarine nursery phase for this species was found to be considerably longer than previously reported, with some specimens staying in the estuary for up to 3.7 years (Bennett et al. 2015). However, once the adults adopted a more marine existence, they would travel widely, as indicated by genetic studies that showed this species to be a single genetic stock with high levels of gene flow throughout its distribution (Bennett et al. 2017).

In the temporarily closed East Kleinemonde Estuary a distinct diel activity pattern was also recorded for white steenbras, with certain individuals utilizing deeper parts of the estuary during the day and shallow regions at night (Bennett et al. 2012, Figure 115). Similarly, in the permanently open Sundays and Kariëga estuaries fish exhibited distinct diel movement patterns, and in this case the movements were associated with the tides (Bennett et al. 2015). More than 90% of the tagged fish showed small scale (tens to hundreds of metres) transverse movements between deep channels and shallow banks that were synchronized with the tide. Thus occupation of the littoral zone was associated with the high tide whereas these same fish moved into channel areas during low tide. The results from the above studies clearly indicated that the shallow littoral zone of estuaries represents a critical habitat for juvenile white steenbras and that estuarine management initiatives need to take these insights into consideration.



**Figure 115.** Daytime, night-time and dawn home ranges (95% UD, grey shaded areas) and core areas (50% UD, black shaded areas) for three tagged juvenile *Lithognathus lithognathus* (UD = Utilization Distribution). The checked areas indicate the littoral zone where nocturnal and dawn foraging was most prevalent (see Bennett et al. 2012 for details).



### Spotted grunter *Pomadasys commersonnii*

The movements of this species were investigated in the Great Fish Estuary using both manual and automated telemetry methods on specimens between 362 and 698 mm TL (Childs et al. 2008a). Individuals with acoustic-coded transmitters spent most of the time (67%) in the estuary, interspersed by a number of marine excursions that lasted mostly between 0.8 and 9.5 days (Figure 116). These excursions were correlated significantly with tide, time of day, fish size and various environmental conditions, especially coastal water temperatures.

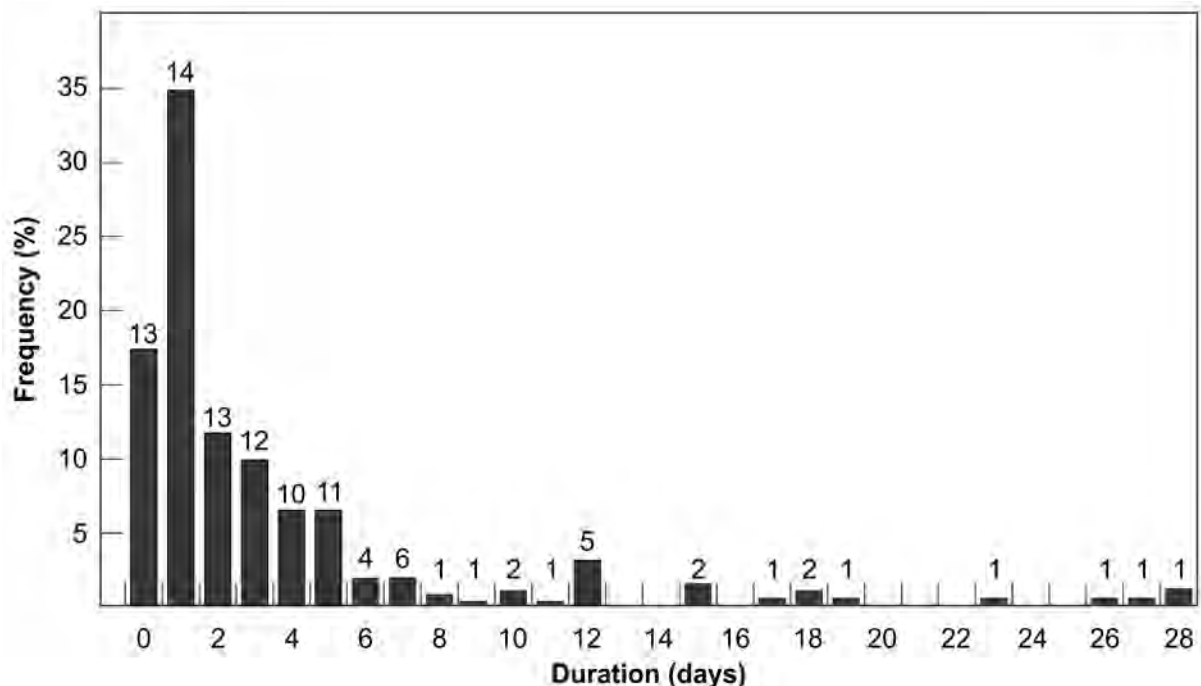
On average, the *P. commersonnii* that undertook 'sea trips' departed the estuary on the nocturnal ebb tide and then returned on the diurnal flood tide (Childs et al. 2008a). Smaller spotted grunter (<400 mm TL) spent more time in the estuary than larger individuals (>400 mm TL) but the above study showed that both juveniles and adults make extensive use of the estuarine environment.

While in the estuary, there was large variation in home range size between individual spotted grunter (Childs et al. 2008b, Cowley 2013). In general, bigger fish had larger home ranges and more core areas than smaller fish. Most (74%) home ranges of the tagged *P. commersonnii* were

located in the lower reaches of the estuary, with the smallest tagged individuals (<400 mm TL) displaying site fidelity to single core areas within about 2 km of the estuary mouth where sand and mud prawn prey densities were highest.

The number of *P. commersonnii* recorded in the Great Fish Estuary was significantly correlated with barometric pressure, wind direction and sea temperature (Childs et al. 2008a). In the Eastern Cape Province, periods of high barometric pressure associated with persistent easterly winds cause cold water to upwell along the coast, leading to rapid declines in inshore marine temperatures. In contrast, low barometric pressure, characterized by predominant westerly winds, are associated with an absence of upwelling events (Schumann et al. 1982). Since *P. commersonnii* are found mostly in waters of between 21 and 23°C, and avoid water <16°C (Childs et al. 2008c), it is not surprising that the average number of tagged fish in the Great Fish Estuary was higher after upwelling events (easterly winds) than non-upwelling periods (westerly winds) (Childs et al. 2008a).

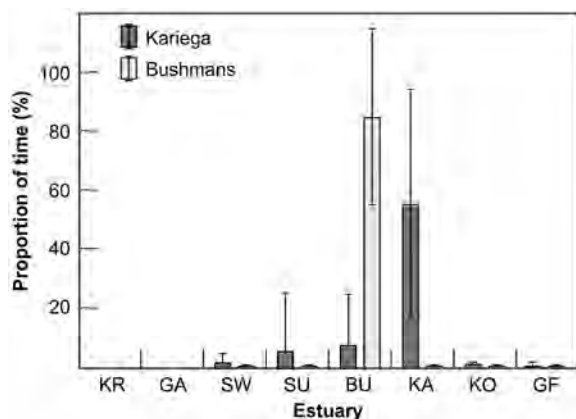
Despite having wide physiological tolerances to salinity (0-37), turbidity (4-356 FTU) and temperature (16-30°C), using real time data from



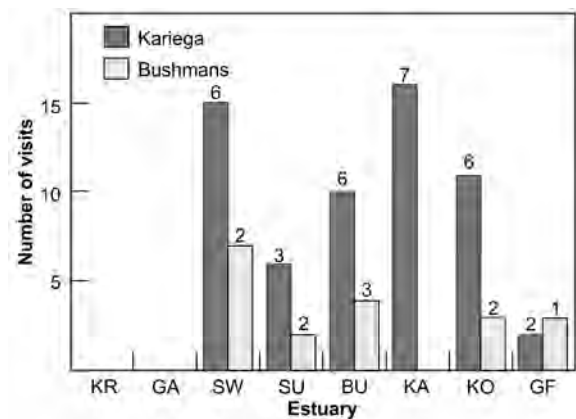
**Figure 116.** The percentage frequency of occurrence of 'sea trips' of given duration made by tagged *Pomadasys commersonnii* in the Great Fish Estuary between September 2003 and February 2004. The number of individuals that undertook a 'sea trip' of a given duration is shown above each bar (after Childs et al. 2008a).

the Great Fish Estuary, *P. commersonnii* appear to follow a suite of more moderate environmental variables using tidal transport. By ‘riding’ flood tides to move up the estuary and ebb tides to move back down the estuary, these fish continually occupy appropriate zones of the estuary where physiological demands are reduced and energy expenditure is minimized (Childs et al. 2008c).

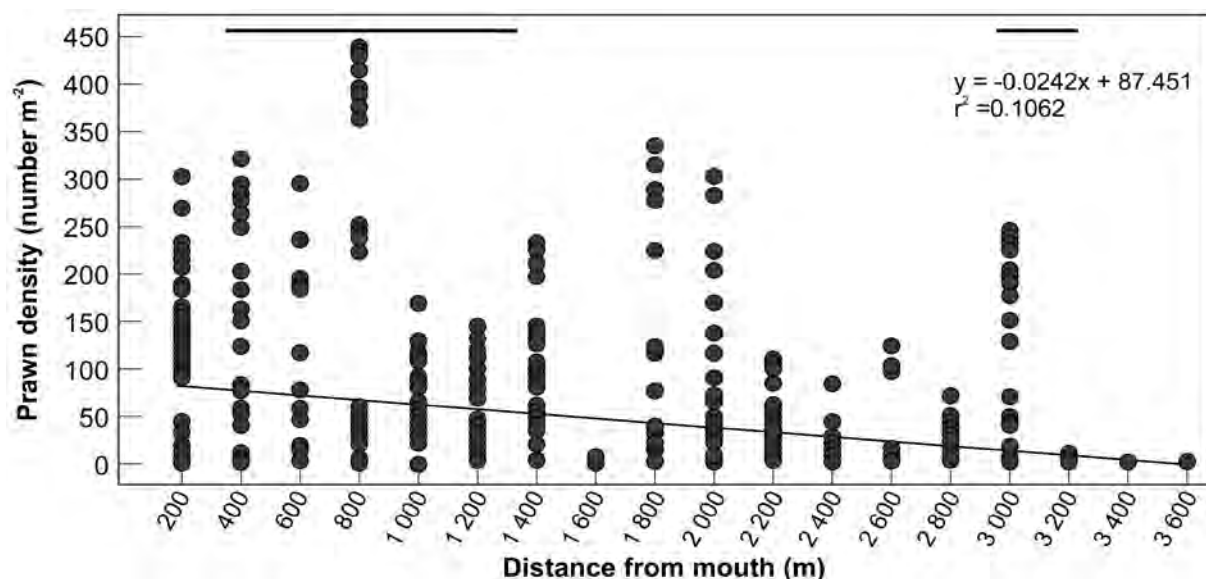
Apart from movements within the estuary, adult *P. commersonnii* also explore nearby estuaries (Dames et al. 2017). This study showed that despite forays into estuaries up to 200 km from where the fish were tagged, most individuals returned or stayed in their tagging estuary (Figure 117). This residency, combined with visits to neighbouring estuaries (Figure 118), highlights



**Figure 117.** Mean proportions ( $\pm$  SD) of time spent in each of eight Eastern Cape estuaries by *Pomadasys commersonnii* tagged in the Kariega ( $n = 15$ ) or Bushmans ( $n = 11$ ) estuaries. The estuaries monitored were the Kromme (KR), Gamtoos (GA), Swartkops (SW), Sundays (SU), Bushmans (BU), Kariega (KA), Kowie (KO) and Great Fish (GF) (after Dames et al. 2017).



**Figure 118.** Numbers of fish visiting the different estuaries (numbers given above the bars) and total numbers of visits to each estuary (bars) by *Pomadasys commersonnii* tagged in the Kariega ( $n = 12$ ) and Bushmans ( $n = 5$ ) estuaries and that subsequently undertook sea trips. The estuaries monitored were the Kromme (KR), Gamtoos (GA), Swartkops (SW), Sundays (SU), Bushmans (BU), Kariega (KA), Kowie (KO) and Great Fish (GF) (after Dames et al. 2017).



**Figure 119.** Sandprawn densities along transects at different positions along the East Kleinemonde Estuary. The regression line (prawn density with distance from estuary mouth) and the locations of the 95% utilised distribution areas of the tagged spotted grunter (horizontal black lines situated at the top of the graph) are shown (after Maree et al. 2016).

the importance of estuarine habitats to this species. Unfortunately this makes the species vulnerable to overexploitation by anglers (Næsje et al. 2007).

In the temporarily closed East Kleinemonde Estuary, the long-term home ranges and movement dynamics of *P. commersonnii* have been assessed (Kerwath et al. 2005), particularly in relation to the distribution and density of their dominant prey within this system, viz. the sandprawn *Kraussillichirus kraussi* (Maree et al. 2016). Kernel home ranges (95% utilized distribution) of spotted grunter varied in size from  $26\text{--}165 \times 10^3 \text{ m}^2$  and were all located in the lower one-third of the 3.6 km-long estuary. There was no effect of season, the diel cycle, or fish length on the home-range estimates, but the distribution of sandprawn prey corresponded with the home-range distribution of tagged fish. Although *C. kraussi* distribution was highly variable within

and among transects and depth classes, sandprawns were most abundant in the lower region of the estuary (Figure 119). This corresponded to the home-range distribution of *P. commersonnii*, thus indicating that the home-range parameters of this fish are strongly influenced by their major prey (Maree et al. 2016).

#### **Zambezi shark *Carcharinus leucas***

This species is known to enter certain estuarine systems on a regular basis, with juveniles often using estuaries (e.g. St Lucia) as a primary nursery area (Bass et al. 1973). However, the exact movements of this species in estuaries was unknown until an adult female measuring 400 cm total length was tagged with an acoustic transmitter in the Breede Estuary (Figure 120) and continuously tracked for 43 hours (McCord & Lamberth 2009). During this time the shark swam as far as

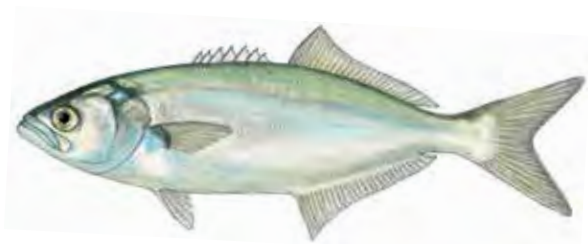


**Figure 120.** An adult *Carcharinus leucas* being tagged in the Breede Estuary (Photo: Alison Towner).

20 km up the estuary but also briefly exited the system for a distance of 2 km out to sea. Most of the time was spent between 5 and 13 km upstream of the estuary mouth. This shark, which was a record size for the species in southern African waters, appeared pregnant at the time of capture and may have been preparing to pup in the estuary (McCord & Lamberth 2009).

### Elf *Pomatomus saltatrix*

Thirty six adult *Pomatomus saltatrix* (Figure 121) were tagged with acoustic transmitters and released into the Langebaan Lagoon during 2006 and 2007 (Hedger et al. 2010). Detection patterns showed that most individuals remained within this estuarine lagoon and coastal embayment for the 30 month long study period. One individual was recaptured 21 months after being tagged off the east coast of South Africa, an along-shore migration of 1 760 km. This result suggests that residency within sheltered coastal habitats and estuaries is optional, with the evidence pointing to a possible west coast population spawning in the vicinity of Saldanha



**Figure 121.** *Pomatomus saltatrix* (© NRF-SAIAB).

Bay (Hedger et al. 2010) and a more migratory component spawning off the east coast of South Africa (van der Elst 1988). However, the evidence from the Langebaan study suggests that even the west coast population is capable of extensive migrations beyond the cool-temperate biogeographic region.

Within Langebaan Lagoon the *P. saltatrix* tended to move seaward during ebb tides, and occupy greater depths during the day when distances covered by the elf increased. In addition, most of the tagged and released individuals tended to remain within the inner embayment but there was a long-term trend of movement from the lagoon into the bay (Hedger et al. 2010).

## Genetic studies

Genetic mixing of estuary-associated marine fish species can occur as a result of adults from various regions coming together for spawning purposes or it can occur at the egg and larval stage. In this latter scenario the coastal water currents disperse the fertilized eggs and preflexion larvae far from the original spawning site, with the postflexion larvae or early juveniles recruiting into new estuaries when compared to the parental stock. Although the exact mechanism for genetic mixing for most species may be obscure, mainly because the adult movements and spawning grounds for most marine fish taxa are unknown, the available evidence suggests that gene flow between estuary-associated marine fish populations is strong.

In the case of the estuarine bream *Acanthopagrus vagus* it was anticipated that strong isolation of the various estuary-dependent populations by distance would reduce connectivity and therefore genetic mixing. However, a preliminary investigation into the geographic genetic structure of this

species along the southern African coast (Figure 122) using mitochondrial DNA cytochrome b sequences revealed no differentiation among the estuarine populations (Oosthuizen et al. 2016). In addition, the star-like genealogy is consistent with a recent population expansion event and there was some evidence to suggest that the *Acanthopagrus* species along the southern African coast is becoming locally endemic.

A more detailed study on the genetic stock structure and level of gene flow was conducted on the white steenbras *Lithognathus lithognathus* using mitochondrial DNA sequencing and genotyping of microsatellite loci in the nuclear genome (Bennett et al. 2017a). Genetic diversity was found to be high throughout the known core distribution of *L. lithognathus* and high levels of gene flow were also documented.

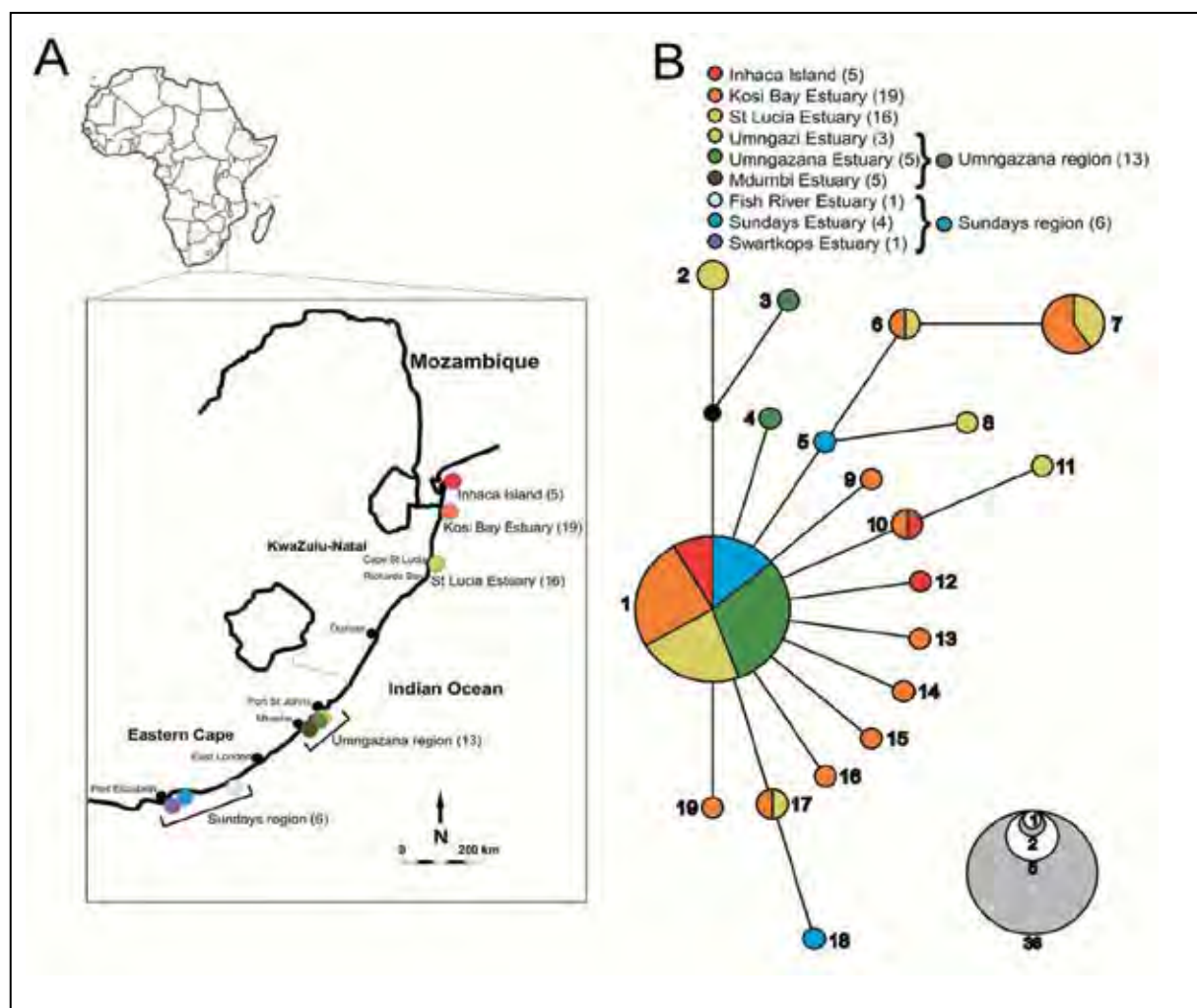
Indications are that this species exists as a single genetic stock, with high levels of gene flow throughout its distribution (Bennett et



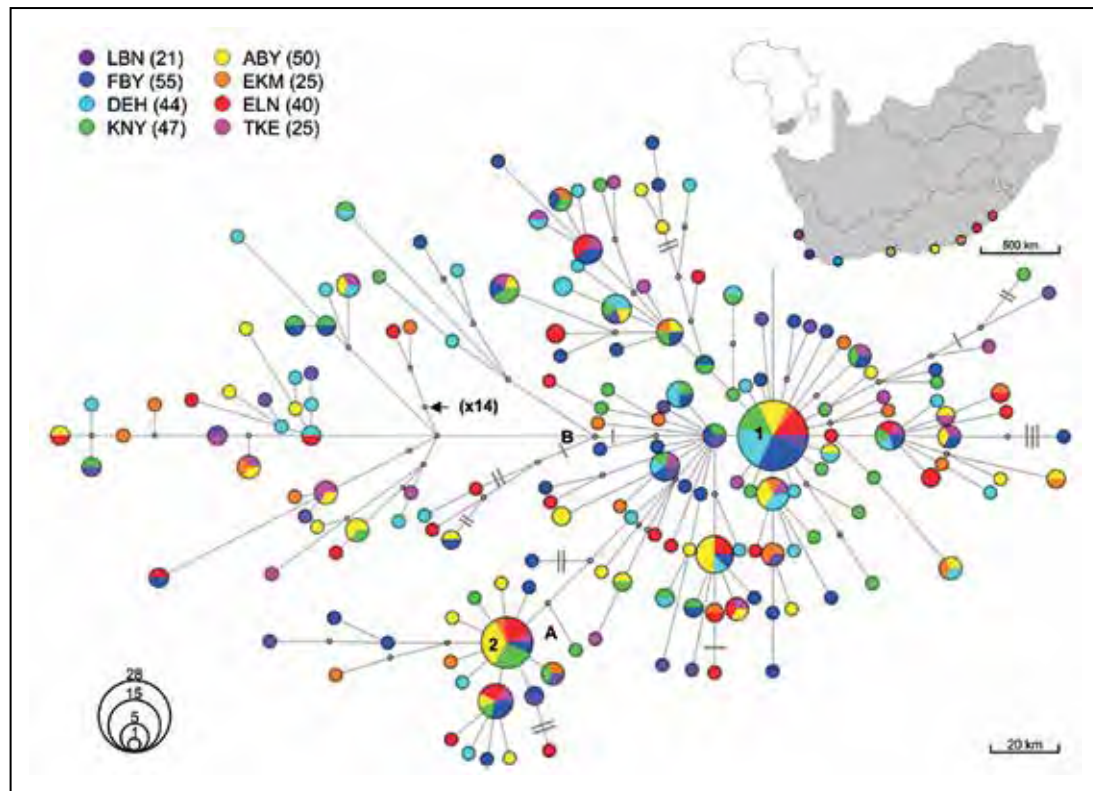
al. 2017a). This result implies that the limited movements by juvenile and subadult white steenbras in association with estuaries and adjacent coastal area, as evidenced by acoustic tracking studies (Bennett et al. 2012, 2015), are not applicable to adults which may move considerable distances during the spawning season (Bennett et al. 2017b).

The star-like topology of the *L. lithognathus* haplotype network (Figure 123), with few common and many rare haplotypes, indicates that this species is undergoing population expansion.

Such expansions are likely a result of climatic oscillations during the Pleistocene period and indications are that the white steenbras population expansion occurred within the last 20 000 years (Bennett et al. 2017a) when temperature increases during the Holocene resulted in a rising sea level and increased estuarine habitat availability for this species. These results suggest that current global warming is not a threat to *L. lithognathus* since previous warming events, which resulted in a higher sea level than at present, did not adversely affect this species.



**Figure 122.** (A) Map of southern Africa indicating the nine sampling localities for the 59 samples of *Acanthopagrus vagus*, and (B) Haplotype network summarizing genealogical relationships among 19 mtDNA ND2 haplotypes identified from 733 bases in the *A. vagus* samples. The colours represent sampling localities, shown with the sample size per locality in parentheses, along the southern African coast. Haplotypes are represented by circles and the size of each circle represents the number of individuals sharing a specific haplotype, scaled according to the provided key. Each line connecting the different haplotypes represents one mutation and black dots represent unsampled/extinct haplotypes. The number next to each circle represents the haplotype number (after Oosthuizen et al. 2016).



**Figure 123.** Minimum spanning haplotype network showing genealogical relationships among 174 haplotypes identified from the mitochondria control region sequences of 307 white steenbras from the eight sampling localities (sample sizes in parentheses). Common haplotypes 1 and 2 are labelled. A is a second cluster centred around the main haplotype 2, while B is a long branch extending from the main clade, and included haplotypes different from haplotype 1 by up to 22 mutations. Sizes of circles are proportional to haplotype frequencies. Colours identify localities and branches indicate one mutational step, with additional steps indicated by transverse bars ( $\times 14$  indicates 14 mutational steps). Intermediate nodes represent unsampled extant haplotypes or ancestral haplotypes (after Bennett et al. 2017a).

## Underwater video studies

Littoral zones within estuaries represent important nursery areas for many species of marine fish but often consist of a mosaic of small habitat patches that are fragmented throughout the estuarine landscape. Fish within small shallow patches of reef, bare sand and reed beds were examined using a remote underwater video within the temporarily closed East Kleinemonde Estuary (Becker et al. 2010).

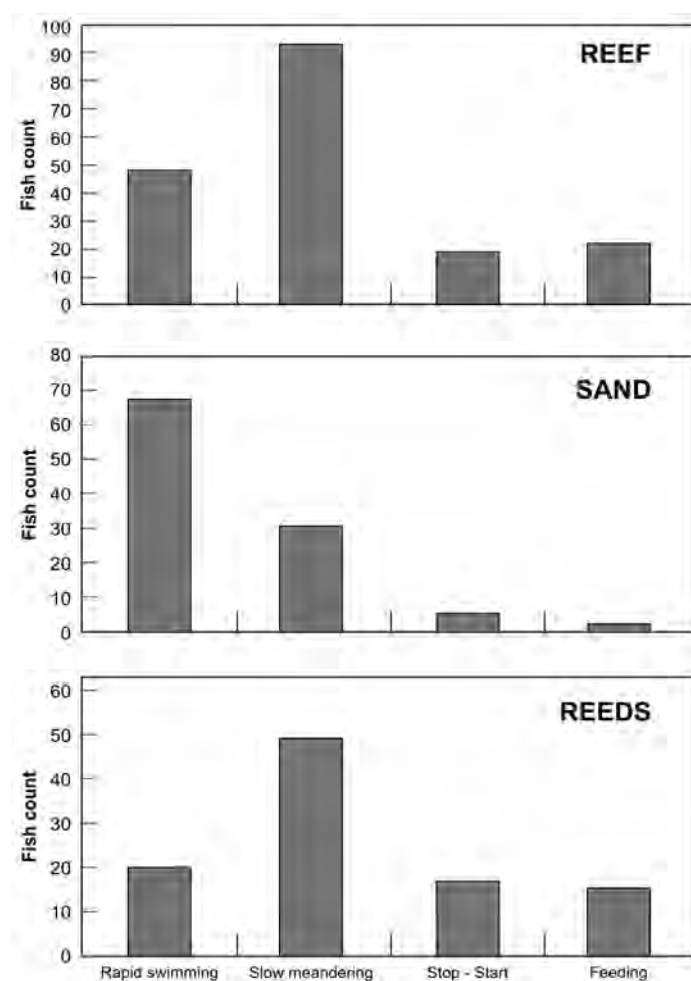
Five feeding guilds were identified in the above study. The omnivorous sparid *Rhabdosargus holubi* was present most often across all habitat types, while small shoaling zooplanktivores such as the clupeid *Gilchristella aestuaria* and atherinid *Atherina breviceps* were very abundant and widespread. While no significant differences in total fish abundance were recorded between the three

habitat types, the composition of assemblages changed according to habitat. Zooplanktivores had a higher affinity to reed habitats and the detritivores were more common in reef and bare sand areas (Becker et al. 2010).

Passive remote underwater camera footage also allowed for behavioural observations to be recorded under natural conditions. Distinct behavioural patterns associated with the different habitats were observed. Fish generally displayed rapid swimming behaviour over sand while slow meandering behaviour was common in both reef and reed habitats (Figure 124). The above study indicated that the value of various habitat patches within nursery grounds is not necessarily indicated only by fish abundance or assemblage composition but also by how these habitats are utilised.

An underwater video camera was also used to investigate the influence of small changes in water depth on selected fish taxa in sandy and eelgrass habitats in the tidal Bushmans Estuary. The camera was deployed to examine the fish assemblage at three eelgrass (*Zostera capensis*) edge and three sand sites over incoming spring and neap tides (Becker et al. 2012). Small changes in tidally driven water depth had significant effects on the abundance of Gobiidae and Mugilidae, with the former family decreasing, possibly due to an exit from the video area to shallower water, and the latter increasing with increasing tidal depth. These patterns were consistent at both the eelgrass and sand sites, as well as during spring and neap tidal cycles. Inconsistent differences were recorded in the abundance of other common fish taxa between the eelgrass edges and bare sand sites.

For a number of taxa there were distinct differences in swimming behaviour between those individuals associated with seagrass beds and those situated over bare sand. The behaviour patterns of the various fish taxa were very similar for spring and neap tides, so only neap tides are depicted in Table 13. Mugilidae, *Atherina breviceps* and *Rhabdosargus holubi* displayed overall 'rapid swim' behaviour over the sand sites, regardless of tidal regime, possibly due to increased vulnerability. However, when these same taxa were located along the edges of the eelgrass beds, the dominant behaviour was 'slow meander', with 'feeding' and 'start stop' behaviour also featuring in the analysis. The Gobiidae swim in a distinctive manner and exhibited a predominance of 'stop start' behaviour at all stages of the tidal cycle in both habitat types (Becker et al. 2012).



**Figure 124.** Count of behavioural categories for fish in each of the three habitat types in the lower reaches of the temporarily closed East Kleinemonde Estuary (after Becker et al. 2010).

Table 13. Percentage contribution of each behavioural category for the four most common fish taxa recorded in both sand and eelgrass habitats in the Bushmans Estuary over the four hours of the incoming neap tide. Italicized numbers in parentheses show the number of observations from which the percentage contributions were generated and the numbers in bold represent the dominant behaviour for each hour (after Becker et al. 2012).

Behaviour	Sand				Eelgrass			
	Hour 1	Hour 2	Hour 3	Hour 4	Hour 1	Hour 2	Hour 3	Hour 4
Mugilidae	(0)	(92)	(94)	(85)	(0)	(4)	(49)	(55)
Slow meander	0	27	21	33	0	0	<b>59</b>	<b>53</b>
Start stop	0	0	<b>52</b>	1	0	0	0	0
Rapid swim	0	<b>55</b>	27	<b>55</b>	0	0	18	27
Feeding	0	17	0	11	0	<b>100</b>	22	20
<i>Rhabdosargus holubi</i>	(0)	(19)	(38)	(32)	(2)	(16)	(39)	(67)
Slow meander	0	11	21	28	0	19	<b>62</b>	<b>61</b>
Start stop	0	5	5	0	0	13	10	10
Rapid swim	0	<b>63</b>	<b>58</b>	<b>66</b>	<b>100</b>	6	28	16
Feeding	0	21	16	0	9	<b>63</b>	0	12
<i>Atherina breviceps</i>	(11)	(21)	(16)	(17)	(35)	(15)	(4)	(12)
Slow meander	27	38	63	41	29	<b>73</b>	<b>50</b>	<b>83</b>
Start stop	0	0	6	0	26	0	25	8
Rapid swim	<b>73</b>	<b>62</b>	<b>31</b>	<b>53</b>	11	27	25	8
Feeding	0	0	0	6	<b>34</b>	0	0	0
<b>Gobiidae</b>	(74)	(29)	(17)	(19)	(23)	(26)	(17)	(11)
Slow meander	0	0	0	0	0	0	0	0
Start stop	<b>100</b>	<b>97</b>	<b>100</b>	<b>100</b>	<b>91</b>	<b>88</b>	<b>76</b>	<b>100</b>
Rapid swim	0	0	0	0	4	4	0	0
Feeding	0	3	0	0	4	8	24	0

## Underwater sonic imaging studies

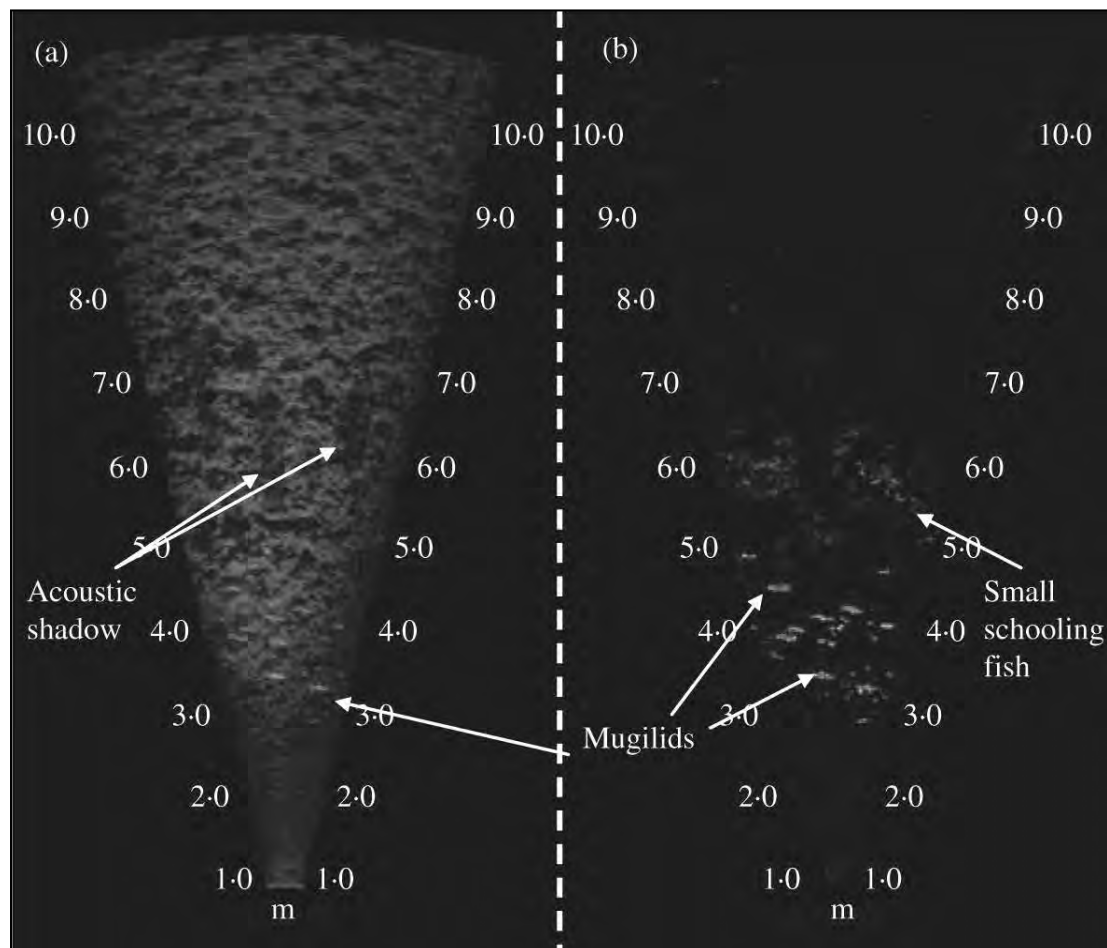
Understanding the size structure and distribution of fish assemblages within estuaries is fundamental to establishing how the ichthyofauna utilizes these systems. The littoral fish population of the East Kleinemonde Estuary was studied using a dual frequency identification sonar (DIDSON) which allowed for direct comparisons in the abundance, distribution and behaviour of a wide size range of fish in the littoral zone (Figure 125) of the system (Becker et al. 2011a). A later study investigated the depth distribution of different fish size classes along the length of the estuary channel (Becker et al. 2017, Figure 126).

Small shoaling fish <100 mm TL (Figure 125) were most abundant, while larger size classes 100-300 mm and 300-500 mm were less abundant but evenly distributed longitudinally within the estuary. Fish <100 mm were most abundant within the mouth region, with large fish >500 mm (probably piscivorous) similarly most abundant near the mouth, possibly due to the location of the smaller prey fish. Differential fish behaviour was observed among the three longitudinal sections, with small fish forming schools in areas of low turbidity and particularly in the presence of large predatory fish (Becker et al. 2011a).

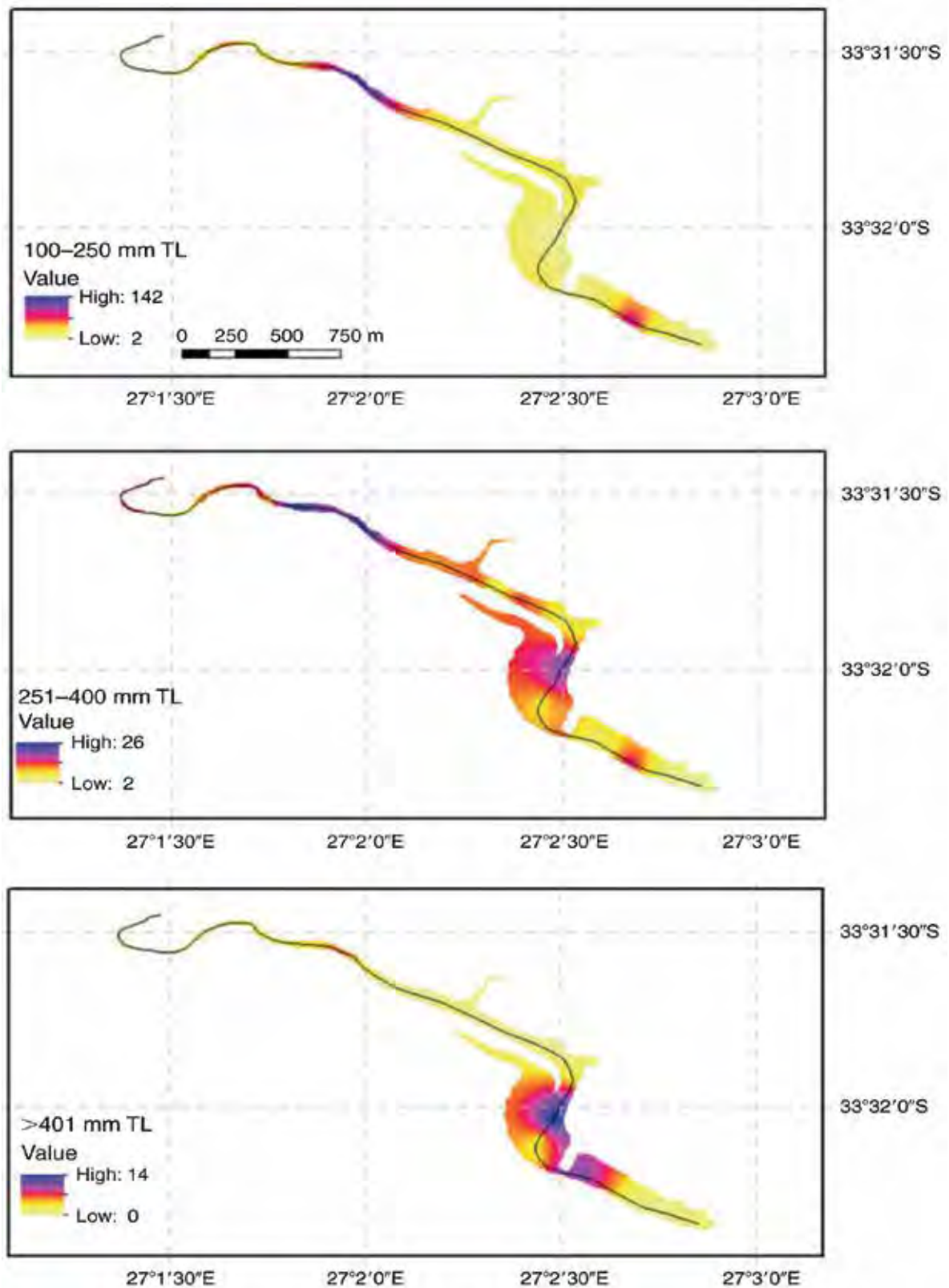


Shallow littoral habitats in estuaries have long been associated with playing a nursery role for small fish. Diel cycles have been linked to the redistribution of fish between habitats and may also influence the movement of various sized fish within the littoral zone of estuaries. Fine scale temporal movements of different size classes of fish onto a shallow (<0.7 m) littoral zone within the closed East Kleinemonde Estuary were examined continuously over 24h periods using a DIDSON. Fish within the size classes of 100-300 mm and 301-500 mm were more abundant in the littoral zone during twilight and at night compared to day, while the largest size class (>501 mm) was rare in this zone but showed no difference in abundance among the three diel periods (Becker et al. 2011b).

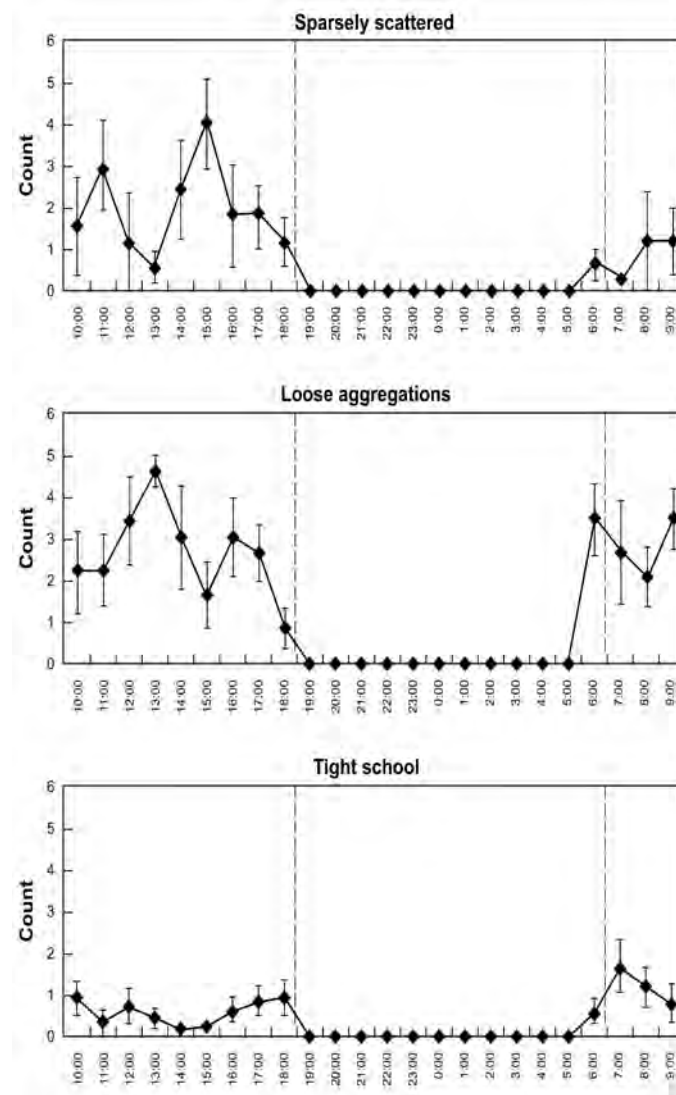
The strongest diel patterns were observed within the small fish (<100 mm) category, which was abundant in the littoral zone during the day but never observed in this habitat after dark (Figure 127). Daily commuting onto and off the littoral occurred within tight time periods (<1 h) that were synchronous with sunrise and sunset respectively. These movements may be linked to the abundance of zooplankton in surface channel waters at night and the avoidance of piscivores in deeper areas during the day. However, large predatory fish did sometimes enter the littoral, thus indicating that piscivorous fish will swim into shallow waters in search of prey. These results support the theory that shallow water habitats do provide a sanctuary for small fish (Paterson & Whitfield 2000a).



**Figure 125.** Two identical visual outputs from a section in the East Kleinemonde estuary using a DIDSON, with the static background (substrate) present (A) and with the background removed (B). The output provides a 'birds-eye view' of the fan shaped sector illuminated by the DIDSON (scale is in meters horizontally away from the DIDSON). A school of mugilids, identified based on their size and behaviour (200-300 mm TL) is highlighted, with their acoustic 'shadow' clearly visible in the image on the left. A group of small schooling species (<100 mm TL) can also be seen in the image on the right, i.e. once the background has been removed (after Becker et al. 2011a).



**Figure 126.** Interpolated surface showing the relative distribution of small (100–250 mm TL), medium (251–400 mm TL) and large (>401 mm TL) fish within the East Kleinemonde Estuary. The colour ramp shows the relative abundance of fish calculated from the mean numbers observed in each 100 m transect section, with purple representing higher abundances and yellow representing lower abundances of fish (note the varying scales for different fish size classes). The larger two size classes were clustered around deeper sections of the estuary. The black line shows the transit followed by the boat (after Becker et al. 2017).



**Figure 127.** Mean hourly frequency of occurrence across six sites ( $\pm$  SE) of small shoaling fish species for each of the three density categories within the littoral zone of the East Kleinemonde Estuary. Dashed lines indicate the timing of sunrise and sunset (after Becker et al. 2011b).

The DIDSON has also been used to document the abundance and direction of movement of fish  $>80$  mm TL in the temporarily open mouth of the small Birha Estuary during spring and neap tidal cycles. While the sizes of fish recorded were consistent across both tide cycles, the numbers of fish passing the camera was significantly greater during the smaller neap tides (Becker et al. 2016).

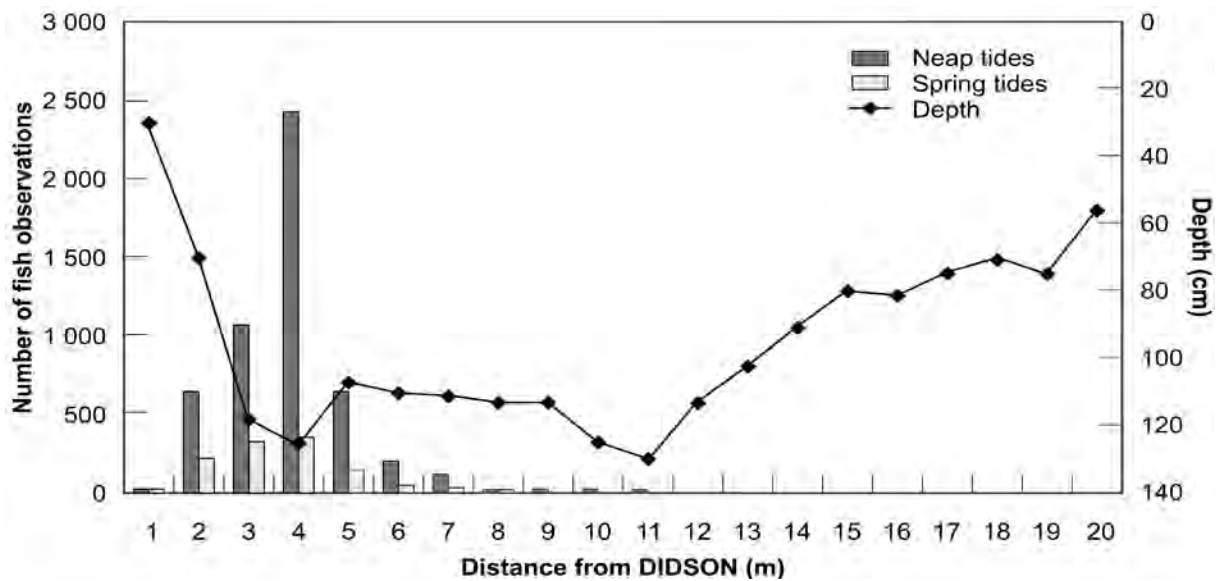
Interestingly, there did not appear to be any definitive fish movement in terms of the direction of tidal flow for either incoming or outgoing fish, i.e. fish were just as likely to be swimming against the tide as to be travelling with it. In addition, schooling behaviour was more pronounced for fish that were travelling into the estuary compared

to fish swimming towards the ocean (Becker et al. 2016).

Fish were mostly recorded within a 3 m wide section of the estuary, despite the channel being approximately 20 m in width (Figure 128). The section where most of these fish were observed was next to a steep rocky sill that bounded the north-eastern bank of the channel and was also close to the deepest point of the channel cross-section (Figure 129). Swimming through the deeper section of the channel allowed fish to move lower down in the water column, thereby avoiding surface predators such as birds and also provided more water volume to evade approaching piscivorous fish predators.



**Figure 128.** Position of the DIDSON (yellow arrow) on the north-eastern side of the Birha Estuary mouth recording fish movements into and out of the system. Most fish swam close to the rocky shelf on the nearside of the photo and avoided the more open sandy area in the central and south-western side of the mouth (see Figure 129 below) (Photo: Alan Whitfield).



**Figure 129.** Cross-section of the Birha Estuary mouth region showing the depth profile (solid black line) and observed number of fish in 1 m increments across the mouth for neap (dark grey bars) and spring (light grey bars) tidal cycles (after Becker et al. 2017).



## 2.7 FISH FORAGING AND ASSOCIATED FOOD WEBS

An understanding of the diets, feeding ecology and trophic interrelationships of fishes in estuaries is fundamental to fisheries management, as well as the development of sound coastal conservation plans. Without detailed knowledge of the often complex food requirements, feeding behaviour patterns, and predator-prey relationships, it is impossible to describe how estuarine fish assemblages function, nor is it possible to interpret or predict changes that might result from any natural perturbations or human impacts. The collection of data on the food and feeding ecology of fishes is therefore of vital importance to those concerned with fisheries management and environmental conservation.

Estuaries have long been recognised as highly productive ecosystems as well as having a prime role as feeding areas for fishes. In order to understand the functioning of these habitats, it is necessary first to describe the trophic interactions within estuaries and then to quantify them where possible. Hence, it is necessary to give the present state of knowledge on the relationships and interactions between fish species (both as juveniles and adults) within estuaries and the interactions between fish and their prey. In addition, the responses of fishes to top piscivorous predators such as birds and crocodiles also needs to be explored.

A prime objective of this section is to examine the ways in which fishes in estuaries interact both with their habitat and with each other, particularly in relation to food and feeding. The ways in which diet and feeding may change with age are discussed, with this aspect being particularly significant with regard to life-history strategies. For example, estuaries are the nursery habitat for many species and hence provide food for at least the first year's growth of individual fish before there is movement to other waters where food type and availability may be very different.

Selected examples are used to illustrate the diverse feeding specializations and dietary flexibility employed by different groups of fishes. Examples of the various trophic levels, from herbivorous to piscivorous, are surveyed and

examples are given of food web structures in selected estuaries and how these may be influenced by different primary producers, as well as by environmental perturbations. The use of stable isotopes in interpreting these trophic structures is emphasized and examples are presented to illustrate how modern techniques have progressed our understanding of fish feeding ecology in estuaries.

### Foraging behaviour and food intake

#### Prey detection

In order to determine the functioning of estuarine habitats and to create food webs, it is necessary to consider prey availability both in terms of abundance and also whether the fish can locate them. Estuaries are often naturally turbid systems and the ability of fishes to detect prey in water where visibility is poor is very important. Species such as *Galeichthys feliceps* have long barbels that perform tactile and chemo-sensory functions, whereas others such as *Argyrosomus japonicus* can use olfactory and lateral line sense organs to detect prey (van der Elst 1988). Whilst some species such as *Platycephalus indicus* are ambush predators lying in wait for their prey, most fishes search for food.

If the food is patchy, it can be an advantage to search in a social group and, while much searching appears to be random, regular diel vertical migrations may help predators to find their prey if it is concentrated in food-rich strata at thermoclines or haloclines. The vertical migrations of obligate and facultative zooplankton have differential results in terms of their position within the water column during the day and night. Obligate forms such as calanoid copepods leave the day-time mid-water areas and congregate near the water surface at night, whereas facultative forms such as amphipods move from the day-time benthic habitat into mid-water areas during the night.

Filter feeding fish species such as *Gilchristella aestuaria* do not have to detect the prey by sight where zooplankton densities and water turbidities are high (Blaber 1979). However, under conditions where low numbers of zooplankton are present and water clarity is high, this species is

forced to use sight to hunt small invertebrates associated with submerged plants (Blaber et al. 1981).

Some large demersal fish species such as *Lithognathus lithognathus* and *Pomadasys comersonnii* appear to select a particular section of the substratum and then plunge their mouthparts and a large section of their head deep into the sediment as they seek out infaunal prey such as prawns, crabs and polychaete worms. By using the gill opercula and buccal cavity as a form of modified 'bellows' they are able to institute a pumping action that forces a jet of water through the mouth, thus 'blasting' invertebrates from their burrows and are then much easier to catch (van der Elst 1988).

### Feeding periodicity

Many fish species in estuaries appear to have the ability to forage during both the day and night but the majority tend to feed mainly diurnally. Whilst this pattern is to be expected for predatory fish species using sight to locate their prey, it is not so obvious for taxa that do not rely on sight for feeding purposes.

Examples of fish feeding periodicity from southern African estuaries include mugilids at St Lucia which tended to have maximum stomach contents between 10h00 and 18h00 (Blaber 1976), sparids in East Kleinemonde, St Lucia and Kosi estuaries feeding mainly between 10h00 and 20h00 (Blaber 1974b, 1984), a clupeid in the Swartkops Estuary between 06h00 and 18h00 (Talbot & Baird 1985a), gerreids in the Kosi system also between 06h00 and 18h00 (Cyrus & Blaber 1984b), carangids in KwaZulu-Natal estuaries between 08h00 and 18h00 (Blaber & Cyrus 1983), and sphyraenids in the Kosi system between 09h00 and 18h00 (Blaber 1982a).

The above taxa include detritivores, omnivores, zooplanktivores, zoobenthivores and piscivores, yet most species appear to favour a mainly diurnal feeding regime. Where both summer and winter feeding periodicity studies have been conducted, similar patterns have emerged but food consumption during winter was always much lower than in summer (e.g. Talbot & Baird 1985a, Whitfield 1984).

One of the few families to reveal a very different trend were ambassids in the Kosi and St Lucia estuarine systems, where peak foraging often occurred during nocturnal and twilight periods, mostly between 18h00 and 06h00 (Martin & Blaber 1983). *Atherina breviceps* in the Bot Estuary also attained peak stomach fullness during nocturnal hours (22h00-24h00) and showed very little evidence of feeding activity during the day (Bennett & Branch 1990). Ambassids and *A. breviceps*, like *Gilchristella aestuaria*, are mainly zooplankton predators, yet the former two taxa exhibit completely different foraging patterns from the latter species.

A detailed study of the feeding periodicity by *Rhabdosargus holubi* in the West Kleinemonde Estuary (Figure 130) revealed that consumption of plant material occurred throughout the daylight hours and reached a peak in late afternoon. However, invertebrates were only eaten in the morning, despite being available throughout the day (Blaber 1974b). Underwater observations using SCUBA revealed that both small and large shoals (10-400 individuals) foraged along the edges of the *Ruppia* beds, biting off pieces of plant material. The lack of any food consumption at night was confirmed using underwater torches which showed that by 21h00 most *R. holubi* were inactive and resting on the bottom, apparently asleep (Blaber 1974b). At night they did not shoal and were mostly evenly spaced.

### Food intake

Food consumption of six small resident estuarine species was studied in Botrivierlei, an estuarine lake. These data revealed that this group of fishes had an annual invertebrate intake of approximately  $6 \text{ g m}^{-2}$  or an average of  $16 \text{ mg m}^{-2}$  per day (Bennett & Branch 1990). In addition, 17% of invertebrate secondary production was consumed by these species during the closed mouth phase, indicating that under these conditions there was no shortage of food. However, a large decline in invertebrate biomass occurred when the estuary mouth opened and extensive areas of the littoral zone were exposed (de Decker 1987), whereupon these fish consumed almost 90% of the remaining invertebrate secondary production. As some of

the marine migrant fish species in this estuary also prey extensively on aquatic invertebrates, it is likely that competition for food will be intense during the open mouth phase. A similar situation has been recorded in temporarily open /closed estuaries around the coast where invertebrate stocks decline considerably during the outflow and tidal phase in these systems (Perissinotto et al. 2010).

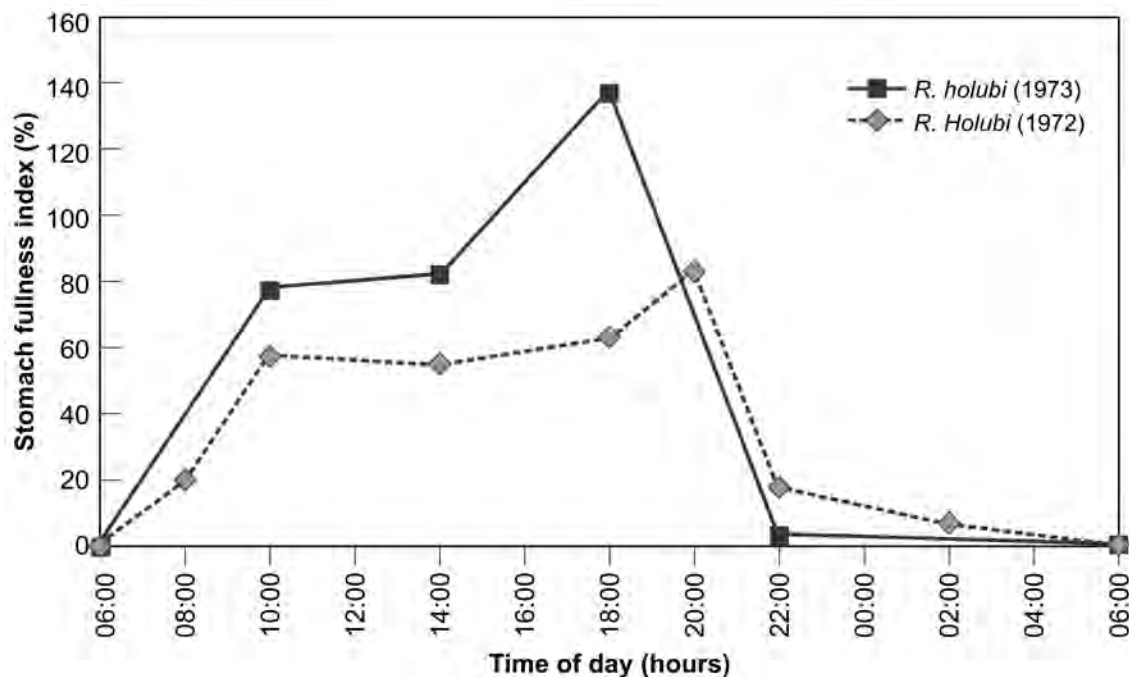
A wide variety of models exist, both for the determination of the gastric evacuation rate and the calculation of food consumption by fish. Several field approaches have been carried out, with the estimated daily food consumption based on fish size usually over-riding seasonal effects. For example, summer food consumption by juvenile *Rhabdosargus holubi* (51-154 mm SL) was estimated to be approximately 5.6% of body mass (Whitfield 1984), whereas early juveniles (27-38 mm SL) of the same species consumed approximately 8.5% of body mass per day during winter (Vumazonke et al. 2008). Similarly juveniles (52-131 mm SL) of *Monodactylus falciformis* consumed approximately 2.5% of their body mass during summer (Whitfield 1984), whereas early juveniles (27-38 mm SL) consumed approximately 8.9% of their body mass per day during winter

(Vumazonke et al. 2008). It appears therefore that body size is a more important driver of food consumption than water temperature, although both are important in influencing annual food intake.

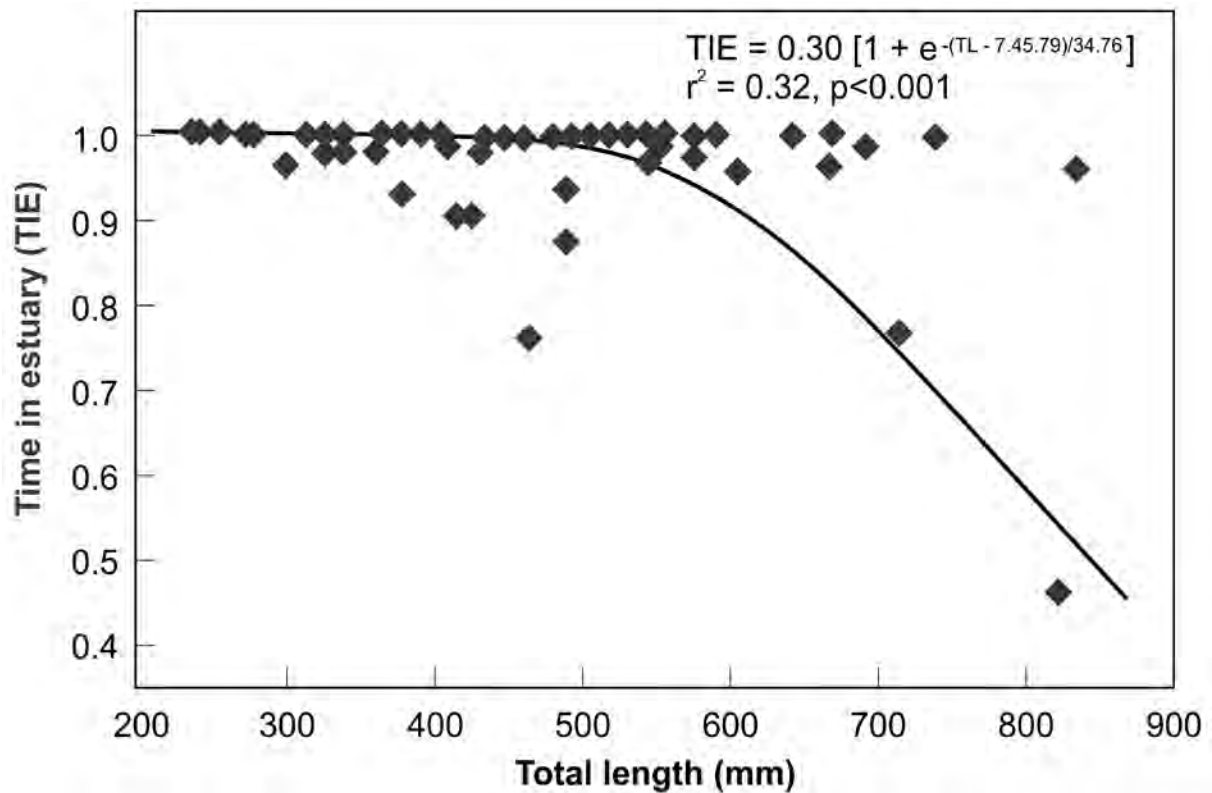
### Feeding migrations

The term 'feeding migration' used here refers to movement from one niche towards another in order to find food. Migration can be linked to different life stages or is the result of competition between other fish or with predators such as birds and mammals.

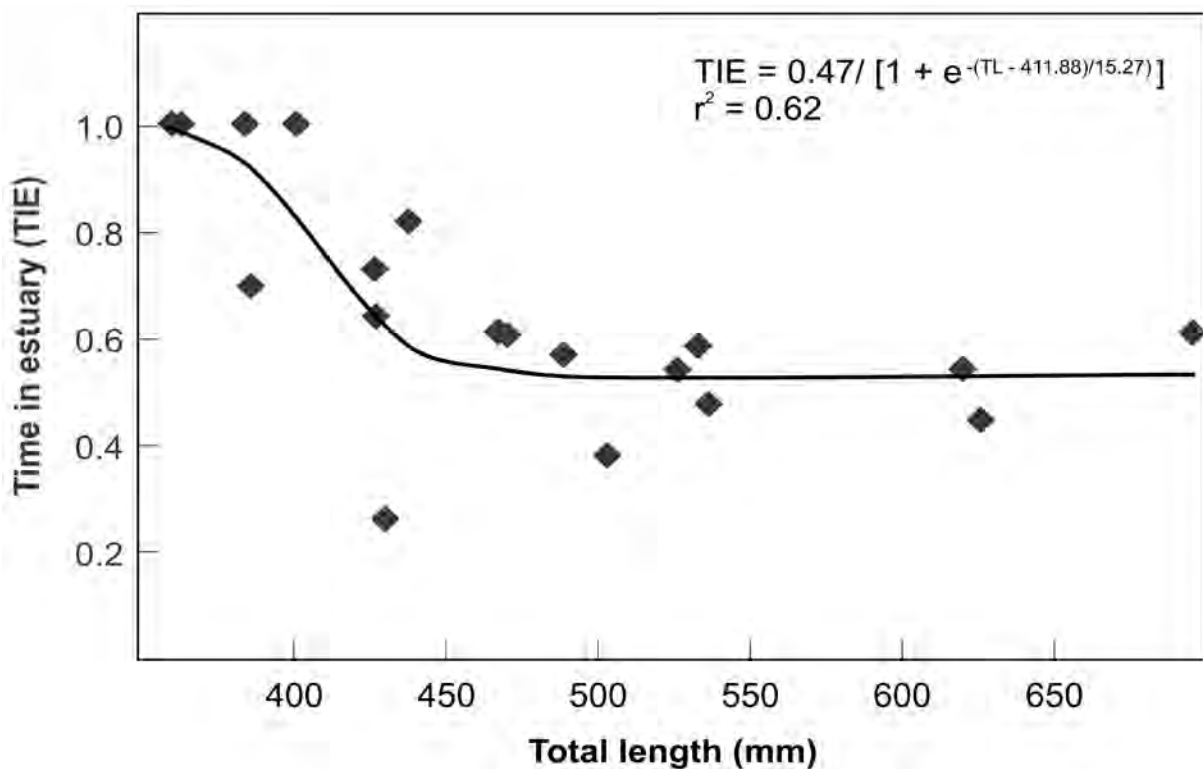
Together with seasonal and estuary-wide migrations, tidal migrations within estuaries are a well-known phenomenon where fish species use the tides in order to forage longitudinally up or down an estuary, or on intertidal flats, or to enter intertidal saltmarsh or mangrove creeks. Some species perform tidal feeding migrations from the estuary channel into the intertidal creeks where they find high numbers of a range of possible prey items, e.g. fish species entered intertidal saltmarshes in the Knysna Estuary at high tide in order to feed on invertebrate resources in these habitats (Le Quesne 2000) or fish entering mangrove habitats for the same purpose (Muller & Strydom 2017).



**Figure 130.** Feeding periodicity of juvenile *Rhabdosargus holubi* in the West Kleinemonde Estuary over 24 h periods in March 1972 and April 1973 (after Blaber 1974b).



**Figure 131.** Changing ecosystem occupation and therefore food resources for *Argyrosomus japonicus* from the Sundays Estuary. This graph indicates the relationship between fish size and the proportion of time spent in the estuary (TIE) and the balance in the marine environment (after Childs et al. 2015).



**Figure 132.** Changing ecosystem occupation and therefore food resources for *Pomadasys commersonii* from the Great Fish Estuary. This graph indicates the relationships between fish size and the proportion of time spent in the estuary (TIE) and the balance in the marine environment (after Childs et al. 2008c).



In the Mhlanga Estuary, the distribution of the majority of fishes was found to be closely associated with that of their dominant food, except for the Mugilidae, where dominant sediment particle sizes influenced family composition in the different reaches (Whitfield 1980a). Zoobenthos feeders such as *Pomadasys commersonnii*, *Leiognathus equula* and *Gerres methueni* were found to be most common in the lower reaches of the estuary where benthic invertebrate stocks were highest. In the upper reaches, where benthic floc was most readily available, the detritivorous *Oreochromis mossambicus* was found to be most abundant. Such distribution patterns imply deliberate movements by fishes to those areas or habitats where food is most plentiful. Zooplanktivorous species such as *Gilchristella aestuaria*, however, showed no distinct zonation pattern in the Mhlanga Estuary, therefore reflecting the relatively even distribution of zooplankton throughout the system (Whitfield 1980a).

Acoustic telemetry studies in a number of Eastern Cape estuaries have provided proof for fish undertaking directed movements and migrations in relation to available food resources, e.g. *Lithognathus lithognathus* was shown to undertake diel movements from deeper channel areas during the day onto shallower sand banks at night to feed (Bennett et al. 2012). Similarly *Argyrosomus japonicus* has been described 'riding the tide' to follow and prey on fish and invertebrates moving up and down the Great Fish Estuary (Næsje et al. 2012). *Pomadasys commersonnii* also 'rides' the tide during foraging excursions (Childs et al. 2008c).

Examples of migrations that result in major ecosystem shifts and therefore a transformation in the type of food sources available to the fish are provided by telemetry studies covering different life stages of each species, e.g. *A. japonicus* and *P. commersonnii* become more marine and less estuarine with increasing size (Figures 131 and 132).

### Ontogenetic changes in fish diets

The diets of most estuary-associated fish species change with growth. The larvae and postlarvae of most fish associated with southern African

estuaries are planktivorous (Whitfield 1985). The timing and extent of changes in food and feeding ecology varies according to the species and is often associated with changes in life style or habitat. Ontogenetic shifts between the postlarval and juvenile diets have been reflected in southern African estuaries, with vertically migrating calanoid copepods appearing to be the trigger that attracts postlarval fishes towards the substratum (Blaber & Whitfield 1977a).

For many species in estuaries the diet of juveniles is also markedly different from that of the adults. The actual timing of switches in diet usually relates to juveniles becoming sub-adults or adults, and leaving estuaries, or may be related to changes in morphology of jaws or teeth or size. Perhaps one of the strongest drivers in dietary change are the very different food resources in estuaries and the sea.

For most species, larger fish target larger prey and hence there will be a gradual change in the type and size of prey as the fish grows. In the following sub-sections selected examples are used to examine how ontogenetic changes in diet enable species to utilise or maximise their use of food in estuarine habitats.

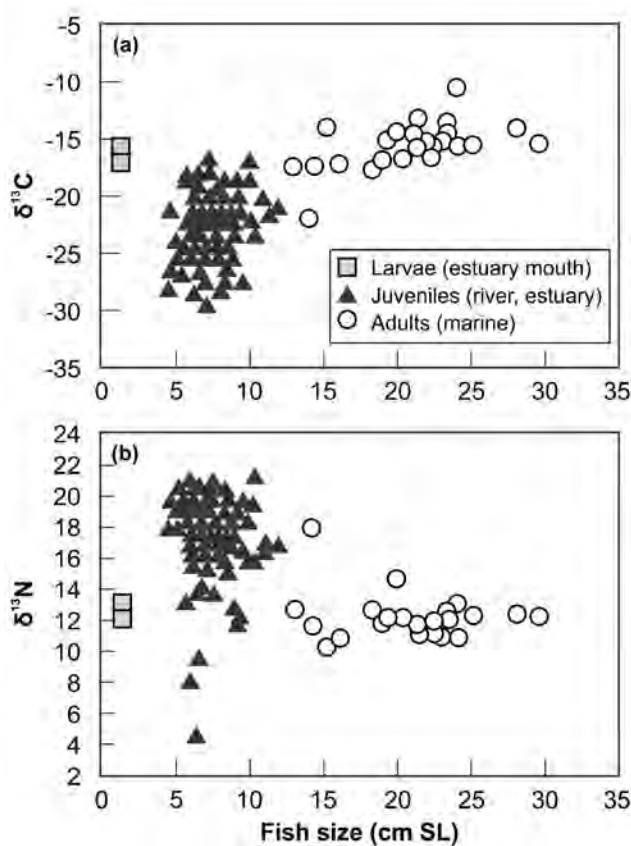
### *Sillago sihama*

In some fish species the ontogenetic dietary shift may be influenced by the abundance and type of prey. For example, the diet of *Sillago sihama* in Richards Bay, Durban Bay and Mlalazi Estuary changes from planktonic prey (mainly larvaceans and copepods) to benthic crustaceans, polychaetes and bivalve siphon tips at about 60 mm in length (Weerts et al. 1997).

Although the prey consumed by *S. sihama* from the above three estuaries was similar, the timing of the change to benthic foods differed. Fish from Mlalazi began feeding on benthos at a smaller size than those from Richards Bay and Durban Bay (Weerts et al. 1997). The delay in switching to a benthic diet and a longer planktivorous phase in Richards Bay and Durban Bay may be advantageous due the presence of very high densities of plankton with high calorific value within these systems. Alternatively the poor zoobenthic stocks and deeper waters in the

Table 14. Percentage frequency of occurrence of food items in the diet of *Rhabdosargus holubi* from the Kowie Estuary and river, and adjacent marine environment (modified from Carassou et al. 2016). Only food items comprising 5% or more for one of the life cycle categories are included in this analysis. Illustrations (not to scale) of an adult, juvenile and late postflexion larva of *R. holubi* are also shown.

Food <i>Fish mean size (mean ±SD)</i>	Larvae <i>1.1 ± 0.1</i>	Juveniles <i>7.3 ± 1.5</i>	Adults <i>21.1 ± 4.4</i>
Copepods (crustaceans)	100	1	0
Filamentous algae	0	78	0
Gastropods (molluscs)	0	5	75
Cirripeds (crustaceans)	0	1	55
Amphipods (crustaceans)	0	36	0
Macrophyte material (detritus)	0	27	5
Holothuroids (echinoderms)	0	0	20
Bivalves (molluscs)	0	9	15
Hydrozoans (cnidarians)	0	0	15
Isopods (crustaceans)	0	15	0
Polychaetes (annelids)	0	11	5
Chironomids (insects)	0	10	0
Ophiuroids (echinoderms)	0	0	10
Brachyurans (crustaceans)	0	5	0
Macrurans (crustaceans)	0	3	5



**Figure 133.** (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values measured in *Rhabdosargus holubi* muscle tissue as a function of fish size in the Kowie river, estuary and adjacent marine environment (after Carassou et al. 2016).

disturbed (dredged) harbour environments may have delayed the benthic switch by *S. sihama* in these particular habitats.

### *Rhabdosargus holubi*

This sparid is endemic to south-east Africa where the juveniles occur mainly in estuaries and the adults at sea. The diet of postflexion larvae comprises mainly zooplankton (Whitfield 1985, Table 14) whereas juveniles usually consume more than 50% (often up to 90%) aquatic macrophytes by weight, with the remainder consisting mainly of small crustaceans and bivalves (Whitfield 1984). The fish cannot, however, digest the vegetation eaten due to the absence of a cellulase or a method of breaking up the plant tissue. Therefore the plant material passes through the gut in an undigested state (Blaber 1974b). Epiphytic diatoms are, however, removed from the plants in the stomach and are subject to digestion (Sheppard et al. 2012). Diatoms may form up to 50% of the weight of plants eaten. It would thus appear that during the juvenile phase of its life history which is spent in estuaries, *R. holubi* is an omnivore with a marked preference for plant material covered with epiphytes.

The migration of *R. holubi* to the sea at the onset of maturity is accompanied by a change in tooth structure and a marked reduction in the amount of plant material in its diet (Buxton & Kok 1983). The tricuspid teeth of the juveniles are well adapted to cutting off pieces of macrophyte, but less useful for feeding on animal prey with hard exoskeletons. As the species grows, the teeth become more molariform and *R. holubi* switches to a diet mainly of bivalve molluscs and barnacles (Buxton & Kok 1983). It appears therefore, that the food requirements of both the juveniles and adults largely determine when the species enters and leaves estuaries and that this change is paralleled by a change in dentition.

*Rhabdosargus holubi*  $\delta^{13}\text{C}$  values from the Kowie system in the Eastern Cape also indicated a clear spatial gradient in the origin of food sources assimilated across habitats, with increasing  $\delta^{13}\text{C}$  along the freshwater-marine continuum (Figure 133). What is also noteworthy is the similarity in both the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signals of *R. holubi* larvae

and adults, with both life stages being trophically tied to marine resources. Within the Kowie Estuary and river, the  $\delta^{13}\text{C}$  ranges of sources and fish overlapped within each habitat along this continuum (Carassou et al. 2016), thus illustrating the fidelity of *R. holubi* to specific habitats. By consuming prey in a particular habitat before migrating, either permanently or temporarily to another habitat, *R. holubi* participates in allochthonous fluxes among riverine, estuarine and coastal marine environments.

### Mugilidae

The diets of juvenile mullet undergo a series of ontogenetic changes when they first enter estuaries at about 10 mm SL (Blaber & Whitfield 1977a). The 0+ mugilids change their feeding habits in the following sequence; zooplankton to zooplankton in the benthos (10-15 mm), zooplankton in the benthos to meiobenthos (10-20 mm), and meiobenthos to sand particles and associated microbenthos (15-25 mm). All mullet species show a similar pattern of change in diet to that of *Planiliza macrolepis* (Figure 134).

Juvenile mullet in estuaries prefer water less than 1 m deep and, since much of the estuarine zooplankton is in, on or near the bottom during the day, the fish are able to capture zooplankton from the benthos. It is a short step from feeding on vertically migratory zooplankton at the benthic stage to ingesting meiobenthic fauna, detritus, benthic floc and microphytobenthos. Once the juvenile mullet are feeding on the benthos, the number of sand grains increases (Figure 135) and microbenthic foods associated with sand grains become overwhelmingly dominant (Blaber 1976).

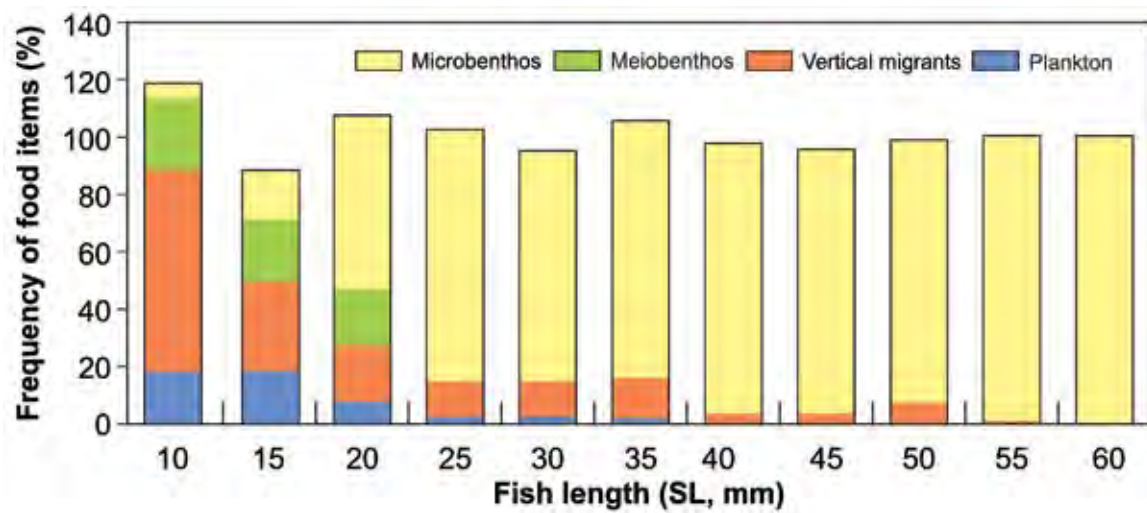
### Foraging specialisations

The extraordinary array of feeding adaptations and mechanisms in fishes allows them to exploit almost all available sources of food. A rich variety of foods exist in estuaries because of the diversity of habitats and the interfaces with freshwater, marine and terrestrial ecosystems. However, there may be large fluctuations in the type and numbers of prey available. There are usually, for example, very marked differences between the sorts of

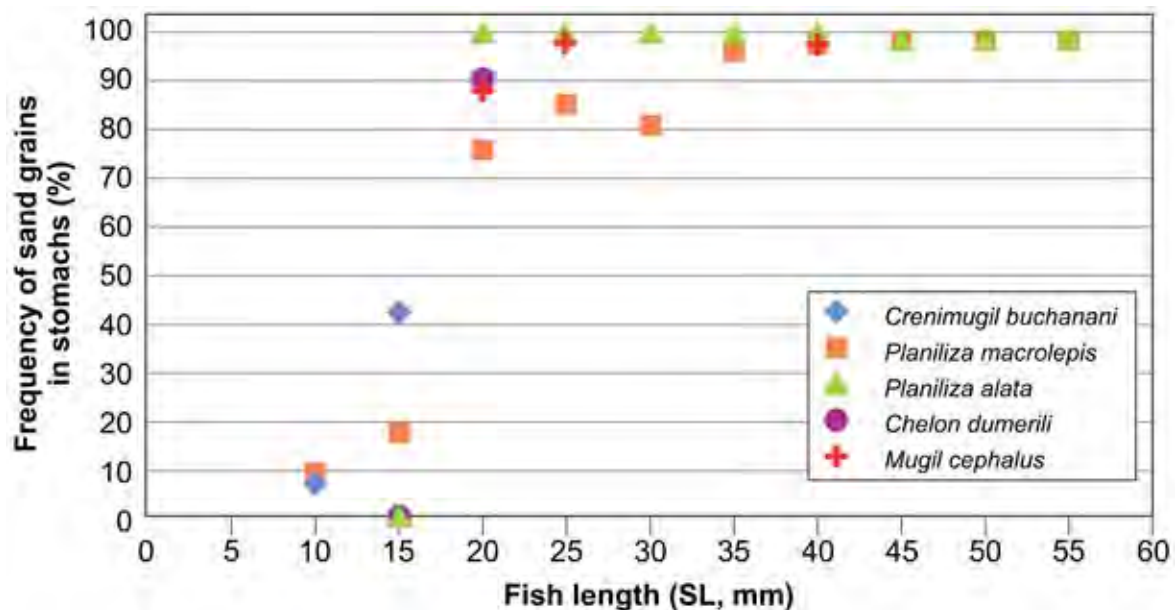
invertebrate prey living in estuarine waters near the mouth and those found in the low salinity headwater reach.

Although most fishes feed on a limited range of prey types, dietary flexibility is a feature of many families. Such flexibility confers important advantages in terms of both fish survival and mobility in estuaries. Nevertheless, there is also considerable scope for dietary specialisation, with the following examples illustrating that common and often

abundant estuarine fish taxa include both highly specialised feeders and those that have more general diets. In both cases the adaptive significance is emphasized. It is evident that, although particular groups may have specialisations enabling them to feed on or capture particular prey, they are not limited to these prey, and are able to switch to other foods if it is necessary or advantageous to do so. The following fish family examples emphasize these issues.



**Figure 134.** Ontogenetic changes in diet with increasing fish length for early juvenile *Planiliza macrolepis* (adapted from Blaber & Whitfield 1977a).



**Figure 135.** The percentage frequency of sand grains in the stomach contents of five species of juvenile mullet from southern African estuaries (adapted from Blaber & Whitfield 1977a).



## Gerreidae

The Gerreidae are a characteristic component of estuarine fish communities in tropical and subtropical regions and show both feeding specialisations and dietary flexibility. As early juveniles between 10 and 20 mm SL, species such as *Gerres longirostris*, *Gerres filamentosus* and *Gerres methueni* prey mainly on copepods (Cyrus & Blaber 1983a). However, above 20 mm SL, an efficient protrusible jaw structure and suction pressure mechanism enables them to feed on a variety of prey on or just below the surface of the substratum (Cyrus & Blaber 1982b).

In a study of the feeding ecology of five species of *Gerres* in the Kosi Estuary of KwaZulu-Natal, Cyrus & Blaber (1983b) showed that they feed largely on the siphon tips of *Hiatula lunulata*, an abundant bivalve in this system. However, benthic sampling at the sites where siphons are dominant in the diet of *Gerres* showed that they were not the most numerous food item present, thus indicating a positive selection for this particular prey.

## Mugilidae

Almost all species of grey mullet are iliophagous and their diet consists largely of benthic floc, microphytobenthos, detritus, meiofauna and smaller epifauna (Whitfield 2016a). A 'cardiac' stomach and long alimentary canal for the digestion of diatoms and detrital material is characteristic of all mugilids (Marais 1980) and, despite the similar dietary composition, all species exhibit marked feeding specialisations that help reduce interspecific competition.

Ontogenetic changes in diet take place at a small size and, from a length of about 50 mm, the diets of juveniles and adults are the same (Blaber 1977). The food of mullet are items that occur most abundantly in shallow quiet waters, especially on substrata with a relatively high organic content. Such conditions are found mainly in estuaries where there is a high input of organic detritus from the river as well as autochthonous supplies. The substratum in such systems is frequently covered with layers of detritus as well as carpets of benthic diatoms and other microalgae in littoral areas. Mullet are well adapted to take advantage of this situation and forage by

taking up the surface layer of the substratum or by grazing on submerged rock and plant surfaces.

Bioturbators such as the sandprawn *Kraussillichirus kraussi* are strong ecosystem engineers that can influence benthic-pelagic coupling in estuaries by modulating energy flow from benthic primary producers (e.g. microalgae) to consumers (e.g. mullet). A laboratory mesocosm experiment conducted by Pillay et al. (2012) showed that increasing *C. kraussi* densities resulted in an increase in sediment turnover and caused reductions in microphytobenthos biomass. This burial of benthic microalgae and therefore the indirect reduction in food availability to *Chelon richardsonii* led to metabolic losses and reductions in growth for this fish species (Figure 136).

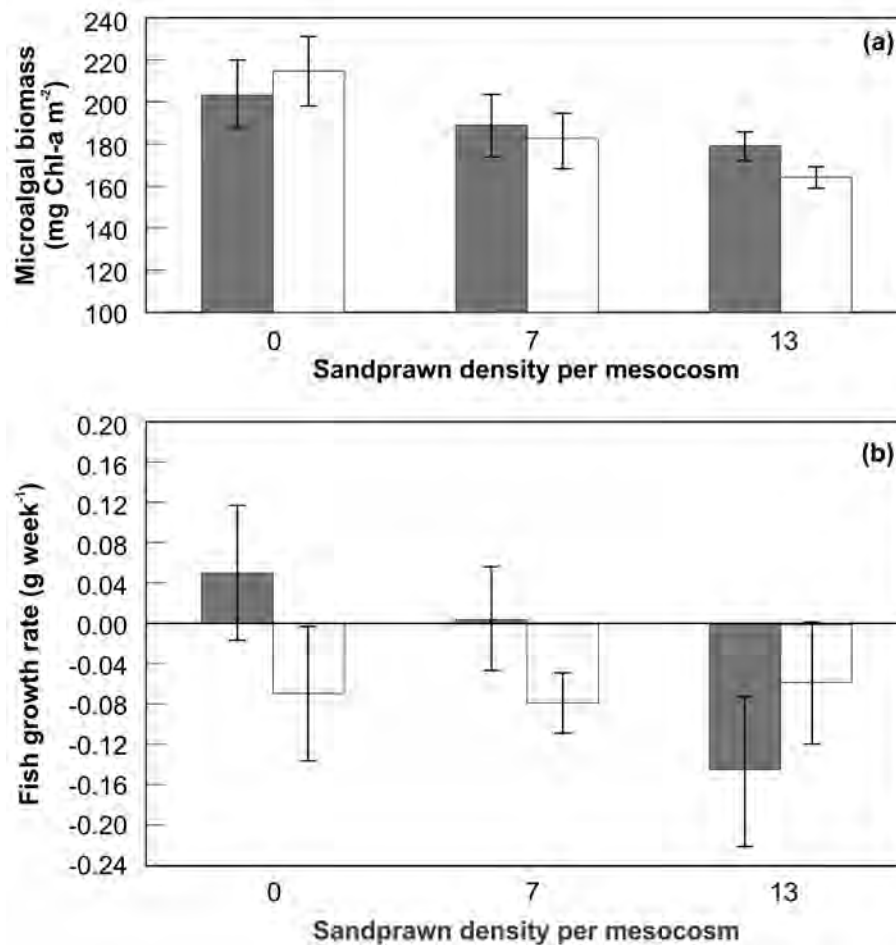
Most mullet species ingest large quantities of inorganic particles together with food items. Blaber (1976; 1977) showed that the most important dietary items of mugilids in local estuaries are foraminiferans, flagellates, pennate diatoms, unicellular and filamentous green algae, blue-green algae, ostracods, and a variety of small invertebrates, e.g. gastropods and harpacticoid copepods. The diets of the various species are similar, but vary from estuary to estuary, and are probably largely determined by the occurrence of particular food items on substrata of the preferred sand particle size for each species.

## Monodactylidae

Foraging can occur during both the day and night (van der Elst 1988) and anywhere within the water column. *Monodactylus argenteus* feed mainly on zooplankton, with individual selection of prey items being the dominant foraging mode. They also consume epibenthic and epiphytic organisms such as amphipods and filamentous algae (Day et al. 1981).

Copepods were the dominant component in the diet of postlarval (19-30 mm SL) *Monodactylus falciformis* in the Swartvlei Estuary whereas juveniles larger than 50 mm feed mainly on small crabs, isopods, amphipods and insects (Whitfield 1984, 1985).

When favoured invertebrate food resources are limited due to major habitat changes within an estuary (Whitfield 1986a), *M. falciformis* is able



**Figure 136.** (a) Microalgal biomass in mesocosms with differing densities of mullet *Chelon richardsonii* and sandprawn *Kraussilichirus kraussi*. (■ = 5 *C. richardsonii*, □ = 10 *C. richardsonii*). (b) Growth rate of *C. richardsonii* in the same mesocosms with differing densities of mullet and sandprawn (■ = 5 *C. richardsonii*, □ = 10 *C. richardsonii*). Means  $\pm$  1SE are shown (after Pillay et al. 2012).

to switch its diet and successfully prey on small zooplantivorous fish species such as the clupeid *Gilchristella aestuaria*. The question then arises – if *M. falciformis* has the ability to be a piscivore of small planktivorous fish species with high energy values, why then does it not utilize this resource at all times?

### Terapontidae

Lepidophagous fishes are those that feed by pulling scales off other living fishes. *Terapon jarbua* are one of a number of fish taxa that obtain nutrition in this manner. This species is abundant in estuaries of the Indo-West Pacific and feeds mainly on fish scales in the St Lucia system (Whitfield & Blaber 1978c).

The dentition of *T. jarbua* is ideal for the removal of scales, with an outer row of sharp conical

teeth and inner villiform layers that would assist in holding any dislodged scales prior to swallowing (Whitfield & Blaber 1978c). In the absence of suitable large fish to ‘parasitize’ by removing scales, *T. jarbua* is able to prey on benthic invertebrates, insects and even small fish.

Laboratory experiments showed that this species is able to digest the scales which comprise mainly keratin (a protein) and yield a higher than expected calorific return to the predator (Whitfield & Blaber 1978c). They are removed only from living fish and usually from fish larger than the individual *T. jarbua*.

These fish often hunt in small schools and form a broad front when attacking a shoal of larger fish (Whitfield 1979). Targeted families include sparids, mugilids, sciaenids, engraulids and cichlids, with the foraging *T. jarbua* moving

continuously from one potential prey school to another. This may account for the presence of fish scales from a variety of fish species in a single *T. jarbua* stomach. This species always attack the lateral surface of large prey fish and scales are removed mainly from the posterior part of the body in the vicinity of the caudal peduncle (Whitfield & Blaber 1978c).

Another foraging method for *T. jarbua* has been described by van der Elst (1988). The thornfish sometimes hides in shallow depressions and, when a suitable fish ventures close by, it stirs the sediment with its tail to create a 'smoke screen'. If the unsuspecting fish approaches to investigate, the *T. jarbua* then rushes out and snatches a mouthful of scales from the startled prey!

### Ecotrophomorphology

The ecomorphology hypothesis assumes that morphology is closely related to, and therefore predictive of, the mode of life. According to the hypothesis, diet should be predicted from the morphology of the fish, particularly from morphological traits related to feeding such as mouth size, jaw shape and dentition (Wootton 1990). The hypothesis also predicts that species with similar morphologies have similar diets. Similarly, body form itself may range from that characteristic of streamlined fishes specialised for rapid acceleration (e.g. Sphyraenidae) to forms characteristic of high manoeuvrability in mid-water areas (e.g. Monodactylidae).

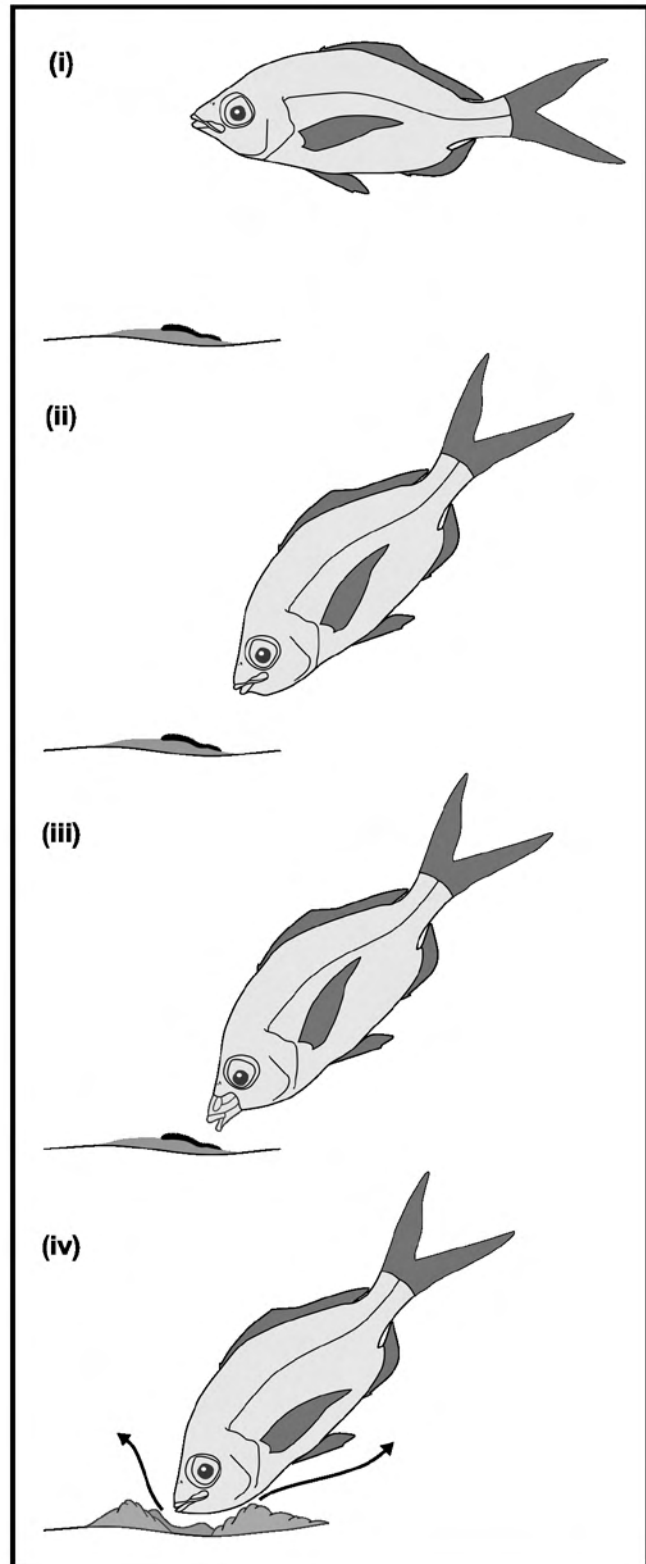
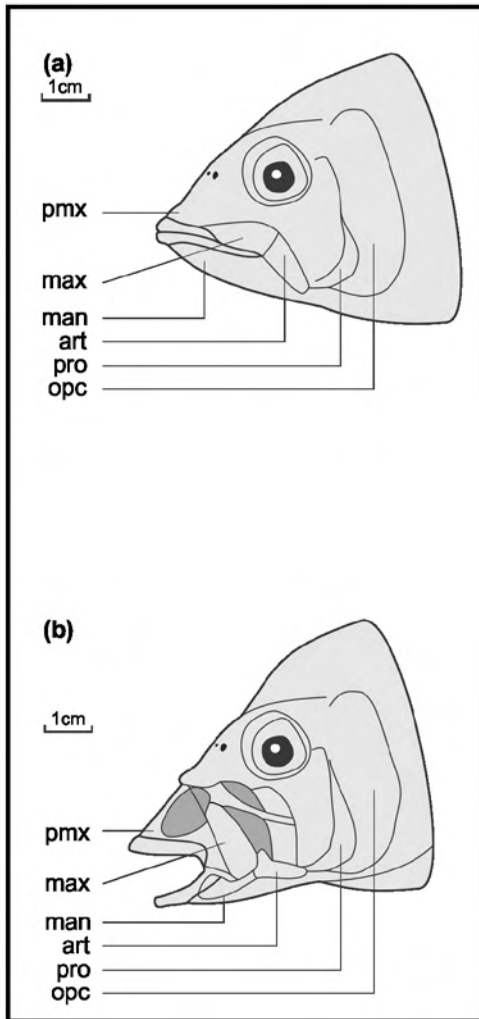
The position, shape and size of the mouth is also related to diet. The ability to protrude the jaw is also common in the more evolutionarily advanced fishes. The advantages of this in feeding probably relate to specific circumstances such as obtaining benthic prey or food from otherwise inaccessible places (Cyrus & Blaber 1982b). Fish may also carry teeth on the tongue, the marginal bones of the jaw, the palatal bones and the pharyngeal bones, the shape of which generally correlates with diet. A good example is *Rhabdosargus holubi* that has tricuspid incisor teeth as juveniles (for consuming large quantities of aquatic macrophytes in estuaries) that are transformed into molariform teeth as adults for crushing shelled invertebrates on marine reefs.

Similarly, in filter-feeding clupeoids and other teleosts, filtering of food takes place on forward-directed projections from the inner margins of the gill arches (known as gill rakers). The shape and abundance of these rakers are related to diet and fish that feed on small food particles usually have numerous long, fine rakers (Blaber 1979), whereas fish feeding on large organisms have fewer, shorter, blunter gill rakers.

A correlation has also been shown between the diet and the gut relative to body length of a fish. This can be illustrated by the relative gut lengths of carnivorous, omnivorous and herbivorous fishes, e.g. estuarine examples of fishes with changing relative gut lengths from each of these trophic categories are available (Marais 1980). Fish consuming high-quality food are able to process it with a gut which is shorter than their total length. Fish whose diet includes a high proportion of material that resists digestion, such as cellulose or lignin, have guts that are several times longer than their body length (Wootton 1990).

In terms of morphology, benthic predators are more varied than any other feeding group and have evolved an assortment of feeding mechanisms. Most benthic species can be described as ambush predators (e.g. gobies which have their mouths directed upwards). Demersal hunters of zoobenthos such as sparids have mouths directed forwards or downwards and actively search for prey on or in the sediment. The majority of the southern African fish species which prey upon moving epibenthic or infaunal invertebrates can be placed in this latter group.

Particle and filter-feeding fishes have also developed a variety of feeding techniques. The fish can be stationary, and pump water into the buccal cavity by means of a series of rapid suction, or they can swim with their mouths open and operculum flaring (Wootton 1990). Thus zooplanktivorous species such as *Atherina breviceps* can forage by means of individual prey selection (biting) in clear water or by filtering zooplankton in turbid water. In contrast, pipefish (Syngnathidae) have developed a type of suction-protrusion feeding strategy on micro-crustaceans by means of their small mouth and tube snout.



**Figure 137.** Head region of *Gerres methueni* with (a) mouthparts retracted and (b) fully protruded (art = articular, man = mandible, max = maxilla, pmx = premaxilla, opc = operculum, pro = preoperculum). A sequence showing prey capture by *Gerres* is also presented, with (i) representing orientation, (ii) the downward pivot, (iii) protrusion of mouthparts and (iv) return to the horizontal (redrawn after Cyrus & Blaber 1982b).



## Trophic categorization

Food webs in estuaries, when viewed from a fish trophic grouping perspective, seem to show a surprisingly small number of energy pathways and therefore a high flow per pathway (Heymans & Baird 1995). This is reflected in the Swartvlei estuarine lake example where only five fish trophic 'compartments' could be recognised and no single compartment was less than 11% of the total fish biomass (Whitfield 1993).

Fish trophic compartments can change in size and number according to both spatial and temporal variation within an estuary. These compartments are also likely to vary as the basal food sources change from the head of an estuary to the mouth. Another factor to consider when attempting to allocate fish species to particular compartments is that species often forage outside the category in which they have been placed, e.g. juvenile *Monodactylus falciformis* in the Swartvlei littoral usually prey on invertebrate fauna associated with the submerged macrophyte beds but can be equally effective at feeding on zooplankton, or even small fishes, if their preferred food items are not available in the littoral (Whitfield 1984).

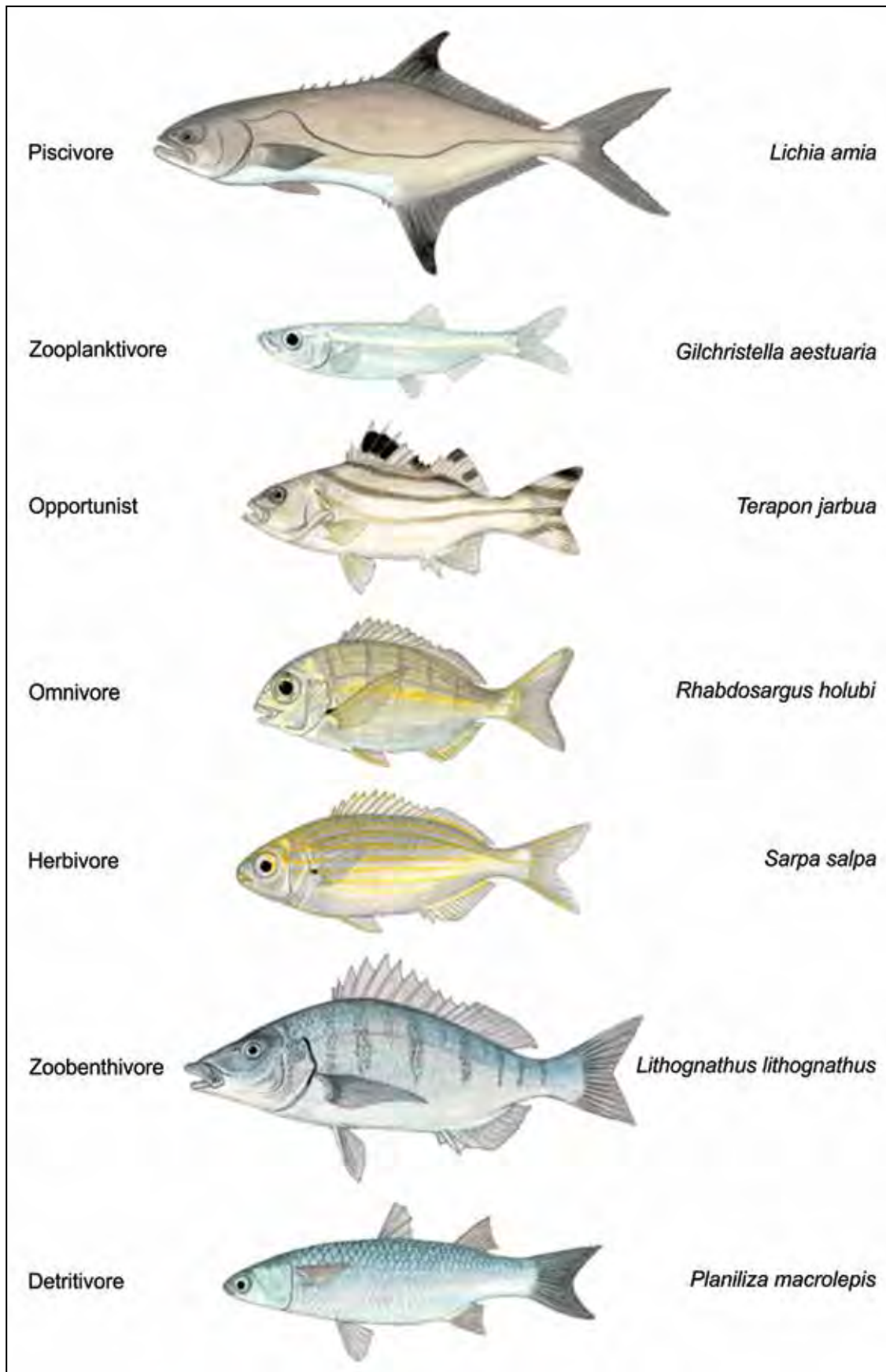
Another method of allocating fish to trophic categories is to use the food sources to characterize which food chain a particular species belongs.

In southern African estuaries, four major food chains have been identified from a fish perspective (Whitfield 1998). The zoobenthic food chain comprises both infaunal and surface dwelling benthic invertebrates. The zooplankton food chain would be dominated by typical planktonic taxa such as copepods but may also include small invertebrates that become part of pelagic waters at certain times. The aquatic macrophyte and filamentous algal food chain would include the epiphytes and epifauna attached to these plants. Finally the detritus food chain would also encompass microphytobenthos and associated meiofauna.

Seven trophic categories or guilds have been identified for fishes in estuaries (Table 15, Figure 138, Elliott et al. 2007) and these are the categories that will be adopted and discussed below. Although the different categories appear definitive, it should be emphasized that dietary studies indicate that almost all fish species will show some evidence of food consumption outside of their dominant food type on a regular or irregular basis. However, for the purposes of the following discussion, species have been placed in categories according to their dominant foraging strategy, i.e. the major stomach content component determines the designated category.

Table 15. Fish trophic guilds in estuaries (after Elliott et al. 2007).

Trophic guild	Definition
Detritivore (DV)	Feeding predominantly on detritus/ benthic floc and/or microphytobenthos
Herbivore (HV)	Grazing predominantly on living macrophyte material or phytoplankton.
Omnivore (OV)	Feeding predominantly on filamentous algae, macrophytes, periphyton, epifauna and infauna.
Zooplanktivore (ZP)	Feeding predominantly on zooplankton (e.g. planktonic crustaceans, fish eggs).
Zoobenthivore (ZB)	Feeding predominantly on invertebrates associated with the substratum, including animals that live just above the sediment (hyperbenthos), on the sediment (epifauna), or in the sediment (infauna).
Piscivore (PV)	Feeding predominantly on finfish but may include large nektonic invertebrates.
Miscellaneous/opportunist (OP)	Feeding on such a diverse range of food that it cannot be readily assigned to any of the above feeding categories.



**Figure 138.** Some examples of southern African estuary-associated fish species in the categories outlined in Table 15 (fish illustrations by Elaine Heemstra and © NRF-SAIAB).

### Herbivorous species

Herbivores are rare among estuarine fishes when compared to marine reef-associated taxa, but a number of estuary-associated species incorporate plants, often aquatic macrophytes together with filamentous algae, as part of their diet. Perhaps one of the most well-known estuarine herbivores is the sparid *Sarpa salpa* (Figure 138), which consumed (by mass) 69% eelgrass (*Zostera capensis*) and 31% filamentous algae and periphyton in the Swartvlei Estuary (Whitfield 1988a).

Estuarine herbivorous fishes in southern African estuaries can be divided into two main groups that are not mutually exclusive, viz. herbivores that also ingest some invertebrate prey and those that are herbivorous for part of their life history. Partially herbivorous taxa include some of the Hemiramphidae, e.g. *Hyporhamphus capensis* that forages predominantly on aquatic macrophytes such as *Ruppia* and *Stuckenia* when these plants are widespread but switches to an animal diet (mainly amphipods and isopods) when aquatic plants are scarce (Coetzee 1981b).

### Omnivorous species

The designation of omnivorous species is compounded by the fact that many of the fishes that feed on aquatic macrophytes and /or filamentous algae are actually targeting the periphyton and epifauna associated with the plants as a food source. Examples of omnivorous fish species in southern African estuaries include the sparids *Rhabdosargus holubi* (Figure 138) and *Diplodus capensis*, both of which ingest a wide spectrum of plant and animal food items, especially aquatic macrophytes, filamentous algae and the associated epifauna and periphyton (Blaber 1974b, Coetzee 1986).

### Detritivorous species

This group, which is sometimes also referred to as iliophagous feeders, consumes mainly microphytobenthos, plant detritus, particulate organic matter, meiofauna and microfauna (e.g. foraminiferans). It is quite possible that much of the particulate organic matter in estuaries originates from macrophytes and microphytes but this has yet to be confirmed. In essence, the small

organisms in or on the surface layer of the substratum, and the associated organic matter are consumed by these fishes. During the foraging process these fishes often ingest relatively large volumes of sediment mixed with food, digest the organic material, and then pass out the inorganic particles in the faeces.

Detritivorous fishes are among the most numerous species in subtropical and tropical estuaries, with the dominant and most speciose group being the Mugilidae (Figure 139). This family is not, however, the only iliophagous group and two other important detritivorous /iliophagous species in subtropical southern African estuaries are the milkfish *Chanos chanos* and the cichlid *Oreochromis mossambicus*.

In a study of the above taxa at Lake St Lucia, Whitfield & Blaber (1978b) showed that various mullet species, *C. chanos* and *O. mossambicus* shared the following food resources, viz. centric and pennate diatoms, filamentous algae, particulate organic matter, foraminiferans, together with small gastropods and crustaceans. Although the diets of the above fish species in Lake St Lucia overlapped, there were also important differences. Whereas *O. mossambicus* fed predominantly on epiphytic pennate diatoms, mugilids and *C. chanos* consumed mainly centric diatoms attached to sand grains. Milkfish preyed more on crustaceans than the other fish taxa and *O. mossambicus* took less animal material than the other species. There was also a higher incidence of sand grains in the stomachs of mullet than *O. mossambicus* or *C. chanos*, thus suggesting that their feeding methods differ.

The role of particulate organic matter in the diets of fishes from estuaries is obscure, but it may sometimes form a considerable proportion of the diets of iliophagous species. In a study of *O. mossambicus* in Lake Sibaya, Bowen (1978) showed that detrital aggregate formed a major component of the diet of this fish but is generally low in protein. He also found that the protein content of the detritus is higher in shallow areas where 0+ juveniles are present and declines with increasing depth, an important consideration for detritivorous fish species in the littoral waters of estuaries.

### Zoobenthivorous species

Included in this category are those fish species that feed primarily on macrobenthic invertebrates but not fishes. Zoobenthos includes animals that live in the sediment (infauna), on the sediment (surface fauna), or just above the sediment surface (hyperbenthos). Although most predatory benthic or demersal fish species usually feed on zoobenthos, it is often difficult to separate these compartments since much of the zoobenthos is sometimes in, sometimes on, and sometimes above the sediment according to time of day, tidal phase, water currents, and various other factors.

*Pomadasys commersonnii* feeds mainly on polychaetes, small bivalves, crabs and prawns in the first year, but from a length of about 200 mm preys mainly on infaunal bivalves and burrowing prawns. The fish uncovers these infaunal invertebrates by blowing water into the sediment using a gill chamber pump action operated through a pointed snout and protrusible mouth. The closely related *Pomadasys kaakan*, which has a less well developed buccal 'bellows' mechanism, forages mainly on smaller crabs, stomatopods, polychaetes and molluscs (Day et al. 1981).

Most sparids have strong molariform teeth suitable for crushing hard-shelled prey such as crabs and molluscs. One of the most widespread estuary-associated marine species in the Indian Ocean region is *Acanthopagrus vagus*. In southern African estuaries juveniles eat mainly amphipods and tanaids while adults feed on bivalves, gastropods, crabs, penaeid prawns and small amounts of macrophytes and fish (Harrison 1991).

*Rhabdosargus sarba* diet consists mainly of a mixture of aquatic macrophytes, bivalves, gastropods, crabs and amphipods (Blaber 1984) and this fish is sympatric with two endemic congeners, *Rhabdosargus holubi* and *Rhabdosargus thorpei*. Their diets differ in the proportions of plant material eaten. *Rhabdosargus holubi* is an omnivore whereas *Rhabdosargus sarba* is almost entirely carnivorous, taking mainly bivalves and crustaceans. Therefore, despite occurring in mixed species shoals, the three *Rhabdosargus* species exhibit differences in feeding ecology.

### Zooplanktivorous species

Zooplanktivores feed predominantly on small crustaceans in the water column. Zooplankton, however, may also include fish eggs and preflexion larvae. The numbers and species diversity of planktivorous fishes in estuaries varies according to the biomass and composition of the plankton, as well as the physical characteristics and location of a particular system.

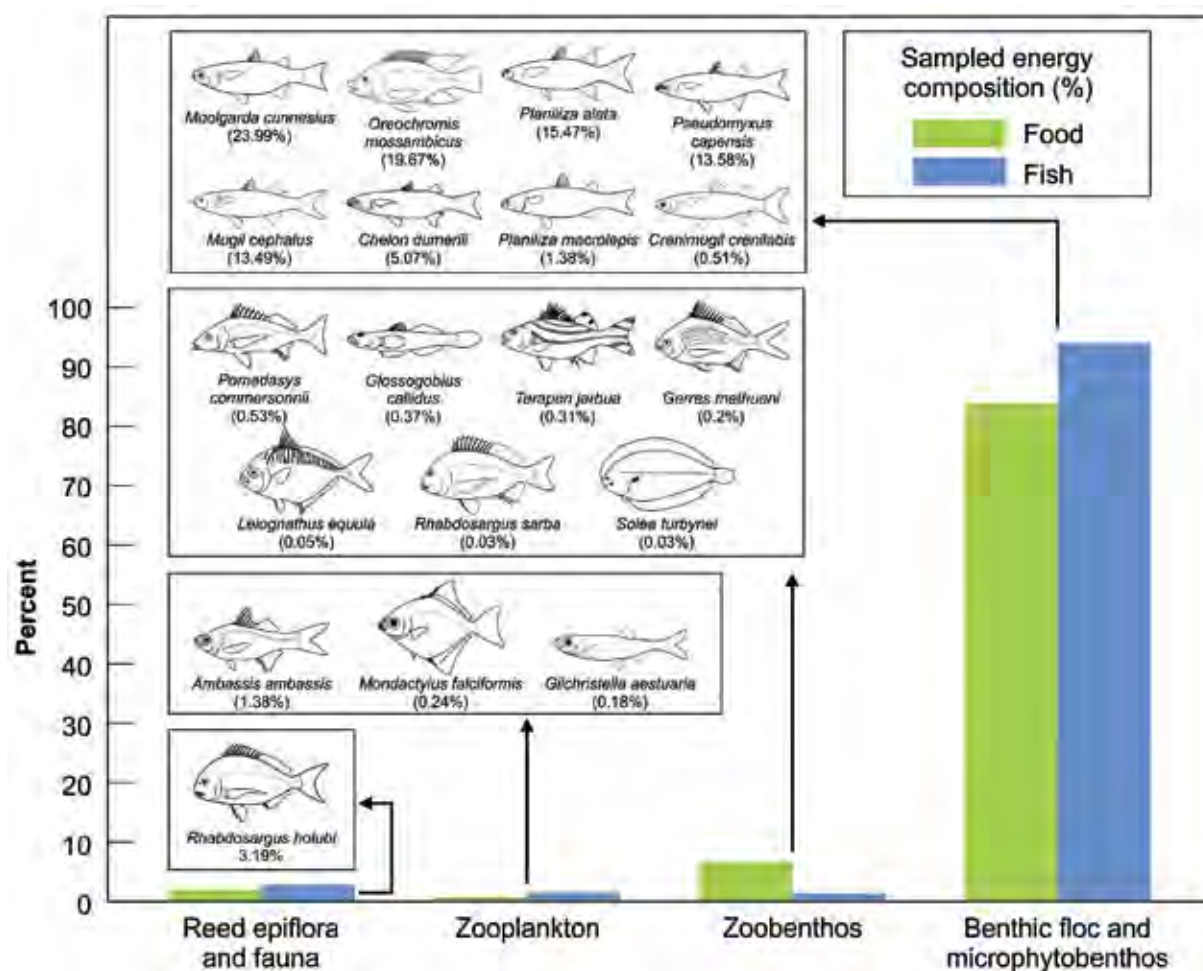
Planktivorous fishes can be divided into those that filter feed using their gill rakers and those that select individual zooplankters. Most of the Clupeidae and Engraulididae fall into the former group, while those that prey on individual plankters are usually smaller fish species or early juveniles from a wide range of families (Blaber 2000). Although the filter feeders are the dominant planktivores in the sea and some larger estuaries, those that select individual prey may be equally abundant in smaller estuaries, particularly systems with low zooplankton stocks.

The size of plankton retained by filter feeders is mainly controlled by the width of the gap between the gill rakers and the length and gap between the the gill raker denticles; with the whole apparatus forming a filtering basket (Blaber 2000). These not only vary according to species but also with the size of the fish. The strong relationships between these parameters and the prey retained have been described for six clupeoids in the St Lucia and Kosi coastal lake systems (Blaber 1979, Blaber & Cyrus, 1981). Generally the narrower the gill raker and denticle gaps, the smaller the sizes of prey taken.

The only species in St Lucia that feeds mainly on phytoplankton is *Hilsa kelee* which has relatively narrow gill raker denticle gaps when compared to the other planktivorous taxa. Most zooplanktivores in St Lucia feed on the estuarine calanoid copepod *Pseudodiaptomus*. However, *Thryssa vitirostris* begins life as a particulate feeder preying mainly on individual *Pseudodiaptomus*, then switches to filter feeding on the same calanoid, before reverting at large sizes to individual selection of small pelagic fish prey (Blaber 1979).

Small estuarine species that are also planktivorous as adults include the ambassids, with most species of this family feeding on animals





**Figure 139.** Simplified food chains for the fishes of the Mhlanga Estuary showing the dominant energy pathways. Arrows go from food to consumer with the percentages based on energy contributions by the respective components (modified from Whitfield 1980b). The aerial photograph shows the lower part of the estuary (Photo: Nicolette Forbes).

taken in the water column or from the water surface such as cladocerans, ostracods, copepods, insects and small fish. *Ambassis ambassis*, *A. natalensis* and *A. dussumieri* are all primarily zooplanktivores. However, competition is reduced by *A. dussumieri* occurring in higher salinities near the estuary mouth with a narrow food spectrum, whereas the other two species have a broader diet, particularly *A. ambassis* that lives mainly in the upper reaches and has a high proportion of insects in its diet (Martin & Blaber 1983).

#### **Piscivorous species**

Piscivores include carnivorous species that feed on

other fishes. Although estuaries provide shelter from major fish predators, several estuary-associated taxa are piscivorous, especially as sub-adults and adults. Examples from southern African estuarine systems include members of the Belontiidae (e.g. *Strongylura leiura*), Carangidae (e.g. *Caranx sexfasciatus*), Elopidae (e.g. *Elops machnata*), Megalopidae (e.g. *Megalops cyprinoides*), Pomatomidae (e.g. *Pomatomus saltatrix*), Sciaenidae (e.g. *Argyrosomus japonicus*) and Sphyrinae (e.g. *Sphyrna barracuda*). While most of the above piscivores feed primarily on fishes, they also consume invertebrates, especially during their juvenile life stages.

### **Regional trophic composition**

A detailed comparative analysis of the fish trophic structure has been undertaken on some 190 South African estuaries spanning three zoogeographic regions and incorporating three broad estuarine types (Harrison & Whitfield 2012). Differences in the fish trophic structure of the various estuary types within each zoogeographic region were documented. These were then linked to the relative biomass contribution of the various trophic guilds and also differences in biomass trophic spectrum profiles of the fishes in each estuary type within each region (Table 16). In spite of these differences in trophic structure, all estuaries were dominated by detritivores, which suggests that the main food source in these systems (detritus) is similar in all biogeographic regions.

According to Whitfield (1999), a key attractiveness of estuaries to fishes lies in the fact that they act as detritus traps, with the organic detritus being either allochthonous or autochthonous in origin (Paterson & Whitfield 1997). Riverine input introduces terrestrial plant material as well as freshwater plants and algae into these systems, while tidal action can carry detached algae, sea grasses, marine plankton and decomposing material in from the sea. The estuary itself provides material from both vascular plants and algae, which may be benthic, epiphytic or planktonic (Day & Grindley 1981).

The contribution of detritivores to the overall fish assemblage was highest in southern African

cool-temperate estuaries and lowest in warm-temperate systems (Table 16). Blaber (1985) states that in all southeast African estuaries, the most numerous fishes are iliophagous species and that detritus, together with epipsammic algae and periphyton, provide a major energy input into the fish community. Whitfield (1980b) also found that, in the temporarily closed Mhlunga Estuary, benthic flocc (including detritus) accounted for 83% of the measured food resources and supported 93% of the sampled fish biomass.

The biomass contribution of detritivores was higher in temporarily closed estuaries than in open systems in all biogeographic regions. Closed estuaries automatically accumulate detritus during the closed phase and this may be responsible for the higher contribution of detritivores in these estuaries relative to open systems (Harrison & Whitfield 2006c). While river flow and tidal action aid in the transportation of detrital material into open estuaries, these mechanisms may also contribute to the loss of detritus to the adjacent marine environment, particularly following river flooding (Marais 1982).

A SIMPER analysis of the data from the Harrison & Whitfield (2012) study showed that in cool-temperate estuaries, the detritivore-category was the main guild that contributed to the similarity within each estuary type. Detritivores were also the most important group in warm-temperate and subtropical estuaries.

In all warm-temperate estuaries, as well as small temporarily closed subtropical systems, omnivores were an important and often dominant guild. Zooplanktivores accounted for some of the similarity within small closed warm-temperate

estuaries and also within all subtropical systems. Zoobenthivores and piscivores contributed to the similarity within moderate-to-large closed and permanently open warm-temperate and subtropical estuaries.

Table 16. Mean ( $\pm$ SD) percentage biomass contribution of fish trophic guilds in small closed estuaries (S), moderate-to-large closed estuaries (M), and permanently open estuaries (O) in the cool-temperate, warm-temperate and subtropical biogeographic regions of South Africa (after Harrison & Whitfield 2012). For trophic guild abbreviations, please see Table 15.

Trophic guild	Cool-temperate			Warm-temperate			Subtropical		
	S	M	O	S	M	O	S	M	O
DV	98.80 $\pm$ 3.57	90.68 $\pm$ 10.99	87.7 $\pm$ 19.60	76.46 $\pm$ 24.91	64.05 $\pm$ 18.08	43.45 $\pm$ 18.28	85.08 $\pm$ 10.76	84.51 $\pm$ 9.35	57.49 $\pm$ 19.78
HV				0.001 $\pm$ 0.003	0.003 $\pm$ 0.01	0.05 $\pm$ 2.39			
OV		0.03 $\pm$ 0.09	0.01 $\pm$ 0.02	12.44 $\pm$ 15.21	9.99 $\pm$ 9.73	3.66 $\pm$ 3.22	4.49 $\pm$ 6.65	2.29 $\pm$ 3.09	1.07 $\pm$ 1.25
ZP	0.01 $\pm$ 0.03	2.72 $\pm$ 3.72	7.80 $\pm$ 16.34	4.05 $\pm$ 5.97	3.10 $\pm$ 2.50	2.02 $\pm$ 2.24	5.14 $\pm$ 6.74	2.79 $\pm$ 2.53	5.67 $\pm$ 5.42
ZB	1.18 $\pm$ 3.57	3.29 $\pm$ 5.09	1.54 $\pm$ 1.94	4.55 $\pm$ 6.82	9.04 $\pm$ 7.54	20.02 $\pm$ 16.97	2.13 $\pm$ 2.24	5.60 $\pm$ 5.71	11.93 $\pm$ 12.65
PV		3.27 $\pm$ 8.15	2.89 $\pm$ 5.16	2.50 $\pm$ 6.73	13.81 $\pm$ 13.90	30.35 $\pm$ 17.22	3.15 $\pm$ 5.46	4.82 $\pm$ 5.39	23.84 $\pm$ 16.39

## Fish food sources and energy flow in estuaries

Estuaries have high productivity per unit of area but material produced within the estuary, or imported from the river or sea, would have little effect on the biota if this matter was not retained within the estuary. A key feature of estuarine systems with respect to fish is therefore an ability to act as detritus traps for both autochthonous and allochthonous production (Whitfield 1988b). This provides rich and abundant food resources for filter and deposit-feeding invertebrate prey, together with detritivorous fish species.

Different parts of the estuarine system have different importance, and littoral plants such as seagrass beds, saltmarsh grasses, mangroves and reeds all contribute to the autochthonous detritus pool. The degree to which these aquatic macrophytes influence the trophic functioning of the

associated fish assemblages is very important to fisheries scientists, conservationists and environmental managers.

### Food web complexity

One of the distinguishing features of most aquatic communities, and that involving estuarine fishes is no exception, is the complexity of trophic structure and the interrelationships within these systems. Despite the large amount of information available on the diets of many estuary-associated fishes, there are relatively few good examples of food webs as they relate to fishes. The trophic structure of estuarine fish communities is not simple and is a result of the influences of both biotic and abiotic factors, the type of estuary, as well as the state of the system.

Although a variety of factors play an important role in influencing the composition of fishes in an estuary, the overall basic trophic structure within these systems is generally very similar (Table 16). Additionally, although numbers of species in a particular type of South African estuary decline between subtropical and cool-temperate regions, the proportional representation between the trophic groups appears to be maintained (Whitfield 1998).

In an early food chain assessment, de Sylva (1975) noted that generalized food chains are basically fueled by either phytoplankton or detrital energy sources (Table 17). Secondary trophic levels are mainly benthos, either infaunal or epifaunal, or perhaps zooplankton or micronekton, or both. Middle fish carnivores include planktivores and benthophagous species, with tertiary fish carnivores dominated by large euryhaline predatory species that use estuaries as feeding grounds. It is noteworthy that there are more estuarine food chains attributed to detritus generation compared

to phytoplankton based production (Table 17).

Possible estuarine detritus food chains, as shown in Table 17, are probably more complex than depicted. The omnivorous nature of some macrofaunal invertebrates such as amphipods and isopods makes these food webs extremely complex. This is because of the importance of bacteria in transferring energy to the microfauna and meiofauna before it reaches the 'detritivorous' macrofauna. Straight food chains such as algae-herbivore-predator or bacteria-bacterivore-predator are an over-simplification of benthic food chains in estuaries and this makes it difficult to place species in definite trophic levels. In addition, most zooplankton species consume both phytoplankton and suspended particulate matter, thus rendering the separation of the plankton and detritus food chain artificial.

In clear estuaries where phytoplankton, aquatic macrophytes, emergent macrophytes and microphytobenthos are present, phytoplankton production is usually lower than that of benthic micro-

Table 17. Classification of important food chains involving fish in southern African estuaries (modified from de Sylva 1975).

<i>Phytoplankton-generated food chains</i>			
Phytoplankton	→ zooplankton	→ benthopelagic fish (e.g. <i>Leiognathus equula</i> )	
Phytoplankton	→ zooplankton	→ planktivorous fish (e.g. <i>Gilchristella aestuaria</i> )	→ large fish predators (e.g. <i>Elops machnata</i> )
Phytoplankton	→ phytoplanktonic fishes (e.g. <i>Hilsa kelee</i> )		
Phytoplankton	→ detritivorous fishes (e.g. <i>Chelon richardsonii</i> )		
<i>Detritus-generated food chains</i>			
Detritus	→ benthos (epifauna)	→ benthophagous fishes (e.g. <i>Sillago sihama</i> )	
Detritus	→ benthos (infauna)	→ benthophagous fishes (e.g. <i>Pomadasys commersonnii</i> )	→ large predators (e.g. <i>Carcharinus leucas</i> )
Detritus	→ small benthos	→ larger invertebrates and small benthic fishes (e.g. <i>Glossogobius callidus</i> )	→ large fishes (e.g. <i>Lutjanus argentimaculatus</i> )
Detritus	→ detritivorous fishes (e.g. <i>Mugil cephalus</i> )		
Detritus	→ macrobenthos	→ large predators (e.g. <i>Himantura leoparda</i> )	
Detritus	→ micronekton	→ intermediate predators (e.g. <i>Ambassis dussumieri</i> )	→ large predators (e.g. <i>Sphyrnaena barracuda</i> )
Detritus	→ zooplankton	→ small fishes and invertebrates	→ larger fishes (e.g. <i>Caranx sexfasciatus</i> )



algae and macrophytes, with detritivory greatly exceeding herbivory (Baird & Ulanowicz 1993). The Eastern Cape Kromme Estuary provided an ideal opportunity to estimate the changes in estuarine food resources and carbon flow through the ecosystem between two periods (Table 18), one prior to the building of the Mpofu Dam just above the estuary (pre-1984) and one after the dam was in place (1988-1992) (Baird & Heymans 1996).

Prior to dam construction, Kromme River flow into the estuary was approximately  $117 \times 10^6 \text{ m}^3 \text{ a}^{-1}$  compared to less than  $2 \times 10^6 \text{ m}^3 \text{ a}^{-1}$  after the dam was completed. The decline in riverine nutrient inputs resulted in a collapse of phytoplankton productivity and an increase in submerged macrophyte production (Table 18) due to improved water clarity. The increased macrodetrital production boosted the invertebrates feeding on this resource, as well as zoobenthivorous and detritivorous fish species (mullet) that benefited from the enhanced availability of detritus and associated micro-organisms (Table 18). Despite the decline in microzooplankton, copepods and mysids, there was an unexpected increase in the zooplanktivorous fishes in the system (Table 18).

One can only assume that these fish species were somehow able to switch their planktonic feeding activities to prey on small crustaceans that were now associated with the extensive eelgrass beds (*Zostera capensis*) within the estuary.

In terms of numbers of species, different types of estuarine systems in southern Africa appear to have approximately similar proportions of species at each broad trophic level (Table 19). There is a consistency in terms of the low representation of herbivorous species and high representation of zoobenthivores in these estuaries. There is also consistency in the representation of planktivorous and detritivorous species but a biomass analysis would probably reveal considerable variation depending on whether a particular estuary is mainly phytoplankton or detritus driven.

Numbers of piscivorous species are also largely consistent between the estuary types (Table 19). It is perhaps noteworthy that the two systems with the most herbivorous fish species (Kowie and Breede) were permanently open, with extensive eelgrass beds in the lower reaches. The system with the least number of herbivores was the temporarily open /closed Mhlanga Estuary which lacks submerged plant beds but has an abundance of

Table 18. Throughputs of carbon ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) for each model compartment in the Kromme Estuary before (pre-1984) and after (1988-1992) the building of the Mpofu Dam (after Baird & Heymans 1996).

Compartment	Pre-1984	1988-1992	Compartment	Pre-1984	1988-1992
Dissolved organic carbon (DOC)	74	39	Mysids	21	0.4
Suspended POC	702	679	Marsh suspension feeders	9	95
Sediment POC	7110	7310	Marsh detritivores	788	1150
Sediment bacteria	2546	2540	Marsh grazers	1	1
Attached bacteria	3	3	Marsh meiofauna	13	13
Free living bacteria	74	33	Meiofauna	70	30
Heterotrophic micro-zooflagellates	36	16	Detritivores	165	936
Phytoplankton	446	49	Suspension feeders	171	412
Halophytes	13800	13800	Carnivorous macrofauna	1	12
Aquatic macrophytes	851	1960	Zooplanktivorous fishes	19	48
Benthic microalgae	361	361	Piscivorous fishes	1	1
Microzooplankton	9	4	Zoobenthos feeding fishes	8	20
Copepods	40	16	Detritivorous fish	13	17

detritivorous food resources (Whitfield 1980b). Thus the high representation of detritivorous fish species in this system (Table 19) is to be expected and is a characteristic of most TOCEs in KwaZulu-Natal.

Food web comparisons between Lake St Lucia and Lake Nhlanga are most interesting. Lake St Lucia is a shallow, turbid and highly productive system with a much richer species diversity than Lake Nhlanga which is oligotrophic with clear water and a relatively low species diversity. In terms of biomass their trophic structures are very different, with St Lucia having more piscivores and zooplanktivores, while Nhlanga has a higher proportion of detritivores and zoobenthic carnivores (Figures 140 and 141, Blaber 2000). Nhlanga has relatively few zooplanktivores, with a major difference between this system and St Lucia being attributed to the high zooplankton productivity of the latter system (Blaber 1979). This results in high numbers of planktivorous fishes in St Lucia and the piscivores that prey upon them (Whitfield & Blaber 1978a).

Detritivorous and benthic invertebrate feeders have similar relative proportions of biomass in each of the above systems. From these data it is apparent that the St Lucia fish food web is both phytoplankton and detritus driven (Blaber

2000), whilst that of Nhlanga is mainly detritus driven with very little phytoplankton production (Allanson & van Wyk 1969).

Studies on energy flow through fish assemblages are hindered by the fact that both known and unknown errors are confronted at nearly every step of the trophic cascade (Gerking 1994), e.g. there are many sources of variation with respect to different sampling methods and there are also problems with net-efficiency conversions for different sampling gear in order to make quantitative estimates of the abundance of fish. Despite the above difficulties and sampling short-comings, some fish production estimates in estuaries have been attempted. A mark-recapture study by Cowley & Whitfield (2002) determined that the population size of small estuarine-spawning fish species in the 17.5 ha East Kleinemonde Estuary was approximately 750 000 and that of larger marine species approximately 140 000. However, the estuarine fish species only contributed 12% to the total fish biomass of 28.4 g m<sup>-2</sup>. Annual productivity for all fish species was 41.3 g m<sup>-2</sup>, with the omnivorous sparid *Rhabdosargus holubi* accounting for >74% of total fish production in this estuary, indicating that most energy flow through the ichthyofaunal assemblage was channelled via this species.

Table 19. The percentage contribution (numbers) of typical indigenous estuary-associated fish species to each trophic category in various types of southern African systems. Only estuaries that were sampled by both seine and gill nets are included in this analysis (EL = Estuarine Lake, TOCE = Temporarily Open/Closed Estuary, POE = Permanently Open Estuary, Herb = Herbivorous, Detr = Detritivorous, Plan = Planktivorous, Zoob = Zoobenthivorous, Pisc = Piscivorous, N = Total number of fish species).

Estuary	Type	Herb	Detr	Plan	Zoob	Pisc	N	Reference
Lake Nhlanga	EL	3	20	24	33	20	30	Blaber (1978)
Lake St Lucia	EL	7	20	16	36	20	61	Whitfield (1977)
Swartvlei	EL	4	23	19	42	12	26	Whitfield et al. (1983)
Tongati	TOCE	6	25	16	34	19	32	Blaber et al. (1984)
Mhlanga	TOCE	2	28	11	48	11	46	Harrison & Whitfield (1995)
Kleinemonde	TOCE	7	21	14	41	17	29	Cowley & Whitfield (2001)
Great Fish	POE	4	26	17	39	13	23	Whitfield et al. (1994)
Kowie	POE	10	19	23	32	16	31	Whitfield et al. (1994)
Brede	POE	10	18	18	38	15	39	Carter (1983)
Average (%)		6	22	18	38	16		

Early juveniles and small fish species are often ignored when assessing energy flow in estuaries. Predation effects by fishes on food chains is also a topic that is seldom studied and the stabilizing influence of early juvenile mugilids on the zooplankton food chain in the Kasouga Estuary has been clearly demonstrated by Wasserman et al. (2013a). Early juvenile *Pseudomyxus capensis*, by feeding on copepods and polychaetes in the mesocosm, created a trophic cascading effect on the ciliate, micro-flagellate, nano-flagellates and bacterial populations. If that is the impact one very small ichthyofaunal component has on prey structure, we can only imagine the role of large predatory fishes on estuarine food webs.

Fish larvae in estuary channels do not necessarily depend on the same carbon sources for their nutrition, even though the dominant prey for all these larvae is derived from the zooplankton (Costalago et al. 2016). For example, in Eastern Cape estuaries there was a significant difference in  $\delta^{13}\text{C}$  values for *Gilchristella aestuaria* larvae in marine dominated estuaries compared to the more freshwater dominated systems. In systems such as the Kromme, where zooplankton stocks were low, the *G. aestuaria* larvae showed greater dependence on suspended particulate organic matter (POM) as a food source (Costalago et al. 2016). In addition, the nutritional condition and growth of *G. aestuaria* larvae from the upper reaches of the freshwater rich Gamtoos and Sundays estuaries was higher than that from other Eastern Cape estuaries where planktonic resources were much lower (Costalago et al. 2015).

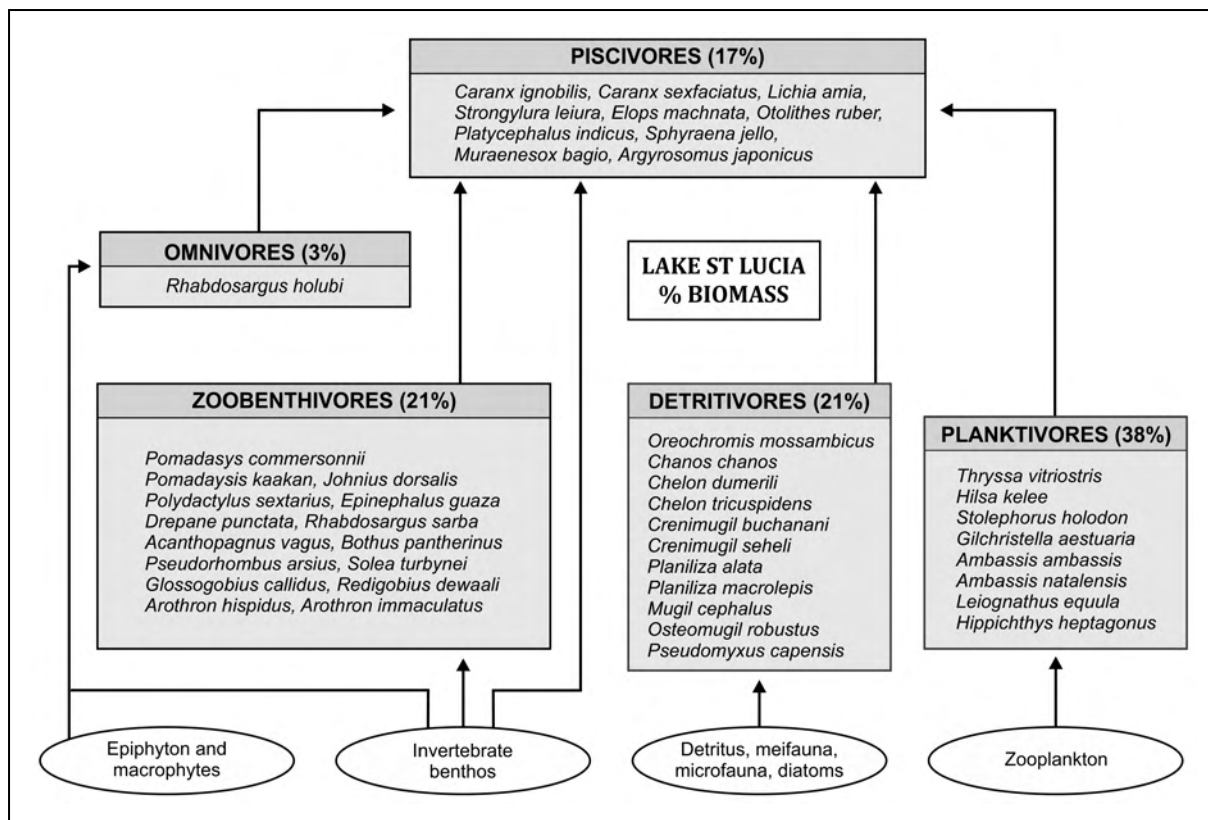
Stable isotope studies can give a strong indication of possible energy sources for fishes within estuaries, e.g. Paterson & Whitfield (1997), using stable carbon isotopes, showed that there were two main energy pathways within the invertebrate and fish assemblages of the Kariëga Estuary. The littoral biota utilized an enriched  $\delta^{13}\text{C}$  primary food source from *Spartina*, *Zostera* and epiphytes, whereas the channel fauna utilized a  $\delta^{13}\text{C}$  primary food source that was depleted in C, most likely a mixture of phytoplankton, terrestrial plant debris and  $\text{C}_4$  aquatic macrophyte detritus. Similarly high  $\delta^{13}\text{C}$  values in the littoral relative to pelagic food sources (e.g. epibionts versus suspended

POM) have been recorded in the Kowie Estuary (Bergamino et al. 2014). This semi-independent functioning of the littoral and channel habitats has also been documented in other estuaries (Froneman 2001).

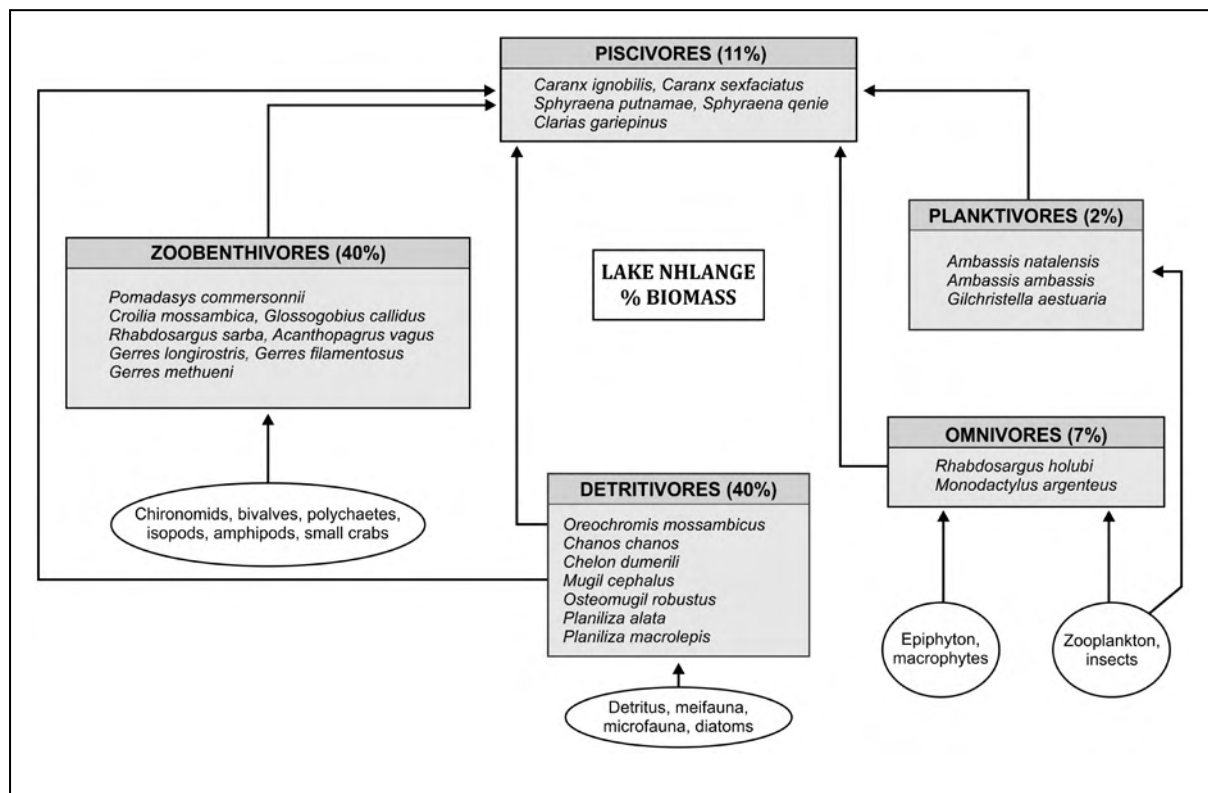
However, energy flow across estuarine habitats can also be greatly facilitated by the movement of fishes within estuaries. An isotope study on a top fish predator in the Kowie Estuary (Figure 142) has shown the role of *Argyrosomus japonicus* in connecting energy flow across littoral, pelagic and benthic habitats in this system (Figure 143). This was facilitated by *A. japonicus* feeding on different fishes and invertebrates in the channel, benthic and littoral areas. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values confirmed the role of *A. japonicus* as a top predator that preys mainly upon smaller fishes such as *Gilchristella aestuaria* in the pelagic zone, *Glossogobius callidus* in the littoral and channel bottom areas, and *Rhabdosargus holubi* together with the shrimp *Palaemon peringueyi* in the littoral zone. The isotope results were consistent with dietary information derived from stomach content analyses of this species in other southern African estuaries, i.e. the most frequently occurring prey species in the stomachs of juvenile *A. japonicus* were the small pelagic fish *G. aestuaria*, benthic dwelling *G. callidus* and the epibenthic shrimp *P. peringueyi* (Whitfield & Blaber 1978a, Marais 1984, Whitfield 1988a).

Thus the foraging of large mobile predatory fish across estuarine environments is an important way in which these different habitats can be closely coupled. The dietary diversity of *A. japonicus*, which is related to the above behaviour, may therefore help to explain the success of this species as a dominant top predator in southern African estuaries, primarily by increasing the amount of food energy available from diverse habitats.

Predation on fishes in estuaries has a direct impact on both the composition and abundance of the ichthyofauna in these systems. Indirectly piscivory influences the feeding ecology of individual species through a top down control and therefore the overall trophic structure and functioning of fish assemblages in estuaries. Piscivorous fishes are dealt with in some detail earlier in this chapter so the focus here will be on the other



**Figure 140.** Simplified trophic structure of the fish assemblage in the estuarine Lake St Lucia (modified from Blaber 2000).



**Figure 141.** Simplified trophic structure of the fish assemblage in the estuarine Lake Nhlangé (modified from Blaber 2000).

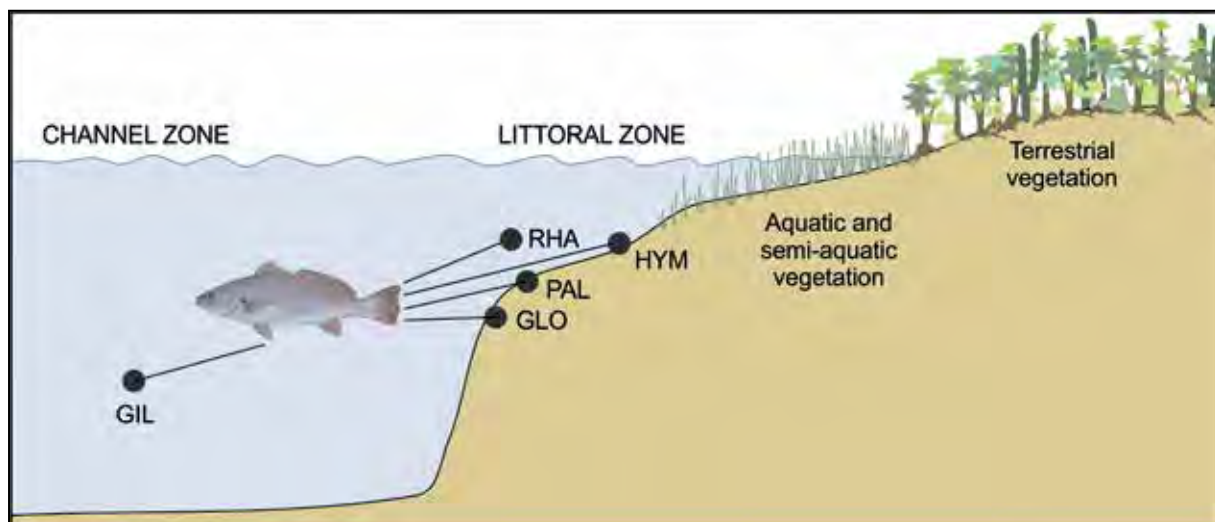


major predator of fishes in southern African estuaries, namely birds. These range in size from small kingfishers <20 g in mass to large pelicans weighing >10 kg.

In Lake St Lucia, the overall abundance of piscivorous birds in different parts of the system appear to be related to littoral fish abundance, as determined by seine netting (Whitfield 1978).



**Figure 142.** View of the oxbow bend in the upper reaches of the Kowie Estuary (Photo: Alan Whitfield).



**Figure 143.** Diagrammatic representation of the location of major dietary components (black dots) of the predatory fish *Argyrosomus japonicus* (pictured) within the Kowie Estuary, thus illustrating the bio-energetic linkages created between the different zones by this species (after Bergamino et al. 2014). Abbreviations for the prey items: HYM = *Hymenosoma orbiculare*; PAL = *Palaemon peringueyi*; GLO = *Glossogobius callidus*; RHA = *Rhabdosargus holubi*; GIL = *Gilchristella aestuaria*.

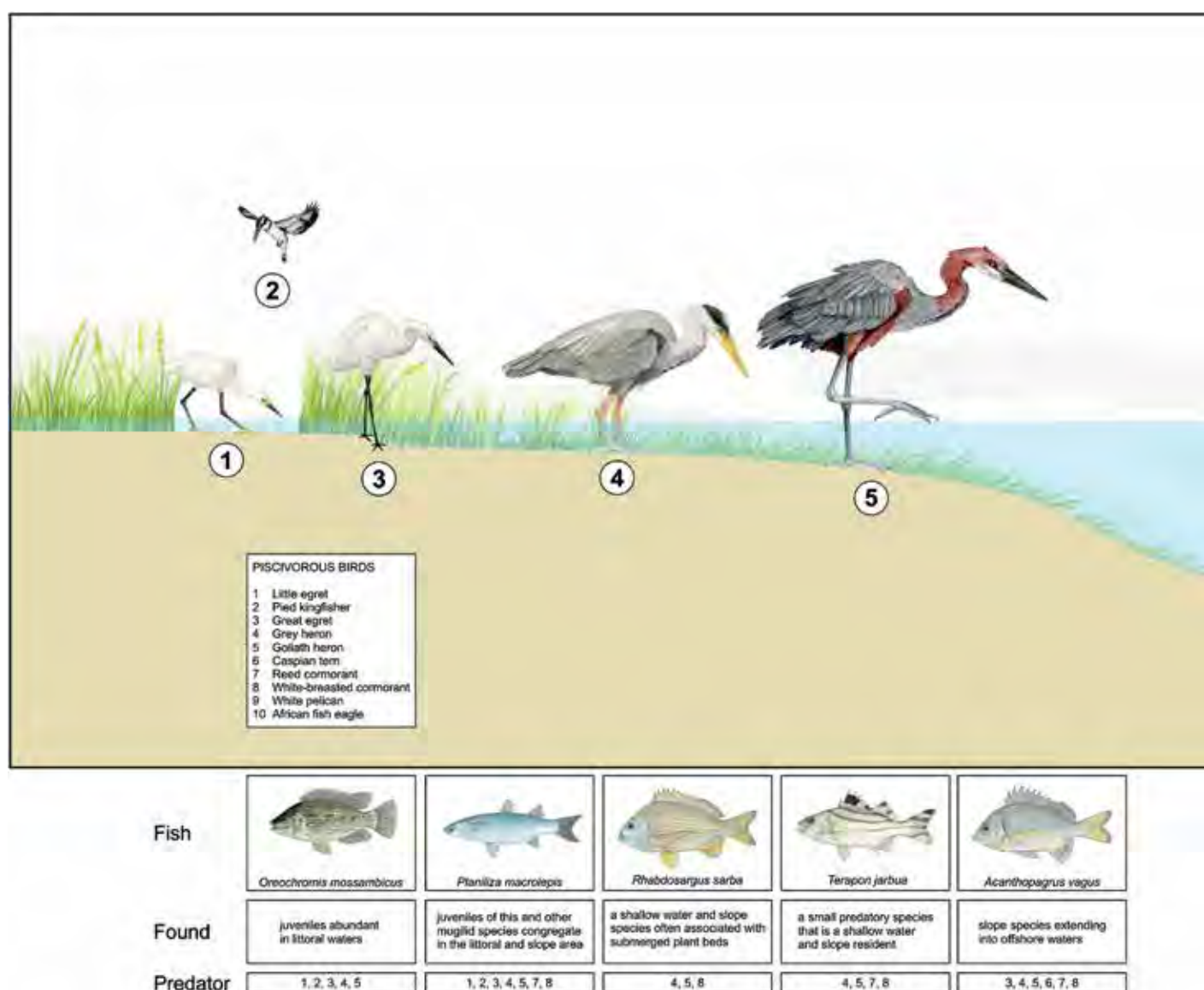
In addition, the breeding of piscivorous birds at the lake appears to be inhibited during hypersaline periods when fish abundance is low (Forrest 1969).

In a detailed study of the diet of piscivorous birds in the St Lucia system, three major avian groupings were identified according to hunting methods, each of which foraged on a range of fish sizes and species, and often in different zones of lake (Figure 144). Wading egrets and herons foraged in littoral waters of different depths, with goliath heron *Ardea goliath* located in the deepest water, the grey heron *Ardea cinerea* and great egret

*Egretta alba* in intermediate depths, and the little egret *Egretta garzetta* in the shallows (Figure 144).

Swimming birds cover the entire lake surface, with reed cormorant *Phalacrocorax africanus* feeding mainly in littoral waters and the white-breasted cormorant *Phalacrocorax carbo* being more widespread (Whitfield & Blaber 1979b). Both these bird species and the white pelican *Pelecanus onocrotalus* preyed upon a wide range of pelagic, demersal and benthic dwelling fishes.

The third category of piscivorous birds belong to the aerial hunters, ranging from the small pied kingfisher *Ceryle rudis* foraging in the littoral,



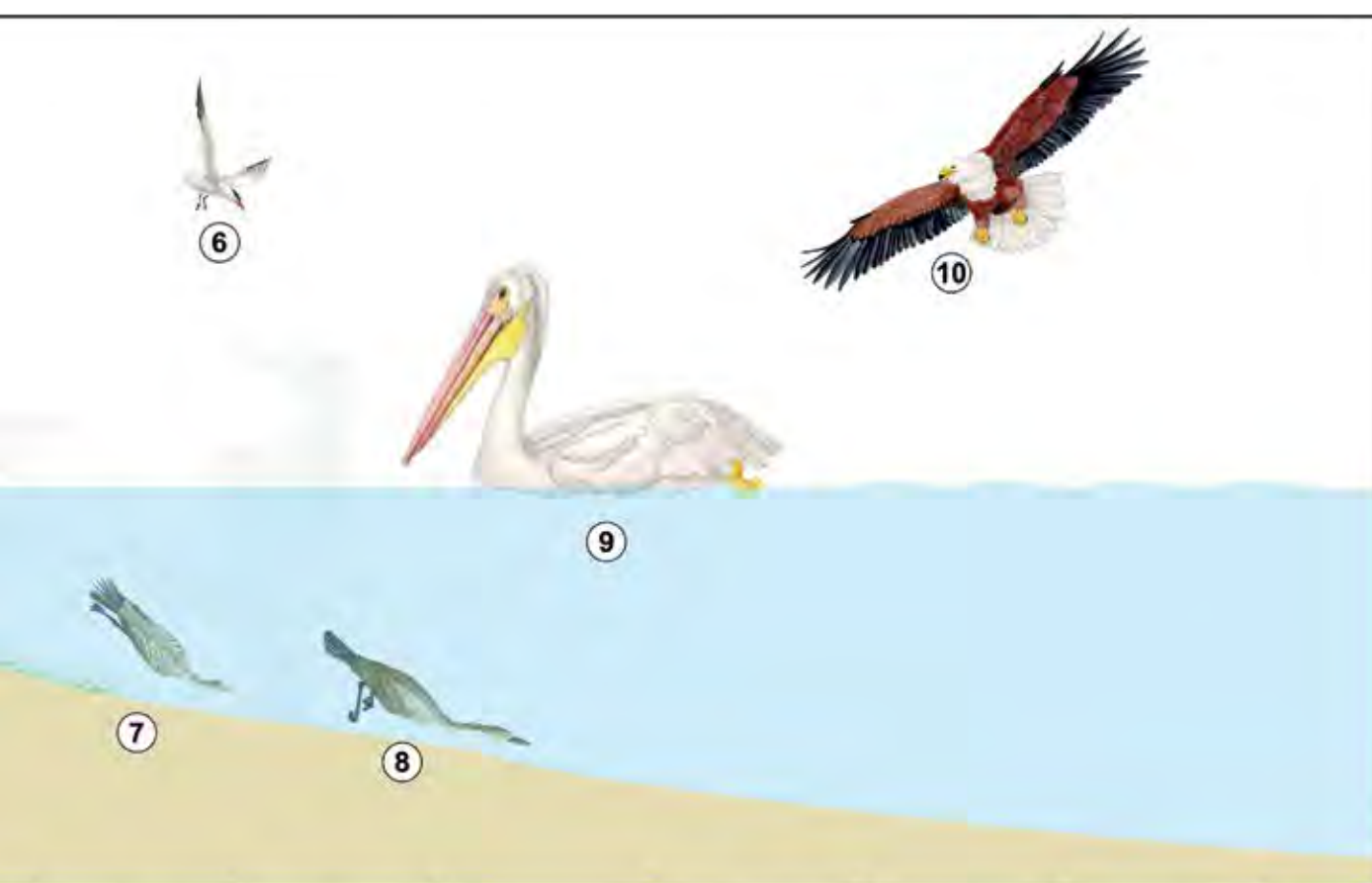
**Figure 144.** Diagrammatic representation of predation by piscivorous birds on fishes in Lake St Lucia. All three broad bird foraging groups are shown, namely waders, aerial divers and swimming species, together with some of the fishes that were favoured by the birds (compiled by Susan Abraham and representing a modified version of an original concept by Tessa Blaber).

to Caspian terns *Hydroprogne caspia* over open waters, and the large fish eagle *Haliaeetus vocifer* which hunted over the entire lake (Whitfield & Blaber 1978d). Examples of birds from all three foraging categories are shown in Figures 145-150.

The fishing behaviour of the wading piscivorous birds in Lake St Lucia was related to the depth at which the birds were able to forage as well as the presence or absence of aquatic macrophytes (Whitfield & Blaber 1979a). Feeding segregation of the little egret *Egretta garzetta*, great white egret *Egretta alba*, grey heron *Ardea cinerea* and goliath heron *Ardea goliath* were driven primarily

by tarsometatarsal length and selection of fish species was targeted mainly on the juveniles of littoral inhabiting *Oreochromis mossambicus* and members of the family Mugilidae (Figure 144).

The two cormorant species at Lake St Lucia also segregated the fish resources according to water depth. The reed cormorant *Phalacrocorax africanus* favoured shallow water within about 100 m of the shore whereas the white-breasted cormorant *Phalacrocorax carbo* was more wide ranging (Whitfield & Blaber 1979b). The white pelican *Pelecanus onocrotalus* also fished across the entire lake surface and preyed heavily on *Mugil*



<i>Ambassis natalensis</i>	<i>Pomadasys commersonii</i>	<i>Mugil cephalus</i>	<i>Leiognathus equula</i>	<i>Gilchristella aeneus</i>	<i>Thryssa vittirostris</i>
a midwater species that occurs across the lake	a slope and demersal offshore species	subadults and adults of this species swim in surface waters when not foraging	midwater zone in offshore waters	midwater zone in slope and offshore waters	midwater species in offshore waters
2, 6, 7	9, 10	9, 10	8, 9,	2, 6	8



*cephalus* during the autumn spawning migration of this species (Whitfield & Blaber 1979b).

Aerial diving birds at St Lucia also segregated the fish resources according to size, with the fish eagle *Haliaeetus vocifer* capable of capturing and carrying fish up to 3 kg in weight, whereas the pied kingfisher *Ceryle rudis* preyed mainly on small fish in the shallows. Prey selectivity by fish eagles was governed primarily by which fish species swam near the water surface (e.g. *Mugil cephalus* and *Clarias gariepinus*) and were therefore vulnerable to capture (Whitfield & Blaber 1978d).

Sudden fish kills resulting from exceptionally low salinity conditions (Blaber & Whitfield 1976) may also cause temporary changes in the energy flow pattern from fishes to piscivorous birds. Similarly, during hypersaline conditions, the decline in fish stocks has a major impact on both the numbers and breeding success of piscivorous birds. In June 1976 a wide variety of birds were recorded feeding on dead or dying fish at Lake St Lucia, some of which were not part of the individual bird species' normal diet. Similarly, an extensive fish kill during a cold period in June 1987 created a subsequent shortage of food, with this being suggested as a reason for the Caspian terns failing to breed during that year (Cyrus & McLean 1994).

A quantitative account of fish predation by piscivorous birds in the temporarily open /closed East Kleinemonde Estuary represents the first global attempt to simultaneously relate bird consumption to production by a fish community in the same estuary (Cowley et al. 2017). Based on comprehensive counts over three years, the piscivorous bird population was estimated to have consumed a maximum of 2 400 kg in 1995/96. Over the same period, fish production in the East Kleinemonde Estuary ( $56 \text{ g m}^{-2} \text{ a}^{-1}$ ) was estimated at 9 780 kg and maximum bird predation therefore amounted to 25% of annual fish production, assuming that all birds counted on the estuary foraged there and that the diet of these birds comprised only fish. The above figures, together with an estimate of fish predation by the dominant piscivorous fish *Lichia amia* of 696 kg, suggests that birds are probably the single most important

natural predator of fishes within this estuary.

Additional support for the view that piscivorous birds constitute a significant predation pressure on fishes in small Eastern Cape estuaries is provided by data from Froneman et al. (2011). These authors estimated that a maximum of 909 kg of fish were consumed by piscivorous birds in the small Riet Estuary (4.5 ha) between August 2005 and July 2006, equating to a consumption rate of approximately  $20 \text{ g m}^{-2} \text{ a}^{-1}$ . Using the same fish productivity estimate of  $56 \text{ g m}^{-2} \text{ a}^{-1}$  (Cowley & Whitfield 2002) from the nearby East Kleinemonde Estuary, the estimated bird consumption of annual fish production in the Riet Estuary is  $\pm 36\%$ . These figures imply that some small Eastern Cape TOCEs may be relatively poor fish nursery areas due to piscivorous birds being proportionately more abundant than in larger systems.

The mean daily piscivorous bird biomass at Lake St Lucia (31 000 ha) was estimated at 8 539 kg between March 1977 and February 1978 (Berruti 1983). The estimated mean daily fish consumption by these birds amounted to  $123 \text{ kg d}^{-1}$  or  $44 895 \text{ kg a}^{-1}$  ( $0.13 \text{ g m}^{-2} \text{ a}^{-1}$ ) for the entire St Lucia system. Average fish production for subtropical South African estuaries has been estimated to be approximately  $30 \text{ g m}^{-2} \text{ a}^{-1}$  (Whitfield 2016), which implies a very low predation pressure by piscivorous birds on fish populations in Lake St Lucia (0.43% of annual fish production) and therefore supports the fish nursery role interpretation for this particular system.

Clearly predation pressures exerted by piscivorous birds on estuarine fish populations appears to be highly variable in southern African systems, and estuarine size appears to be a critical factor in interpreting that pressure. The lack of quantitative information on both piscivorous bird and fish populations from southern African and global estuaries precludes a broader assessment of the role of these estuaries as nursery areas for fishes, particularly for those marine species whose juveniles make extensive use of these systems for food and shelter in their early years.

The Nile crocodile *Crocodylus niloticus* is the only major reptilian predator of fishes in southern African estuaries. Crocodiles were once





**Figure 145.** The African fish eagle *Haliaeetus vocifer* is an aerial piscivore that can capture a wide size range of fish (Photo: Tris Wooldridge).



**Figure 146.** An example of a wading piscivorous bird associated with estuaries, the goliath heron *Ardea goliath* with a captured estuarine bream *Acanthopagrus vagus* (Photo: Tris Wooldridge).



**Figure 147.** An example of a swimming piscivorous bird associated with estuaries, the whitebreasted cormorant *Phalacrocorax carbo* (Photo: Tris Wooldridge).



**Figure 148.** Although an aerial piscivore, the pied kingfisher *Ceryle rudis* spends much time perched on branches above the water looking for fish (Photo: Tris Wooldridge).





**Figure 149.** The little egret *Egretta garzetta*, a wading piscivore in shallow waters, with a freshly captured sole *Heteromycteris capensis* in its beak (Photo: Tris Wooldridge).



**Figure 150.** The giant kingfisher *Ceryle maxima* is capable of catching fish larger than any of the other kingfisher species found in association with southern African estuaries (Photo: Tris Wooldridge).



**Figure 151.** An adult Nile crocodile *Crocodylus niloticus* consuming a large *Mugil cephalus* at St Lucia (Photo: Alan Whitfield).

distributed in all major rivers and estuaries in the subtropical region of the subcontinent but are now only abundant in Lake St Lucia, with isolated populations present in a few estuaries to the north and south.

The prey of the Nile crocodile changes with size so that their dependence on fish as a dietary item also varies according to age and the availability of suitably sized fish. Crocodiles at St Lucia have been recorded preying on the following fish species, estuarine bream *Acanthopagrus vagus*, dusky kob *Argyrosomus japonicus*, sharptooth catfish *Clarias gariepinus*, flathead mullet *Mugil cephalus*, pike conger *Muraenesox bagio*, spotted grunter *Pomadasys commersonnii*, bull shark *Carcharinus leucas*, and lesser guitarfish *Rhinobatos annulatus*.

Heavy predation on adult *Mugil cephalus* in the St Lucia estuarine system by the Nile crocodile has been documented during the mullet spawning migration to the sea (Whitfield & Blaber 1979d). This opportunistic foraging activity appeared to be well anticipated by the crocodiles that gathered in large numbers in the Narrows just prior

to the *M. cephalus* shoals arriving in the area en route to the sea. Boat counts of crocodiles in the Narrows rose from less than 10 in February/March 1976, to 10-20 just prior to the arrival of the mullet shoals in April, to more than 50 in May when the *M. cephalus* passed through the Narrows (Whitfield & Blaber 1979d).

Crocodiles in the Narrows feed both singly and in groups. Nash (pers. comm.) observed nine crocodiles 2-3 m in length feeding on a school of migrating *M. cephalus*. The fish were invariably caught below the water surface and then carried to the shallows where the grip on the mullet was altered so that it could be swallowed head first (Figure 151). Foraging success by the crocodiles was very high, with very few misses recorded. The above situation represented co-operative foraging since, the more crocodiles feeding simultaneously, the greater is the confusion within the mullet school and the easier is the capture of these fast swimming and leaping fish by individual crocodiles. However, on one occasion two crocodiles captured the same fish and a 'tug of war' ensued for ownership of the catch.



Based on a mean daily fish intake of 1.1 kg of fish for a 2.5 m crocodile (modal size group in the Narrows), and the numbers of crocodiles counted in the Narrows from the air, an estimated 3.8 t of fish was consumed between the 23 April and 31 May 1976 (Whitfield & Blaber 1979d).

An interesting observation was made by Dunsterville (1968) on interactions between a Nile crocodile and a grey-headed gull *Larus cirrocephalus* at the top of the Narrows. The crocodile captured a large spotted grunter *Pomadasys commersonnii* of >1 kg in weight and took the fish to a mud bank to swallow. The grey-headed gull then proceeded to 'dive-bomb' the crocodile in an attempt to get it to drop the fish. The crocodile then retreated into the water where it

proceeded to complete its meal.

On a more successful avian piracy note, a white pelican *Pelecanus onocrotalus* was seen struggling to swallow a large mugilid at Lake St Lucia. A fish eagle *Haliaeetus vocifer* then attacked the pelican to gain access to the fish (Behr 1968). After a short struggle the eagle succeeded in wresting the mullet away from the pelican and then flew off with the pirated fish. In another bird piracy incident at Lake St Lucia, a goliath heron *Ardea goliath* was struggling to swallow a large fish when two white pelicans closed in on the heron to rob it of its prey. The heron dropped the fish which was picked up by one pelican. As the other pelican passed by, the heron aimed a powerful peck at the pelican's head, killing it instantly (Fourie 1968).



## Chapter 3

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### Estuary-associated fish species profiles

#### 1.1 INTRODUCTION

THE FISHES ASSOCIATED with southern African estuaries may be divided into four broad categories according to origin and spawning habits. Marine species usually breed at sea although some taxa have also been recorded spawning in the mouth region of selected estuaries. The juveniles of most marine species covered in this chapter utilize estuaries as nursery areas. Estuarine species generally spawn within the estuarine ecosystem, but several taxa have also been recorded breeding in both the marine or freshwater environment. For some of these fishes the entire life cycle occurs in estuaries, whereas for others part of the cycle is spent in either the sea or adjacent freshwater habitats. Freshwater species usually spawn in rivers, streams, lakes or pans, although some taxa (e.g. *Oreochromis mossambicus*) have also been recorded breeding in estuaries. Indeed, *O. mossambicus* in estuarine lakes and temporarily closed estuaries breed prolifically in what appear to be ideal habitats for this species. The fourth group comprises catadromous anguillid eels which spawn at sea but spend most of their life in river systems. Only the most common anguillid eel on the subcontinent is covered here.

A primary aim of this chapter is to provide a source of biological and ecological information on commonly encountered fishes in southern African estuaries. Some of the rare and unusual species occurring in estuaries have also been included to provide a more complete coverage of the range of fishes utilizing ecosystems on the subcontinent. Although the species profiles of some of the more abundant fishes are reasonably comprehensive, very little is known about the biology and ecology of a number of species, especially those that are small and cryptic. Hopefully this treatise will serve to stimulate research on these taxa, including some of those that are perceived to be rare or endangered.

The scientific and common names for marine and freshwater fish species are based on those used by Smith & Heemstra (1986a) and Skelton (2001) respectively, with the scientific names updated using Eschmeyer et al. (2019). In this chapter only a limited number of external diagnostic features are described for each species, with the lateral scale count (LS) being used wherever possible. In addition, selected anatomical features which are characteristic of each species are also given. For all the bony fishes (Osteichthyes) Roman numerals indicate spines and Arabic numerals indicate soft rays.

The fish illustrations were prepared by David Voorvelt and other professional illustrators, mainly from preserved specimens housed in the National Fish Collection of the South African Institute for Aquatic Biodiversity. However, the illustrations often benefitted from fresh material, colour plates or transparencies when available.

Wherever possible, standard length (SL) of bony fish and total length (TL) or disc width (DW) for cartilaginous fish illustrations are used. Fish lengths above 10 cm are given in centimetres whereas those below 10 cm are given in millimetres. The term body length (BL) is used for fish larvae.

Distribution maps are given for each of the 99 species covered and have been compiled from the published literature, museum records and unpublished data collected by the author. The distributions shown here apply to the confirmed occurrence of species in estuaries and the marine environment. It should be emphasized that although fishes have the potential to colonize all estuaries within a particular distributional range, their actual occurrence in individual systems is determined by a wide variety of environmental factors, e.g. species that favour clear water are unlikely to occur in highly turbid estuaries and

turbid water species are usually absent from clear estuaries within a particular biogeographic region.

In addition, there are likely to be seasonal variations in the distributional patterns of certain species, with the range of some tropical taxa extending southwards during summer and retreating northwards during the winter. Conversely, some

of the more temperate species may extend their distribution northwards during winter but are then forced southwards with the onset of summer. For the purposes of this book the maximum range for each species is depicted on the distributional map, i.e. full summer and winter ranges are included in the overall distribution.

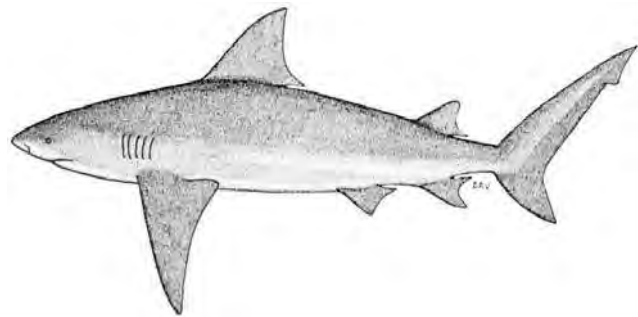
### 3.2 MARINE GUILD

Family: CARCHARHINIDAE

Species: *Carcharhinus leucas*  
(Müller & Henle 1839)

Common name: Bull shark, Zambezi shark

Illustrated specimen length: 166 cm TL



#### Selected anatomical features

Tooth count: Upper jaw; 26 lateral, 2 central

Lower jaw; 24 lateral, 2 central

First dorsal fin height up to 3.1 times

second dorsal fin height

Maximum recorded length in southern

African waters:  $\pm 400$  cm TL

#### Distribution

*Carcharhinus leucas* is a predominantly inshore warm-water shark, known from all the major oceans (Bass et al. 1986) and extending to 150 m depth (Compagno et al. 1989). Within local waters this species ranges from Mozambique to the Breede Estuary in the southwest (McCord & Lamberth 2009).

#### Biology and ecology

Growth of this species slows with age, being  $15\text{--}20\text{ cm y}^{-1}$  for the first five years,  $10\text{ cm y}^{-1}$  for years 6–10,  $5\text{--}7\text{ cm y}^{-1}$  for years 11–16, and  $<4\text{--}5\text{ cm y}^{-1}$  thereafter (Branstetter & Styles 1987). Sexual maturity is attained at approximately 20 years of age and a length of between 180–190 cm (Wintner et al. 2002). The summer mating season is prolonged (Cliff & Dudley 1991) and probably occurs in subtropical coastal waters (Bass et al. 1973). The young are born during summer of the following year after a gestation period of approximately 10–11 months (van der Elst 1988).



Gravid females often congregate in the mouth of the St Lucia and other large turbid estuaries to give birth to about 9 young, each measuring about 55 cm precaudal length (Cliff & Dudley 2010). *Carcharhinus leucas* juveniles forage in estuaries, occasionally visit the sea, or ascend into rivers (Day et al. 1981). Large numbers of juveniles occur in the turbid Mzimvubu Estuary which they use as a nursery area (Cowley pers. comm.).

Juvenile bull sharks in Lake St Lucia have been regularly recorded in salinities ranging from 10–47 (Bass et al. 1973). The absence of *C. leucas* from the northern sections of the lake when salinities were above 50 suggests that this species leaves areas of extreme hypersalinity. Juveniles sometimes move into the larger river systems of tropical and subtropical Africa, and specimens have been captured hundreds of kilometres up



large river systems (Skelton 2001). Adult *C. leucas* do enter the lower reaches of some southern African estuaries (e.g. Mzimvubu) but do not appear to penetrate the upstream rivers. Although bull sharks are associated with a wide range of turbidities, this species is strongly attracted to turbid waters in rivers, estuaries and the marine environment (Cliff & Dudley 1991).

D'Aubrey (1971) noted that young *C. leucas* from KwaZulu-Natal feed mainly on teleost fish, with a higher proportion of elasmobranchs in the diet of larger specimens. According to Bass et al. (1973) this reflects not so much a change in food preference as a change in the availability

of different types of prey in estuaries compared to the sea. Bull sharks in Lake St Lucia and other KwaZulu-Natal estuarine systems consume mainly mugilids and haemulids, although a wide variety of other teleost fish species such as *Argyrosomus japonicus*, *Acanthopagrus vagus* and *Rhabdosargus sarba* are also captured.

Although small sharks, skates and rays dominated the diet of *C. leucas* in the marine environment, dolphins, turtles and crabs are also taken. The presence of terrestrial mammalian remains in the stomach contents of bull sharks from both the estuarine and marine environment suggest that this species is also a scavenger.

Family: PRISTIDAE

Species: *Pristis zijsron* (Bleeker 1851)

Common name: Longcomb sawfish

Illustrated specimen length: 109 cm TL

#### Selected anatomical features

Rostral tooth count: 24-28 pairs of lateral saw teeth

Space between basal two teeth 3-6 times space between distal two teeth

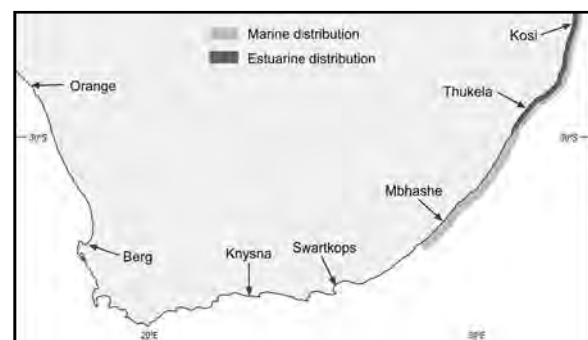
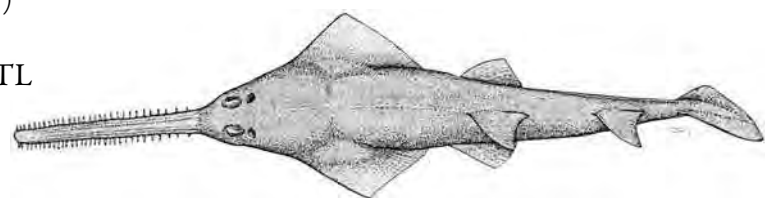
Maximum recorded length in southern African waters:  $\pm 550$  cm TL

#### Distribution

*Pristis zijsron* has a mainly tropical Indo-West Pacific distribution, extending from New South Wales in Australia to South Africa. Within local waters it was an inshore marine species that entered some of the larger estuaries and rivers during the early 1900s (Compagno et al. 1989). A relative of this species, *Pristis pristis*, is found in the estuaries and larger rivers of Mozambique (Skelton 2001) and may also have entered South African estuaries. Unfortunately both *P. zijsron* and *P. pristis* are now regarded as being extinct in local waters (Everett et al. 2015).

#### Biology and ecology

Due to previous misidentification, the biological and ecological information supplied by Wallace (1967a), Compagno (1986a) and van der Elst



(1988) for *P. pectinata* from southern African waters applies to *P. zijsron*.

Sexual maturity for *P. zijsron* occurs between 380 at 430 cm TL (Compagno 1986a, Peverell 2008). All sawfishes are ovoviviparous with adult female *P. zijsron* having been recorded entering the St Lucia Estuary and Richards Bay to pup. Each of the 15-20 young is about 60 cm long at birth and has its saw enveloped in a membrane to avoid injuring the mother (van der Elst 1988).

The young often remain in estuaries and bays

which are used as nursery areas. Gill netting in the St Lucia and Richards Bay estuarine systems during the 1960s and 1970s revealed that significantly smaller specimens were captured in these estuaries when compared to those recorded in the inshore marine environment (Everett et al. 2015).

The longcomb sawfish occurs in salinities ranging from oligohaline to euhaline and where temperatures are above 20°C. This mainly littoral species has been recorded in turbid and clear water areas, as well as over both muddy and sandy substrata.

The diet of *P. zijsron* in southern Africa consists of slow swimming and shoaling fish, especially mugilids that are killed or stunned by thrashing the saw from side to side. This is evident from fish scales that are often found impaled on the

rostral teeth and from foraging behaviour observed whilst in captivity. *Pristis zijsron* can feed in highly turbid water, and has also been recorded preying on prawns, crabs and bivalves (van der Elst 1988).

Extinction probability analysis indicates that sawfish no longer occur in South African waters (Everett et al. 2015). Human impacts on many estuarine systems, particularly angling and environmental degradation, gill netting along the KwaZulu-Natal coast for bather protection, and illegal fish harvesting at St Lucia and Richards Bay, are probably the primary reasons for the disappearance of sawfish from the subcontinent (Everett et al. 2015). The loss of this important top piscivore is likely to impact on food webs within systems such as St Lucia.

Family: TORPEDINIDAE

Species: *Torpedo fuscomaculata* (Peters 1855)

Common name: Blackspotted electric ray

Illustrated specimen length: 27 cm TL

#### Selected anatomical features

Small caudal fin and small papillae around the spiracles

Dull grey above with variable markings, underside white

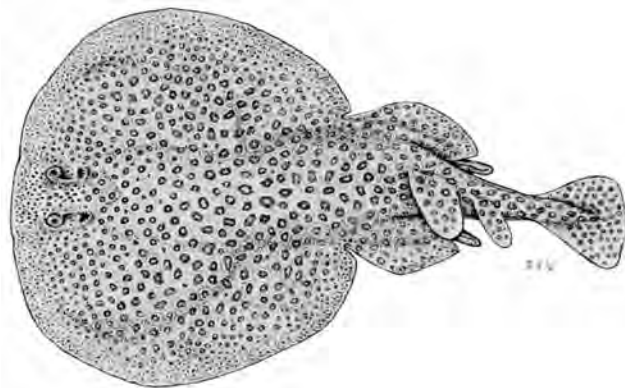
Maximum recorded length in southern African waters:  $\pm 64$  cm TL

#### Distribution

*Torpedo fuscomaculata* is described by Compagno et al. (1989) as ranging from Cape Agulhas to southern Mozambique. Although this species has also been reported as occurring in the Seychelles, Mauritius, Madagascar and Zanzibar (Wallace 1967b), the identity of these specimens is uncertain (Compagno et al. 1989). The closely related marbled electric ray *Torpedo sinuspersici* also occurs in estuaries and is sometimes confused with *T. fuscomaculata*.

#### Biology and ecology

The blackspotted electric ray is sometimes a common inhabitant of the shallow lower and middle reaches of estuaries, but also occurs down to the



upper slope of the continental shelf at approximately 440 m depth. *Torpedo fuscomaculata* is ovoviviparous and the young are born in summer (Compagno et al. 1989), sometimes in estuaries (Smith 1965).

The ray is propelled by the caudal fin and not the enlarged fleshy pectoral fins. This species is

generally sluggish and individuals sometimes get stranded in the intertidal areas of estuaries on the outgoing tide. According to Smith (1965) they can survive for hours when left stranded on moist sand by the receding water. The absence of this species from estuaries where average salinities are less than 15 suggests that it may be sensitive to mesohaline and oligohaline conditions.

*Torpedo fuscomaculata*, has two large kidney shaped electric organs in the disc on either side of the head. These organs are capable of generating strong electric shocks which are administered at will (Compagno 1986b) but decline in effectiveness if repeated at very short intervals (Smith 1965). This species has been observed to stun both demersal and pelagic fishes but probably target fish on or near the bottom.

The blackspotted electric ray is a solitary species which frequently buries itself beneath the substratum during the day but is active at night when most foraging takes place. The jaws have small cuspidate teeth and the mouth is highly

distensible. Electric shocks are probably used, not only to stun fish prey, but also as a deterrent to potential predators such as sharks.

A 31 cm TL specimen captured in the Kariega Estuary was found to have swallowed a 13 cm SL Cape stumpnose *Rhabdosargus holubi* (Paterson 1995). From the size of the mouth, it is apparent that the ray immobilises its prey and the highly distensible jaw mechanism enables it to cope with the swallowing of large fish. According to Compagno et al. (1989) they consume merlucciids, cynoglossids, engraulids, sparids, gonorhynchids, carangids and triglids in the marine environment.

Laboratory observations by Paterson (1995) indicate that bottom dwelling gobies and clinids were preferred to midwater species and that most feeding takes place at night. He also noted that the blackhand sole *Solea turbynei* was not preyed upon by *T. fuscomaculata* despite its benthic habits, and in many cases this sole was observed burying itself in the sand layer covering the ray.

Family: MYLIOBATIDAE

Species: *Myliobatis aquila* (Linnaeus 1758)

Common name: Common eagle ray

Specimen width: 36 cm DW

#### Selected anatomical features

Snout broad and short, pectoral tips blunt

Disc brown to black above, underside white

Maximum recorded disc width in southern

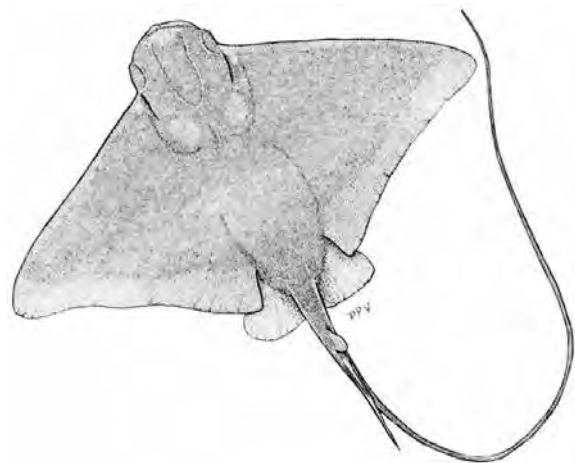
African waters:  $\pm 150$  cm

#### Distribution

The common eagle ray ranges from the Mediterranean and eastern Atlantic around Cape Point to KwaZulu-Natal. It is described by Compagno (1986c) as a mainly coastal species that readily enters shallow bays and estuaries. Within the marine environment it occurs in shelf waters down to at least 95 m (Compagno et al. 1989).

#### Biology and ecology

*Myliobatis aquila* is commonest in warm-temperate Eastern and Western Cape waters where it is



often found in groups (Compagno et al. 1989). This species is most abundant during summer and usually swims just below the water surface when not foraging, sometimes breaking the surface with its wings. Individuals can be trapped by the closure of estuary mouths and appear to tolerate the declining salinity levels within such systems. A powerful swimmer, the eagle ray occasionally leaps from the water, the purpose of which is not fully understood (van der Elst 1988).

Sexual maturity is attained at a disc width of 50 cm, with females tending to be larger than males. This species is ovoviviparous and after a

gestation period of almost a year, females give birth to 3-7 live young in shallow water (van der Elst 1988), sometimes in estuaries (Smith 1965)

Foraging occurs mainly in bottom waters since their diet consists mostly of bivalves, gastropods, brachyurans, echinurids, anomurans, polychaetes, tunicates and small bony fish such as gobies and eels (Compagno et al. 1989). The upper and lower jaws have seven rows of plate-like teeth for crushing the molluscan and crustacean prey. As a deterrent to predators, *M. aquila* has one or two serrated spines near the base of its tail.

Family: DASYATIDAE

Species: *Himantura leoparda*

(Manjaji-Matsumoto & Last 2008)

Common name: Honeycomb stingray

Specimen width: 34 cm DW

#### Selected anatomical features

Disc 1.0-1.1 times disc length; tail 2.6-3.0 times longer than disc

Conspicuous dark spots or reticulations on a light brown disc, underside white

Maximum recorded disc width in southern African waters:  $\pm 200$  cm

#### Distribution

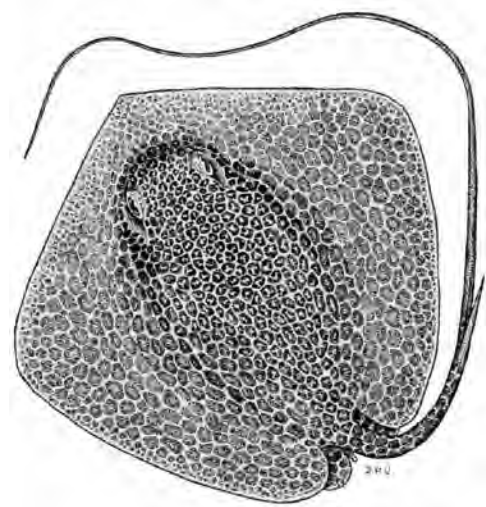
The honeycomb stingray is a widespread Indo-West Pacific species (Compagno 1986b). Within southern Africa it extends from the Eastern Cape to Mozambique, being more abundant in the subtropical waters of KwaZulu-Natal than the warm-temperate region farther south. This stingray is common off sandy beaches and in shallow estuaries, extending from the intertidal zone to offshore banks down to 50 m (van der Elst 1988).

#### Biology and ecology

*Himantura leoparda* occurs in KwaZulu-Natal waters throughout the year, although it is most abundant during the summer months (Wallace 1967c). They attain sexual maturity at a disc width of approximately 100 cm, which corresponds to an age of 4-5 years. During the summer 3-5 young

are born after a one year gestation period (van der Elst 1988).

The honeycomb stingray has been recorded in salinities ranging from 2-35 and shows considerable tolerance of reduced salinities and turbid conditions found in muddy estuaries such as Lake St Lucia. Respiration in silty environments is facilitated by the large spiracles situated on top of the head behind the eyes and through which clean water is taken in.





Foraging may occur singly or in small groups, with a tendency to move into littoral estuarine waters at night. The strong, pavement-like teeth are used to crush molluscs, crabs and prawns that constitute the major portion of the ray's diet. Tube worms are also occasionally eaten (van der Elst 1988).

Family: ELOPIDAE

Species: *Elops machnata* (Forsskal 1775)

Common name: Skipjack

Illustrated specimen length: 33 cm SL

#### Selected anatomical features

Fin elements: Dorsal 22-27;

Anal 15-18; Pectoral 17-18

Lateral scales: 90-103

Maximum recorded length in southern

African waters:  $\pm 85$  cm SL

#### Distribution

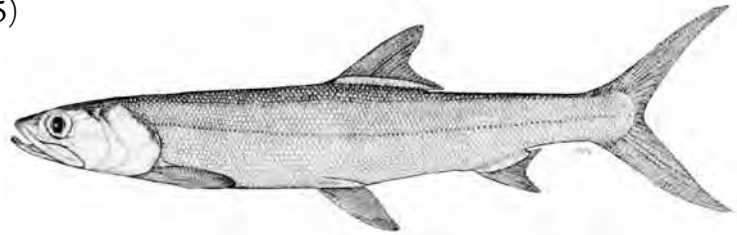
The skipjack has a range extending from the Breede Estuary northwards to the Red Sea, India, and into the western Pacific (Smith 1986a). Within southern Africa, both juveniles and adults are well represented in the larger subtropical estuaries and some systems along the Eastern Cape coast. Large individuals have also been recorded in warm-temperate southern Cape estuaries (Smith 1965) but early juveniles are absent from these systems.

#### Biology and ecology

Little is known about gonadal development or spawning phases in the life cycle of this species in southern Africa. Wallace (1975b) found a single reproductively active specimen in KwaZulu-Natal but no ripe individuals were recorded. According to van der Elst (1988) large shoals of breeding adults are found off Mozambique during winter.

The transparent leptocephali larvae enter KwaZulu-Natal and Eastern Cape estuaries between 20 mm and 40 mm BL during spring and summer (Melville-Smith & Baird 1980, Harris & Cyrus 1995), often congregating in the upper reaches. Although juveniles <20 cm SL are often recorded in estuaries they are not abundant.

*Himantura leoparda* has 1-3 stout spines near the base of the tail. These spines are poisonous and are used as a defence mechanism. Despite this mechanism, the species has been recorded as part of the diet of *Carcharinus leucas* (Cliff & Dudley 1991). Honeycomb stingrays may attain at least 24 years of age, by which stage they weigh almost 120 kg (van der Elst 1988).



The recorded salinity range of this fish is 0-95, with the larva sometimes entering freshwater areas above the ebb and flow of certain estuaries, e.g. in the Great Fish and Nahoon rivers. Adults were recorded in Lake Nhlange at salinities <1 (Blaber & Cyrus 1981) and no individuals were documented dying during the May 1976 oligohaline fish kill in Lake St Lucia (Blaber & Whitfield 1976). This species did, however, perish in salinities above 95 in the temporarily closed Seekoei Estuary (Whitfield 1998).

*Elops machnata* has been recorded in a wide range of turbidities, from less than 10 NTU to more than 80 NTU. It is classified by Cyrus & Blaber (1987a) as a turbid water species because almost 70% of the specimens captured at St Lucia occurred in 51-80 NTU waters.

Skipjack forage mainly during the early evening, either individually or in small groups (van der Elst 1988). The diet of specimens greater than

28 cm SL in southern African estuaries has been well studied and indications are that this mainly visual predator utilizes both fish and crustaceans as food (Whitfield & Blaber 1978a, Marais 1984, Hecht & van der Lingen 1992). Although relatively slow swimming clupeids (e.g. *Gilchristella aestuaria*) are favoured prey items, faster swimming mugilids are also captured. Penaeid prawns and mysids are the dominant invertebrate taxa consumed.

It would appear that increasing turbidity levels cause a modification of its foraging strategies from capturing fast moving prey organisms with a higher escape probability (e.g. fish) to slow moving taxa with a lower escape probability (e.g. mysids) (Hecht & van der Lingen 1992). The large tubular mouth and well developed gill rakers create an effective sieving apparatus that allows for ram ventilation and the effective capture of large or small pelagic prey in highly turbid waters.

Family: MEGALOPIDAE

Species: *Megalops cyprinoides* (Broussonet 1782)

Common name: Oxeye tarpon

Illustrated specimen length: 26 cm SL

#### Selected anatomical features

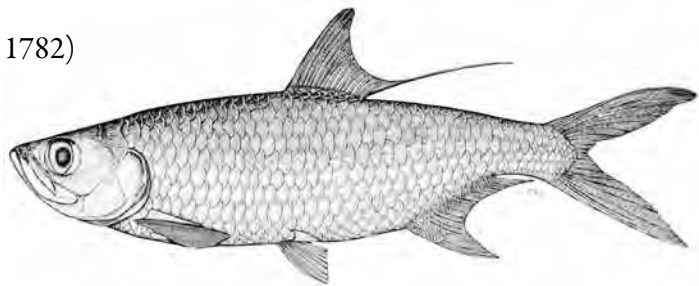
Fin elements: Dorsal 17-20;

Anal 24-31; Pectoral 15-16

Lateral scales: 36-40

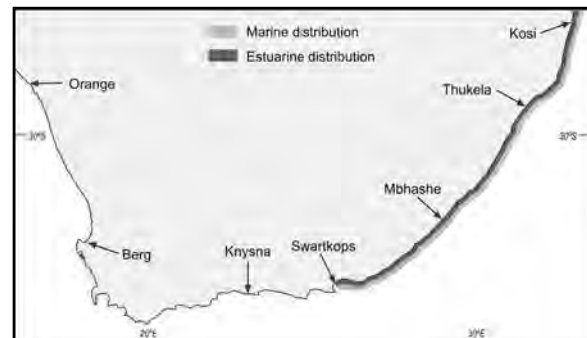
Maximum recorded length in southern

African waters:  $\pm 70$  cm SL



#### Distribution

*Megalops cyprinoides* is a tropical Indo-West Pacific species extending into the subtropical waters of southern Africa. It favours estuaries but has been reported from as far inland as the lower Shire River in Malawi, and the Save-Runde junction in Zimbabwe (Skelton 2001). Stray specimens reach as far south as Algoa Bay and are usually associated with estuaries in the region (Smith 1986b).



#### Biology and ecology

This predominantly solitary species is found in marine, estuarine and fresh water environments (van der Elst 1988). Breeding occurs at sea with the leptocephali larvae entering estuaries at a length of between 17 mm and 31 mm BL (Harris & Cyrus 1995).

Postlarvae and early juveniles of the oxeye tarpon appear to be attracted to floodplain brackish or freshwater lakes and pans which they enter when these systems are linked to the adjacent estuary. Skelton et al. (1989) recorded juvenile

*M. cyprinoides* (27-39 mm SL) entering the freshwater Mkhuze swamps from Lake St Lucia following a summer river flood.

Crass (1964) collected trapped adult *Megalops cyprinoides* (maximum size = 54 cm FL) in southern Lake Bhangazi, a freshwater system that is only connected to Lake St Lucia (via a swamp) following episodic rainfall events. Early juveniles could migrate up this swamp from South Lake during such periods but adults would remain trapped in Lake Bhangazi unless a major water level increase occurred.

This species is strongly euryhaline with a southern African salinity range from 0-38 but has been recorded elsewhere in salinities up to 100. Tarpons are among the few marine fishes known to breathe air, rising regularly to the surface to do so. The swim bladder is modified for this purpose (Skelton 2001).

*Megalops cyprinoides* is a powerful swimmer, able to hunt at speed and consuming small pelagic fish, the juveniles of larger species, and shrimps (van der Elst 1988). Foraging by the oxeye tarpon can occur both at night and during the day, with all prey, regardless of size, being swallowed whole due to the absence of cutting teeth.

Family: MURAENIDAE

Species: *Strophidon sathete* (Hamilton 1822)

Common name: Slender giant moray

Illustrated specimen length: 79 cm TL

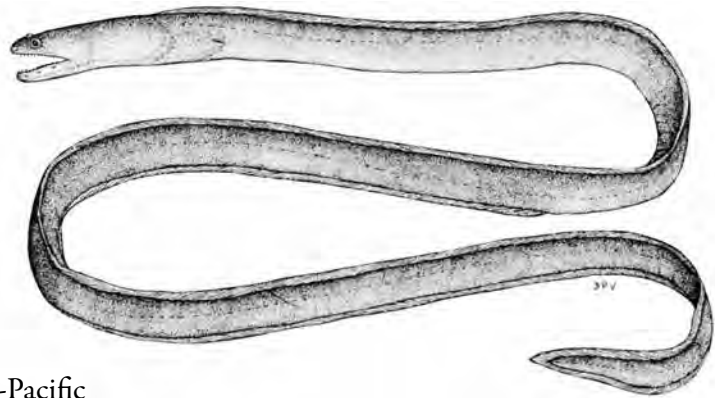
#### Selected anatomical features

Body depth  $\pm 40$  in total length

Body length 1.5-2.0 in tail length

Maximum recorded length in southern

African waters:  $\pm 300$  cm TL



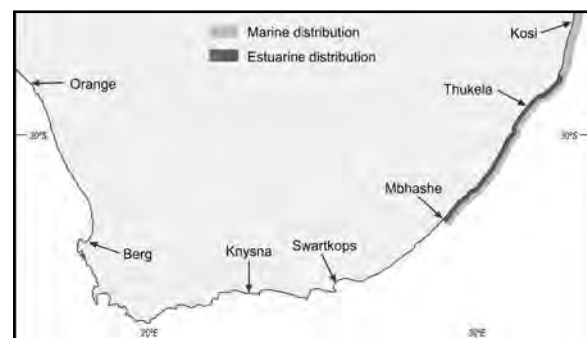
#### Distribution

This moray is a widespread tropical Indo-Pacific species, extending into the subtropical waters of southern Africa where it is more abundant in the sea than estuaries. Specimens have been collected as far south as the Mbashe Estuary (Castle & McCosker 1986).

#### Biology and ecology

Although the slender giant moray is often captured by KwaZulu-Natal anglers in estuaries, very little is known about this species. *Strophidon sathete* is usually solitary and confined to coastal waters and offshore banks (van der Elst 1988). In terms of estuaries, this species favours large systems with muddy bottoms. According to Harris & Cyrus (1995) *S. sathete* leptocephali larvae (19-100 mm BL) enter the St Lucia Estuary when it is open.

This moray is resident in the turbid St Lucia Narrows (Millard & Broekhuysen 1970). The brownish body colouration provides effective camouflage in muddy systems where it feeds on



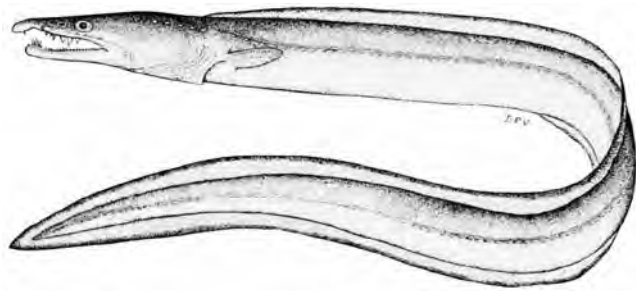
demersal fish, prawns and small crabs (van der Elst 1988). Some of the sharp conical teeth in both jaws are depressible (Smith 1965), a feature that may aid prey retention. Despite its strong marine links, this species is highly euryhaline and can tolerate a range of salinities from 10-70.

Family: MURAENESOCIDAE

Species: *Muraenesox bagio* (Hamilton 1822)

Common name: Pike conger

Illustrated specimen length: 48 cm TL



#### Selected anatomical features

Dorsal rays before anus: 47-49

Body depth 16-22 in total length

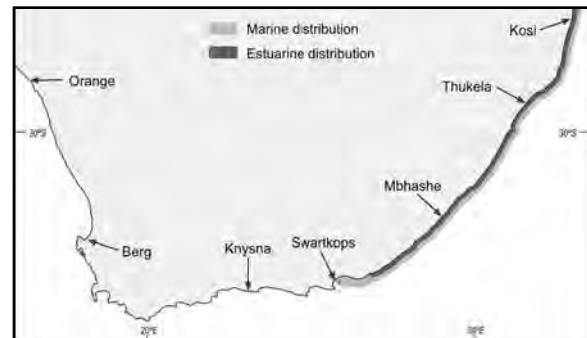
Lateral line pores before anus: 33-39

Maximum recorded length in southern

African waters:  $\pm 175$  cm TL

#### Distribution

The pike conger is an Indo-Pacific species, extending into Eastern Cape waters, with a coastal distribution extending to 100 m depth (Castle 1986a). In southern Africa it is most common in larger KwaZulu-Natal estuaries, particularly muddy systems such as Lake St Lucia, Richards Bay and Mhlathuze.



#### Biology and ecology

This species reaches sexual maturity at approximately 100 cm TL and spawning occurs at sea during spring and early summer (van der Elst 1988). Leptocephali larvae 73-85 mm BL have been recorded entering the St Lucia Estuary (Harris & Cyrus 1995), a system that can harbour large numbers of adults within the lake compartments.

The pike conger is a predominantly solitary species which may shelter in burrows or depressions (van der Elst 1988). It is often found over muddy bottoms and is particularly common in turbid areas of Lake St Lucia and Richards Bay. The recorded salinity range of *M. bagio* is 0-35 (Whitfield 1996a) but it has not been recorded entering southern African rivers.

This species was absent from the upper sections of Lake St Lucia when salinities increased above 35, indicating an intolerance to hypersaline conditions. However, it was abundant in the same parts of the system when salinities were <20.

*Muraenesox bagio* is a predator and scavenger of dead or decaying fish. Both jaws are armed with several rows of sharp teeth, some of which are enlarged into canines. When the mouth is closed, these larger teeth slot into cavities in the opposite jaw. Prey taxa include *Johnius dorsalis*, *Pomadasys kaakan* and mugilids, as well as prawns (van der Elst 1988). Fish species consumed by adult pike conger (90-143 cm TL) in Lake St Lucia include *Solea turbynei*, *Johnius dorsalis* and *Leiognathus equula* (Whitfield & Blaber 1978a).

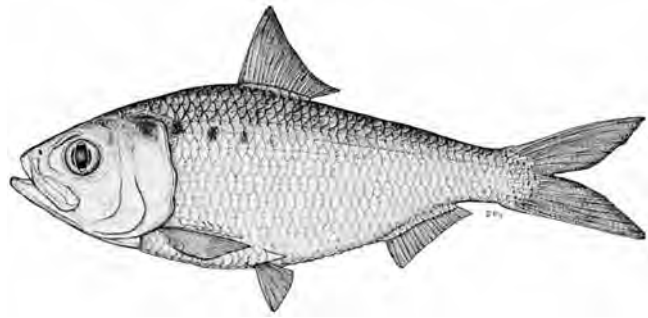


Family: CLUPEIDAE

Species: *Hilsa kelee* (Cuvier 1829)

Common name: Kelee shad

Illustrated specimen length: 19 cm SL



### Selected anatomical features

Fin elements: Dorsal 16-19;

Anal 17-23; Pectoral 13-16

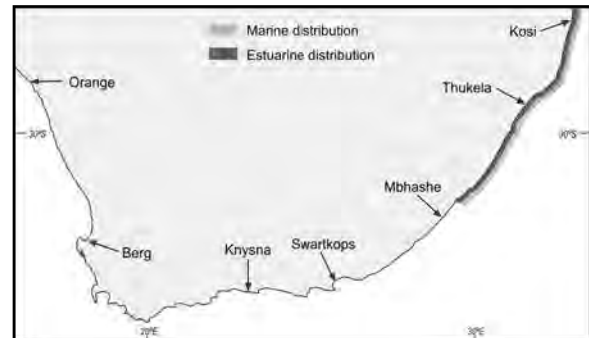
Lateral scales: 39-44.

Maximum recorded length in southern

African waters:  $\pm 27$  cm SL

### Distribution

The kelee shad is a widespread tropical Indo-West Pacific species (Whitehead & Wongratana 1986a), extending as far south as the Eastern Cape. Within subtropical southern African estuaries this species is sometimes abundant in the larger turbid northern KwaZulu-Natal systems.



### Biology and ecology

*Hilsa kelee* starts maturing after one year at a length of approximately 15 cm SL (van der Elst 1988). Spawning usually occurs in the marine environment although ripe-running specimens have been recorded in Durban Bay during December (Wallace 1975b). The breeding season covers the period September-February, with spent individuals sometimes entering estuaries.

Recruiting juveniles 20-40 mm SL usually occupy the lower reaches of estuaries (van der Elst 1988). Juveniles (30-50 mm SL) were recorded in Lake St Lucia during February 1978 and grew approximately 10 mm per month to reach a length of 110 mm SL by August 1978 (Blaber 1979).

The kelee shad is a pelagic shoaling fish that frequents deeper areas of an estuary where salinities range from 3-35 (Whitfield 1996a). This species avoids hypersaline and freshwater conditions, and was recorded dying when salinities declined below 3 and water temperatures were  $< 12^{\circ}\text{C}$  (Blaber & Whitfield 1976).

In the St Lucia system, Blaber (1979) found that the diet of *H. kelee* juveniles was dominated by centric diatoms, calanoid copepods and gastropod veligers. A variety of other zooplankters were also consumed, including cyclopoid copepods, amphipods and brachyuran zoeae. Adults were also pelagic filter feeders and the diet was dominated by calanoid copepods and centric diatoms.

There was no strong positive selection for particular food items in Lake St Lucia and *H. kelee* was found to have a relatively fine filtering apparatus, with the gill raker and denticle gap altering little after a fish length of about 70 mm SL (Blaber 1979). He also determined that *H. kelee* forages throughout the 24 h cycle, with a peak in the early evening.

Although kelee shad are an important food source for large predators such as the king mackerel (*Scomberomorus commerson*) and various species of tuna in the marine environment (van der Elst 1988), very few are consumed by piscivorous fishes in estuaries (Whitfield & Blaber 1978a).

Family: ENGRAULIDAE

Species: *Stolephorus holodon* (Boulenger 1900)

Common name: Thorny anchovy

#### Selected anatomical features

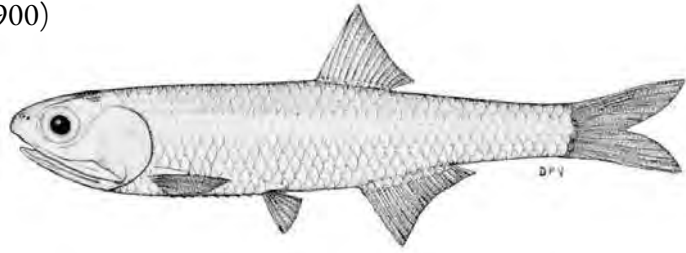
Fin elements: Dorsal 15-17;

Anal 20-23; Pectoral 12-14

Lateral scales: 38-40

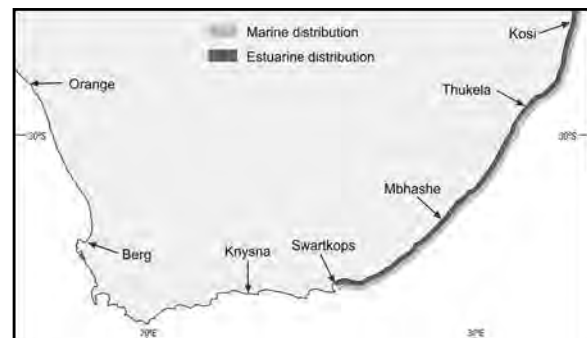
Maximum recorded length in southern

African waters:  $\pm 90$  mm SL



#### Distribution

An inshore marine and estuarine species *Stolephorus holodon* is endemic to eastern and southern Africa, ranging from Kenya to the Eastern Cape Province (Whitehead & Wongratana 1986b). Although the larvae, juveniles and adults of *S. holodon* have been recorded in the lower reaches of a number of southern African open estuaries, this species seldom penetrates the middle and upper reaches of these systems.



#### Biology and ecology

*Stolephorus holodon* reaches sexual maturity at a length of approximately 50 mm SL, with gonads being inactive in winter and ripe during summer (Blaber 1979).

Spawning by this shoaling species usually occurs in the nearshore marine environment, but *S. holodon* eggs have also been recorded in the St Lucia estuarine system (Connell 1996). The eggs are oval in shape and were present in Lake St Lucia in small numbers between September and April 1994. However, higher numbers of eggs were present in the St Lucia Estuary mouth region towards the end of September 1993 (Connell 1996) and *S. holodon* as a species ranked second of all fish larvae sampled in the mouth of Durban Bay (Harris & Cyrus 1999). Ichthyoplankton sampling in the nearshore marine environment adjacent to the St Lucia Estuary revealed moderate numbers of

preflexion, flexion, postflexion and juveniles of this species (Harris et al. 1999).

The thorny anchovy is a moderate osmoregulator and has been recorded in salinities from 7-40. The apparent absence of this species from Lake St Lucia during oligohaline (<5) and hypersaline (>40) periods suggests that *S. holodon* is sensitive to extreme salinity.

The diet of the planktivorous *Stolephorus holodon* in Lake St Lucia was dominated by the copepod *Pseudodiaptomus*, with gastropod post-veligers, mysids and bivalve spat also being consumed (Blaber 1979).

Although this fish is consumed by *Argyrosomus japonicus* in Lake St Lucia, the thorny anchovy is unimportant as a dietary item when compared to *Thryssa vitrirostris*, the other engraulid prey of the dusky kob in the lake.

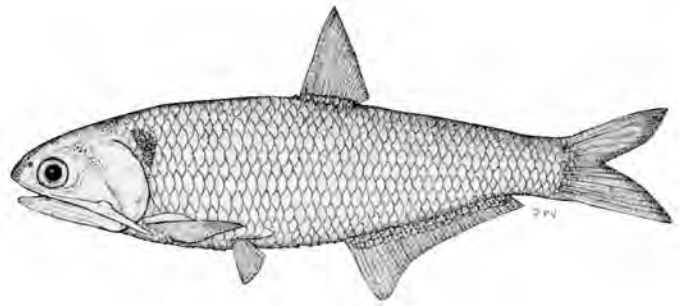
Family: ENGRAULIDAE

Species: *Thryssa vitrirostris*

(Gilchrist & Thompson 1908)

Common name: Orangemouth glassnose

Illustrated specimen length: 14 cm SL



### Selected anatomical features

Fin elements: Dorsal 13-14;

Anal 34-43; Pectoral 12-13

Lateral scales: 40-44

Maximum recorded length in southern

African waters:  $\pm$  18 cm SL

### Distribution

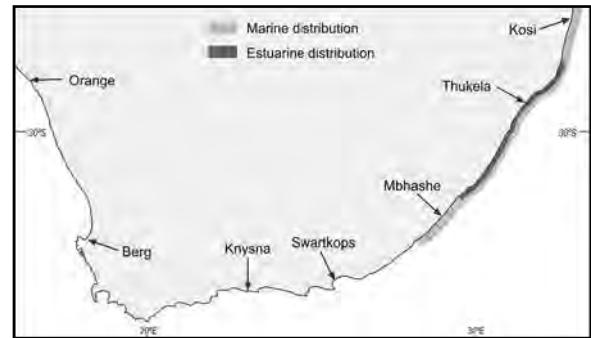
This anchovy is most common in tropical and subtropical bays of the Indian Ocean region, from South Africa to the Persian Gulf and India (Whitehead & Wongratana 1986b). Within southern African estuaries *T. vitrirostris* is abundant in the larger turbid northern KwaZulu-Natal systems and rare in warm-temperate estuaries. The closely related longjaw glassnose, *Thryssa setirostris*, also occurs in the estuaries of KwaZulu-Natal but in much lower numbers.

### Biology and ecology

Sexual maturity by *T. vitrirostris* is attained after one year at a length of approximately 80 mm SL (Blaber 1979). Spawning usually occurs in the nearshore marine environment but has been recorded in certain estuarine lakes and bays (Wallace 1975b). At Lake St Lucia, large numbers of reproductively active fish (12-18 cm SL) appeared between July and September 1977 but actual spawning events were not recorded.

Following spawning, it appeared that most of the adults left Lake St Lucia for the sea, although small numbers of reproductively spent individuals did remain within the system (Blaber 1979). Larvae first appeared in the lake during spring and the subadults emigrated during the following winter when the adults arrived in the lake. No individuals of this species were recorded in the system following prolonged estuary mouth closure.

*Thryssa vitrirostris* is a strong osmoregulator and has been recorded in salinities ranging from 1-67. Hypersaline conditions in Lake St Lucia



during 1970 may have accounted for an absence of viable larvae during that spawning season (Wallace 1975b). This is a turbid water species, with 98% of the specimens captured in Lake St Lucia being associated with water turbidities >50 NTU (Cyrus & Blaber 1987a).

The diet of *T. vitrirostris* <20 mm SL in the St Lucia system was dominated by copepods, and those between 20 mm and 90 mm SL consumed copepods, mysids and a variety of other planktonic organisms (Blaber 1979). Large shoals of the orangemouth glassnose feed in synchrony, each individual opening its mouth wide and using its elaborate gill rakers to strain zooplankton from the water (van der Elst 1988).

Adults greater than 100 mm SL prey mainly on small fish (<30 mm SL), especially the clupeid *Gilchristella aestuaria* which shares the same habitat. Foraging in the turbid waters of Lake St Lucia occurs between the bottom and mid-water level and takes place during both the day and night (Blaber 1979). The diet of adults in the marine environment consists mainly of fish and crustaceans (e.g. mysids and cumaceans).

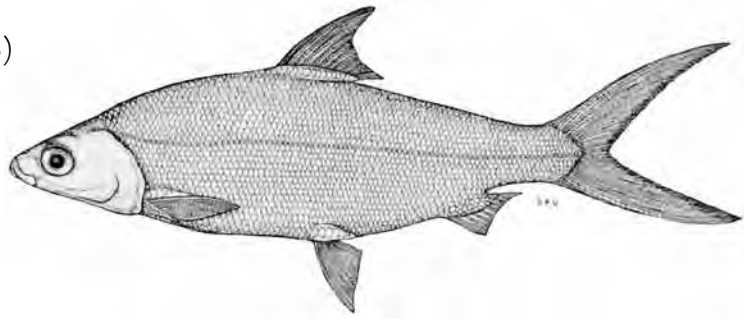
This species is intensively utilized by piscivorous fishes such as *Argyrosomus japonicus* in Lake St Lucia (Whitfield & Blaber 1978a) and is an important food source for gamefish in the marine environment (van der Elst 1988).

Family: CHANIDAE

Species: *Chanos chanos* (Forsskal 1775)

Common name: Milkfish

Illustrated specimen length: 18 cm SL



### Selected anatomical features

Fin elements: Dorsal 13-17;

Anal 8-10; Pectoral 15-17

Lateral scales: 78-90

Maximum recorded length in southern

African waters:  $\pm 120$  cm SL

### Distribution

The milkfish is widely distributed in those tropical and subtropical waters of the Indo-Pacific region which are enclosed by the 20°C isotherm (Bagarinao 1994). This species is sometimes common in the larger subtropical estuarine lakes and bays on the KwaZulu-Natal coast, with a few individuals having been recorded in the warm-temperate region as far south as Swartvlei.



### Biology and ecology

Adults of this species are most common in Lake St Lucia during the summer and appear to leave this system between June and September, possibly due to declining water temperatures (Whitfield & Blaber 1978b). Sexual development of the females begins at 50 cm TL and males at about 90 cm but both sexes are reproductively active by the age of 4 years (van der Elst 1988).

Spawning occurs at sea, usually at night, and is strongly seasonal (Bagarinao 1994). The fertilized eggs are pelagic, spherical and approximately 1 mm in diameter, with transport mainly occurring by passive advection. Once the larvae are >9 mm BL (2 to 3 weeks old) they move inshore via active migration which is a feature of the early life stages (Bagarinao 1994). The larvae (10-15 mm BL) enter South African estuaries during summer where a metamorphosis into pigmented juveniles occurs (Harris & Cyrus 1995).

Juvenile and subadult milkfish occur in both clear and turbid estuarine systems along the southern African coast. In Lake St Lucia they

have been recorded in salinities ranging from 1-72 (Whitfield 1996a) and appear to tolerate temperatures from 13-41°C (Bagarinao 1994). Temperatures lower than 23°C decrease food intake, growth and development of larvae and juveniles (Villaluz & Unggui 1983).

Shoals of *C. chanos* are frequently seen feeding over shallow estuarine banks, with their dorsal fins and tails protruding from the water (Smith 1965). The diet in Lake St Lucia consists mainly of benthic meiofauna such as foraminiferans, gastropods, bivalves, tanaids, ostracods, copepods and zoeae larvae, together with particulate organic matter and detritus (Whitfield & Blaber 1978b). According to van der Elst (1988) milkfish feed mainly on particulate organic matter and benthic micro-organisms, with occasional small crustaceans, worms and fish also being consumed.

*Chanos chanos* was not recorded as a prey item of any of the piscivorous fish in Lake St Lucia (Whitfield & Blaber 1978a), possibly due to their relatively large size in this system, together with an exceptionally powerful swimming ability.

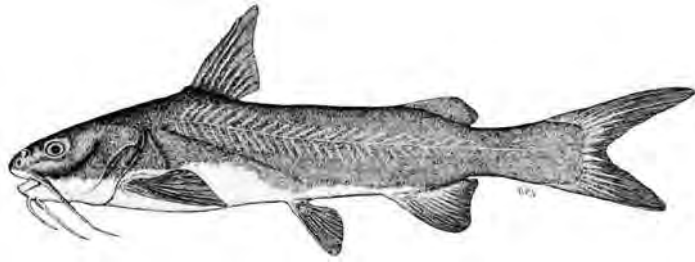


Family: ARIIDAE

Species: *Galeichthys feliceps*  
(Valenciennes 1840)

Common name: White seacatfish

Illustrated specimen length: 23 cm SL



### Selected anatomical features

Fin elements: First dorsal I, 7;

Anal 17-21; Pectoral I, 9-11

Lateral silvery stripe sometimes present

Maximum recorded length:  $\pm 45$  cm SL

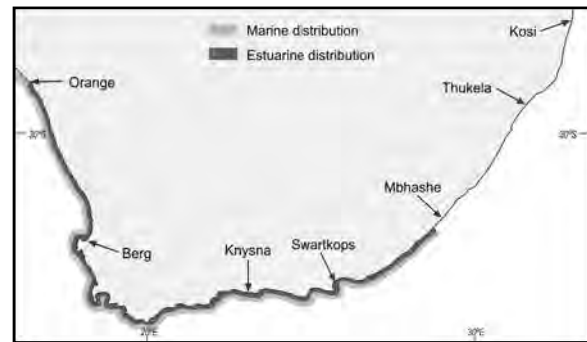
### Distribution

This southern African endemic frequents both the sea and estuaries, from Namibia to the Eastern Cape. Although *G. feliceps* occurs mainly in water less than 30 m deep, it has been recorded down to 60 m (Tilney & Hecht 1990). This sluggish species prefers protected waters and is frequently found in underwater caves and below rocky ledges in the marine environment (van der Elst 1988). Within estuaries they are most abundant in turbid, muddy areas, with the early juveniles often associated with plant beds.

### Biology and ecology

White seacatfish females mature at 24 cm SL and males at 26 cm SL. Little is known of the spawning behaviour of this species, but it is the only marine fish in southern African estuaries with paternal buccal incubation. The eggs are relatively large (16 mm in diameter) and the average brood size is 49 (Tilney & Hecht 1993). Ventilation of the eggs by the adult is carried out using the branchial pump mechanism, with a considerable current of water passing over the embryos during breathing movements. Hatching occurs at between 75 and 80 days, with the juveniles being released after 140 days at 54 mm TL (Tilney & Hecht 1993).

*Galeichthys feliceps* males lose up to 24% of their total body mass during the incubation period as they do not feed while mouth brooding. Males with eggs frequent estuaries during spring and summer, with a peak between September and December (Marais & Venter 1991). The sex ratio of 1:1 for adults in the marine environment contrasts to the 7:1 ratio in favour of males in Eastern Cape estuaries and is indicative of the



nursery function of these systems for this species.

Although *G. feliceps* is most frequently recorded in the lower and middle reaches of permanently open estuaries, this species is also found in certain estuarine lake systems (Whitfield 1993). *Galeichthys feliceps* is a strong osmoregulator but large numbers were recorded dying in the temporarily closed Bot Estuary at a salinity of approximately 3 (Bennett 1985) and in the Seekoei Estuary when salinities rose above 90 (Whitfield 1998).

Foraging is exclusively benthic and the well-developed barbels, together with a large mouth, aid prey detection and consumption in muddy waters. The diet of *G. feliceps* in estuaries is dominated by anomurans and brachyurans, with macrurans, mysids, isopods, gastropods, cephalopods, polychaetes and fish also being consumed (Marais 1984, Coetzee & Pool 1985, Tilney & Hecht 1990).

In the marine environment this species preys mainly on brachyurans, echinurids and polychaetes. The high incidence of teleost scales in the diet of juveniles was found to be a consequence of scavenging and not lepidophagy (Tilney & Hecht 1990). White seacatfish can consume large amounts of food, with up to 19% of body mass being recorded in the stomachs of some specimens. (Marais 1984).

Family: BELONIDAE

Species: *Strongylura leiura* (Bleeker 1851)

Common name: Yellowfin needlefish

Illustrated specimen length: 44 cm SL

### Selected anatomical features

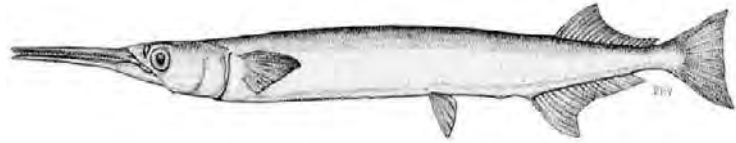
Fin elements: Dorsal 18-21;

Anal 22-26; Pectoral 11-12

Predorsal scales: 121-152

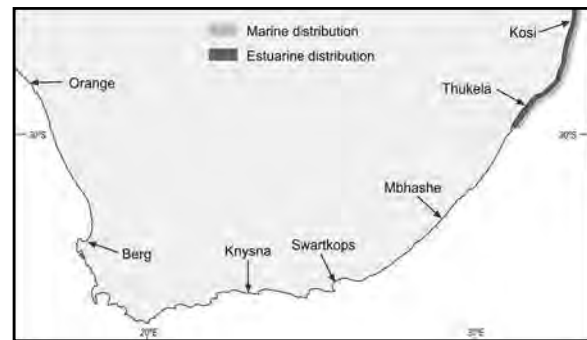
Maximum recorded length in southern

African waters:  $\pm 73$  cm SL



### Distribution

The yellowfin needlefish has a mainly tropical and subtropical Indo-West Pacific distribution, ranging from southern China and northern Australia to KwaZulu-Natal (Collette 1986a). Despite a preference for surface waters, this species is rarely recorded in offshore areas within its distributional range.



### Biology and ecology

This needlefish is an inshore marine and estuarine species which spawns in KwaZulu-Natal waters during spring and summer. Although females in a ripe condition have been captured in Lake St Lucia during October, none of the typically large eggs or larvae have been recorded in KwaZulu-Natal estuarine systems. It has been suggested that since the postlarvae are seldom found in inshore habitats, the early developmental stages probably occur offshore (van der Elst 1988).

*Strongylura leiura* has been recorded in salinities ranging from 3-38 (Whitfield 1996a) and occurs in both clear and turbid estuaries, thus suggesting an indifference to water clarity. The prime limiting factor in the distribution of this tropical species in southern African estuaries is probably its absence from estuaries where winter water temperatures fall below 14°C, since it is not found south of Durban (Collette 1986a).

The yellowfin needlefish is most abundant in the surface waters of estuarine lakes and bays where it is often seen chasing small fish in the

shallows. It is capable of considerable bursts of speed, and when disturbed can 'skip' across the water surface using powerful thrusts from its tail (van der Elst 1988). More than 80% of the yellow-fin needlefish captured in gill nets at Lake St Lucia occurred in the upper 30 cm of the water column, and this probably accounts for the high selectivity by fish eagles for this species (Whitfield & Blaber 1978d).

The diet of *S. leiura* in estuaries is dominated by surface dwelling and midwater fishes such as mugilids, engraulids, hemiramphids, atherinids, ambassids and clupeids, with terrestrial insects floating on the water surface also being consumed (Hill et al. 1975, Whitfield & Blaber 1978a).

The parasitic cestode *Ptychobothrium belones* was found in the intestines of 63% of the *S. leiura* examined in Lake St Lucia and are probably due to *Hyporhamphus capensis* prey being an intermediate host (Whitfield & Heeg 1977). The primary host is likely to be one of the calanoid copepod species in the lake that are frequently consumed by *H. capensis*.

Family: HEMIRAMPHIDAE

Species: *Hemiramphus far* (Forsskal 1775)

Common name: Spotted halfbeak

Illustrated specimen length: 16 cm SL

#### Selected anatomical features

Fin elements: Dorsal 13-15;

Anal 11-13; Pectoral 11-12

Predorsal scales: 36-41

Maximum recorded length in southern

African waters:  $\pm 47$  cm SL



#### Distribution

*Hemiramphus far* occurs throughout the tropical and subtropical waters of the Indo-West Pacific. Within southern Africa this species is common from Maputo Bay to Knysna, with a few records west to False Bay (Collette 1986b).



#### Biology and ecology

Sexual maturity is attained at a length of 25 cm SL and the breeding season lasts from October to March (Smith 1933). Spawning usually occurs in the marine environment but has also been recorded in estuarine bays such as Knysna. Females produce up to 12 000 large eggs ( $\pm 3$  mm diameter) per season. The eggs have numerous glutinous filaments by which they attach to floating objects and aquatic plants (van der Elst 1988).

The larvae have no prolongation of the lower jaw, and adult proportions are only attained at 50-60 mm TL (Smith 1933). A peak in juvenile (50-100 mm TL) numbers in the Knysna Estuary occurs during January and February (Whitfield & Kok 1992).

Although *Hemiramphus far* has a recorded salinity range of 0-35, individuals are usually confined to the lower reaches of estuaries where salinities are higher. Within Knysna this species occurs throughout the estuary but is most abundant in the lower reaches (Whitfield & Kok 1992).

The small mouth bears very fine teeth but the lower jaw extension makes the capture and consumption of large invertebrates and small fishes difficult. The diet consists primarily of aquatic plants and pelagic invertebrates, the latter being gathered by raising the short upper jaw so as to skim the water surface. Small shrimps, crab larvae, and even insects floating on the surface are part of the diet of this species (van der Elst 1988).

Family: PLATYCEPHALIDAE

Species: *Platycephalus indicus* (Linnaeus 1758)

Common name: Bartail flathead

Illustrated specimen length: 21 cm SL

#### Selected anatomical features

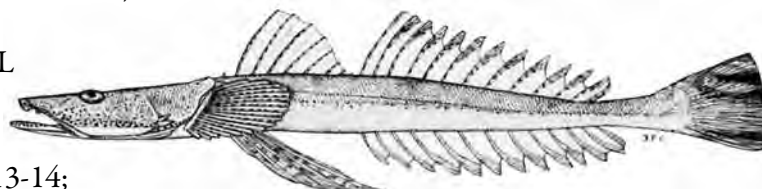
Fin elements: Dorsal I/VII-VIII/I+13-14;

Anal 13; Pectoral 18-20

Lateral scales: 68-82

Maximum recorded length in southern

African waters:  $\pm 86$  cm SL



### Distribution

The bartail flathead is a widespread, mainly tropical Indo-West Pacific species found in estuaries and shallow water to about 15 m (Knapp 1986). Within southern Africa, this species ranges from the Mossel Bay area eastwards into the subtropical waters of KwaZulu-Natal. In permanently open estuaries this species is most common in the lower reaches.

### Biology and ecology

Sexual maturity is attained at 36 cm SL. Although a single ripe-running female was recorded in the St Lucia Estuary during November, spawning is not considered to be an estuarine function. The spawning season ranges between July and November (Wallace 1975b) but juveniles are seldom recorded in estuaries.

The recorded salinity range of the bartail flathead is from 1-58 (Whitfield 1996a) and this species also shows considerable tolerance to fluctuating turbidities (van der Elst 1988). *Platycephalus indicus* is common in both sandy and muddy estuaries where its colouration blends well with these surroundings making it inconspicuous, especially when it buries itself below the mud



surface with only its eyes exposed (van der Elst 1988). The function of the brightly patterned caudal fin is unknown.

*Platycephalus indicus* is an ambush predator (i.e. it does not actively pursue its prey), feeding on shrimps, penaeid prawns, crabs, mysids, polychaete worms, and small fishes such as *Johnius dorsalis*, *Solea turbynei*, *Thryssa vitrirostris*, *Gilchristella aestuaria* and a wide variety of gobies (Whitfield & Blaber 1978a, Day et al. 1981, Marais 1984). The extremely broad mouth, diversity of habitat types occupied (including marine surf zones), and camouflage colouration assists in the capture of a wide variety of invertebrate and fish prey.

Family: KUHLIIDAE

Species: *Kuhlia mugil*

(Bloch & Schneider 1801)

Common name: Barred flagtail

Illustrated specimen length: 95 mm SL

### Selected anatomical features

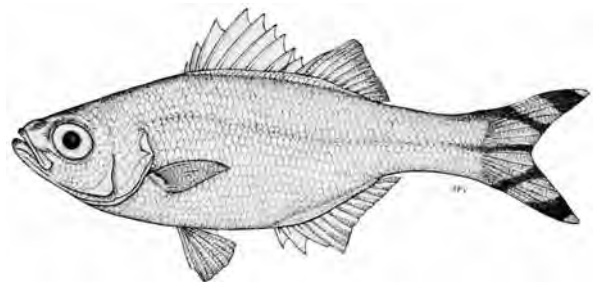
Fin elements: Dorsal X, 9-11;

Anal III, 9-11; Pectoral 14

Lateral scales: 48-56

Maximum recorded length in southern

African waters:  $\pm 16$  cm SL



### Distribution

The barred flagtail is abundant throughout the coastal regions of the tropical Indo-Pacific, from the Galapagos to Africa, extending as far south as Cape Agulhas (Smith 1986c). The closely related rock flagtail *Kuhlia rupestris* also occurs in northern KwaZulu-Natal estuaries but can be



distinguished from *K. mugil* by the absence of five dark stripes through the caudal fin.

### Biology and ecology

This species is often recorded from subtropical estuaries, sometimes extending into almost fresh water (Smith 1965). Spawning occurs throughout the year off the KwaZulu-Natal coast and the

juveniles mainly use tidal pools as nursery areas (Smith 1986c).

The adults are common in the surf zone habitat, with shoals sometimes congregating in the sheltered lee of reefs (van der Elst 1988). The diet consists mainly of zooplankton such as crab larvae and krill, but small fish are also eaten by large individuals.

Family: TERAPONTIDAE

Species: *Terapon jarbua* (Forsskal 1775)

Common name: Thornfish

Illustrated specimen length: 11 cm SL

### Selected anatomical features

Fin elements: Dorsal XI-XII, 9-11;

Anal III, 7-10; Pectoral 13-14

Lateral scales: 69-93

Maximum recorded length in southern

African waters:  $\pm 26$  cm SL

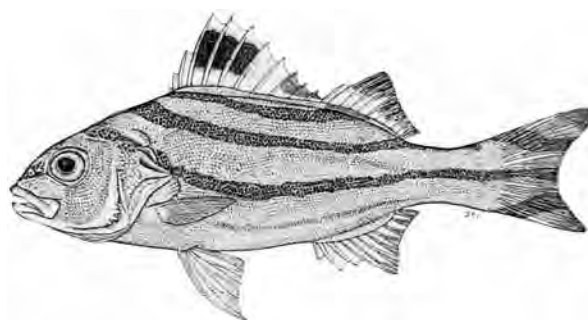
### Distribution

The thornfish is widely distributed in the tropical and subtropical Indo-West Pacific region, extending into the warm-temperate waters of the southeast coast of Africa. This species occurs in both the marine and estuarine environment but is more abundant in the latter.

### Biology and ecology

Sexual maturity is attained at 13 cm SL, with spawning occurring in KwaZulu-Natal waters during the late spring and summer (Day et al. 1981). Juveniles 10-30 mm SL enter estuaries between November and May (Wallace & van der Elst 1975). Shoals of juveniles 10-20 mm SL are sometimes caught in the lower reaches of Eastern Cape estuaries during the summer but appear to leave these systems before the onset of winter.

Occasional specimens are found as far west as Knysna where they were associated with a warm water power station outlet. The juveniles and adults of this species are often abundant in KwaZulu-Natal estuaries, sometimes extending into freshwater areas adjacent to these systems (Heemstra 1986a).



*Terapon jarbua* is a strong osmoregulator and has been recorded in salinities ranging from 0-72 (Whitfield 1996a). Although it can survive oligohaline conditions under warm water conditions (Blaber & Cyrus 1981), low salinities in combination with low temperatures (12°C) cause mass mortalities (Blaber & Whitfield 1976). This species is associated with water turbidities ranging from less than 10 NTU to greater than 80 NTU (Cyrus & Blaber 1987c). Based on field and laboratory choice chamber experiments (Cyrus & Blaber 1987a, 1987b), *T. jarbua* can be regarded as being indifferent to water turbidity.

New recruits (<30 mm SL) feed mainly on copepods and amphipods, but a wide variety of other organisms are also consumed (Whitfield 1985). Larger juveniles and adults have been recorded feeding mainly on fish scales removed from living fishes, as well as both terrestrial and



aquatic invertebrates (Whitfield & Blaber 1978a). *Terapon jarbua* always attacks the lateral surface of the prey species and scales are removed mainly from the posterior region of the body, particularly around the caudal peduncle. Underwater observations of their hunting behaviour have been

described by Whitfield (1979) in estuaries and by van der Elst (1988) in the marine environment. The former observations indicate a predominantly active foraging mode by small schools of juveniles, whereas the latter describes a solitary mode of feeding by adults.

Family: POMATOMIDAE

Species: *Pomatomus saltatrix* (Linnaeus 1766)

Common name: Elf

Illustrated specimen length: 24 cm SL

#### Selected anatomical features

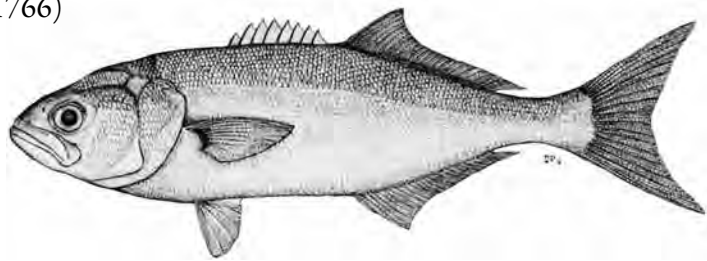
Fin elements: Dorsal VII-VIII+I, 23-28;

Anal II, 23-27; Pectoral 16

Lateral scales: 90-100

Maximum recorded length in southern

African waters:  $\pm 80$  cm SL



#### Distribution

The elf occurs in all oceans between latitudes 50°N and 50°S (Smith & Smith 1986a). Within southern Africa it is known to occur on the west coast but is particularly common along the south and east coasts, declining in abundance towards Mozambique (van der Elst 1976).



#### Biology and ecology

Most *P. saltatrix* become sexually active at 24 cm TL for males and 25 cm TL for females. The life cycle of this species involves lengthy migrations each winter from the Eastern Cape to Kwa-Zulu-Natal. Following maturation in spring, spawning takes place between September and January, with a peak in November (van der Elst 1976).

The Thukela Bank has been identified as one spawning area, with other southern African breeding grounds also likely. The pelagic larvae drift passively in shelf waters and are transported southwards, partially assisted by the Agulhas Current (Beckley & Connell 1996).

The 0+ juveniles spend their first year in the warm-temperate coastal waters, with some individuals utilizing estuaries in the region. Juveniles (<40 mm TL) enter the Knysna Estuary between

September and December (Whitfield & Kok 1992). Subadults and adults leave warm-temperate estuaries at the end of summer to join shoals on the annual migration to KwaZulu-Natal waters (Day et al. 1981).

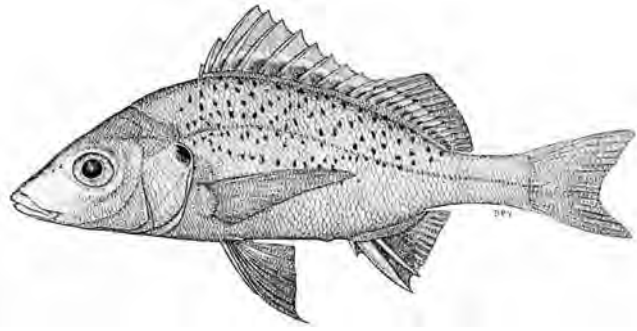
The recorded salinity range of elf is 8-49 (van der Elst 1976, Whitfield 1996a), with most specimens found in the lower reaches of permanently open estuaries where salinities are similar to those in the sea. However, small numbers have been recorded in South Lake, more than 30 km from the sea under mesohaline conditions. Mortalities of *P. saltatrix* were recorded in the temporarily closed Bot Estuary when salinities declined to 3 (Bennett 1985).

Family: HAEMULIDAE

Species: *Pomadasys commersonnii*  
(Lacepède 1801)

Common name: Spotted grunter

Illustrated specimen length: 13 cm SL



### Selected anatomical features

Fin elements: Dorsal XI, 14-15;

Anal III, 9-10; Pectoral 17-19

Lateral scales: 52-54

Maximum recorded length in southern

African waters:  $\pm$  69 cm SL

### Distribution

The spotted grunter is a mainly shallow water (<30 m depth) western Indian Ocean species (Smith & McKay 1986). Within southern Africa it is common along the eastern coast, with occasional specimens recorded as far west as False Bay during summer (Day et al. 1981).

### Biology and ecology

Most males are mature by 30cm and females by 36 cm SL. Spawning usually occurs at sea between August and December (Wallace 1975b) although breeding has been recorded in the marine dominated Durban Bay. Viable eggs have also been collected in the St Lucia system during August and September (Connell 1996). Partially spawned fish penetrate short distances into estuaries and on rare occasions ripe-running specimens seem to stray into this environment from adjacent spawning areas (Wallace 1975b).

Egg and larval development occurs at sea, with juveniles first entering estuarine nursery areas at 20-30 mm TL (Wallace & van der Elst 1975). In certain Eastern Cape estuaries, juveniles <50 mm SL are abundant in the upper reaches during the summer months, often extending their distribution into fresh water (Ter Morshuizen et al. 1996a). According to Wallace & van der Elst (1975) the recruitment into KwaZulu-Natal estuaries is maximal during early spring and summer.

First year juveniles grow approximately 12-15 mm per month in the first year (Wallace 1975a), at which stage they return to the sea. Growth rates of these 0+ juveniles is most rapid in an isosmotic salinity (12) rather than lower (5) or higher



(25 and 35) salinities (Deacon & Hecht 1999). Following sexual maturity, mass increments range from 600-700 g per annum. Fish which reach the maximum recorded size of 87 cm TL are approximately 15 years of age (Wallace & Schleyer 1979).

*Pomadasys commersonnii* has been recorded in salinities from 0-90 and can survive salinities <1 for prolonged periods (Blaber & Cyrus 1981). However, mass mortalities of this species have been recorded in the Kosi and St Lucia systems when salinities declined below 4 and coincided with water temperatures below 13°C (Blaber & Whitfield 1976). Similarly, the entire population was eliminated from the temporarily closed Seekoei Estuary when salinities increased above 90 (Whitfield 1998).

The thermal preference and growth of 0+ juveniles was found to be optimal between 24°C and 25°C (Deacon & Hecht 1995, 1996). Laboratory studies on dissolved oxygen consumption by *P. commersonnii* have been conducted by du Preez et al. (1986a) and faecal and non-faecal energy losses by this species have been investigated by du Preez & Cockcroft (1988a). Field sampling and laboratory experiments have shown that the spotted grunter is indifferent to water turbidity (Cyrus & Blaber 1987c, Hecht & van der Lingen 1992).

Juveniles newly recruited into estuaries prey mainly on pelagic copepods and mysids (Woolridge & Bailey 1982), prior to adopting a predominantly benthic foraging mode. Adults of this important angling species are primarily crepuscular and nocturnal, foraging predominantly on

benthic dwelling anomurans and bivalves (Marais 1984, Hecht & van der Lingen 1992). Mud prawns *Upogebia africana* are extracted from their burrows using a gill chamber pump action which rapidly blows water out of the mouth, causing infauna to become suspended and then captured.

Family: HAEMULIDAE

Species: *Pomadasys kaakan* (Cuvier 1830)

Common name: Javelin grunter

Illustrated specimen length: 12 cm SL

#### Selected anatomical features

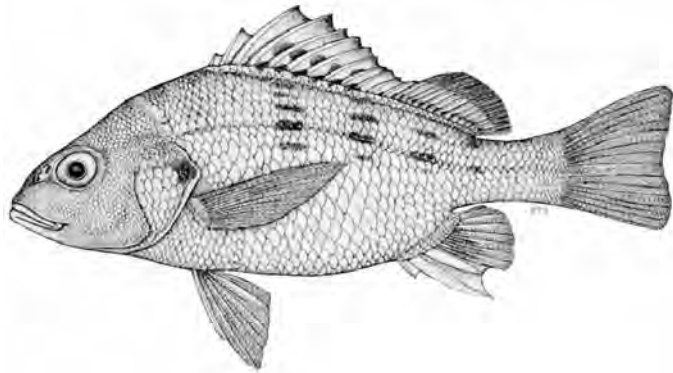
Fin elements: Dorsal XII, 13-15;

Anal III, 7-8; Pectoral 17-18

Lateral scales: 43-47

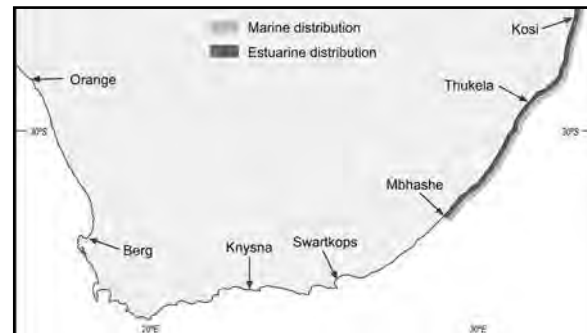
Maximum recorded length in southern

African waters:  $\pm 51$  cm SL



#### Distribution

The javelin grunter has a mainly tropical Indo-West Pacific distribution, extending into the subtropical waters of southern Africa (Smith & MacKay 1986). This species is rare in most estuaries within the region but are sometimes common in the larger, more turbid northern KwaZulu-Natal systems (e.g. Richards Bay). Water temperature appears to be a primary determinant governing the distribution of *P. kaakan*, with the species avoiding estuaries where winter water temperatures fall below 14°C



#### Biology and ecology

The length at sexual maturity is unknown since *P. kaakan* is mainly inactive in the estuarine environment. According to van der Elst (1988) spawning takes place during winter, often in the vicinity of estuary mouths. A small sample obtained from the Thukela Banks in June included specimens with ripe running and partially spawned gonads (Wallace 1975b). A few reproductively spent individuals have been recorded entering estuaries.

Length frequency distributions in the KwaZulu-Natal estuarine environment indicate that recruitment of juveniles first occurs at lengths <40 mm TL, with most of the population being <12 cm TL (Wallace 1975a).

This species is tolerant of salinities between 4 and 44. Although it has been recorded in the riverine dominated Thukela Estuary it is usually absent from Lake St Lucia under oligohaline conditions. According to Cyrus (1992) *P. kaakan* is indifferent to turbidity.

Early juveniles feed extensively on copepods, later changing to a demersal diet of small crabs and polychaetes (van der Elst 1988). During foraging, *P. kaakan* blasts the benthos with a jet of water ejected from the mouth. The moderately developed gill rakers may assist with the filtering of food organisms during feeding, but quantities of fine sediment are also ingested (van der Elst 1988).

Family: HAEMULIDAE

Species: *Pomadasys olivaceus* (Day 1875)

Common name: Piggy

Illustrated specimen length: 10 cm SL

#### Selected anatomical features

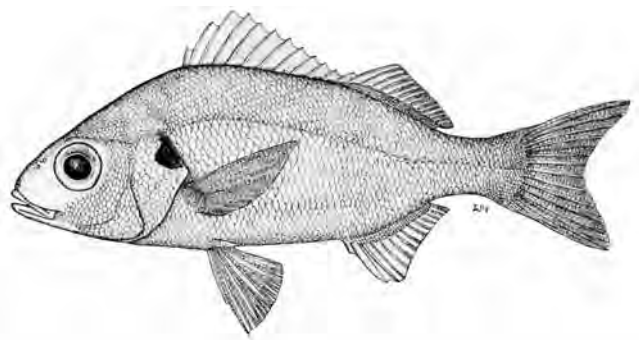
Fin elements: Dorsal XII, 15-17;

Anal III, 11-13; Pectoral 16-17

Lateral scales: 51-54

Maximum recorded length in southern

African waters:  $\pm 21$  cm SL



#### Distribution

The piggy has a mainly tropical Indo-West Pacific distribution but also occurs in cool-temperate waters of the Cape west coast. The juveniles of this predominantly marine species occur in large shoals around shallow-water outcrops whereas the adults are generally associated with deeper offshore reefs (van der Elst 1988). Juveniles are sometimes common in warm-temperate estuaries, especially in the vicinity of submerged plant beds (Smith & McKay 1986).

#### Biology and ecology

*Pomadasys olivaceus* matures at about 14 cm FL (Joubert 1981). Spawning takes place in deep water (van der Elst 1988) and the breeding season is prolonged (March-December). Juveniles (<50 mm TL) occurred throughout the year in Algoa Bay (Lasiak 1983b) but only between April and January around inshore reefs along the KwaZulu-Natal coast (Joubert 1981). This size group was most abundant in the Knysna Estuary during December (Whitfield & Kok 1992).

Beam trawls off the Swartkops Estuary mouth revealed that piggy juveniles were the dominant species captured, comprising 76% of the total catch (Beckley 1984b).

Although *P. olivaceus* is generally confined to the lower half of estuaries, stragglers have been recorded from the upper reaches of the Knysna and Swartvlei systems where salinities often decline below 10. The piggy is sensitive to rapid changes in temperature, with extensive mortalities having been recorded when cold upwelling events occur along the coast (Smith & McKay 1986).

Juveniles in estuaries feed mainly on amphipods, with polychaetes, small crabs and prawns also being important (Day et al. 1981). Within the sea, juveniles forage on shrimps, penaeid prawns, polychaetes and mysids, whereas adults consume mainly stomatopods, small fish, shrimps, penaeid prawns and crabs (Joubert & Hanekom 1980).

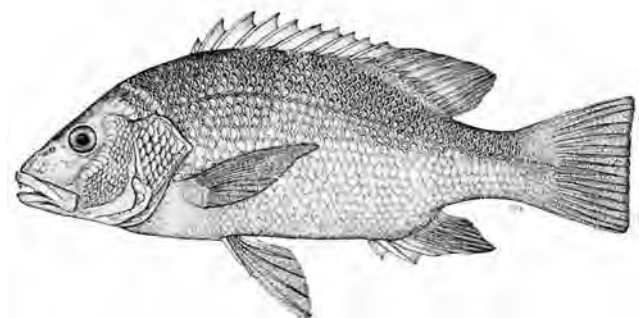
The piggy is an important forage fish and is preyed upon by piscivores such as *Lichia amia* in estuaries (Marais 1984) and *Pomatomus saltatrix* in the sea (van der Elst 1988).

Family: LUTJANIDAE

Species: *Lutjanus argentimaculatus*  
(Forsskål 1775)

Common name: Mangrove snapper

Illustrated specimen length: 22 cm SL



### Selected anatomical features

Fin elements: Dorsal X, 13-14;

Anal III, 7-8; Pectoral 16-17

Lateral scales: 46-47

Maximum recorded length in southern

African waters:  $\pm 85$  cm SL

### Distribution

*Lutjanus argentimaculatus* ranges from the Red Sea and tropical Indo-West Pacific region, south to Port Elizabeth (Anderson & Allen 1986). The juveniles are sometimes common in subtropical southern African estuaries, especially permanently open systems where mangroves are present.

### Biology and ecology

Sexual maturity is attained between 45 and 60 cm TL, with spawning occurring during summer in offshore marine waters. The larvae are widely dispersed by ocean currents and when the juveniles are about 50 mm TL they migrate into littoral nursery areas. Within estuaries this species favours rocky areas or the prop roots of mangrove swamps (van der Elst 1988). Adults and sub-adults return to the sea where they occur down to a depth of 100 m.



The recorded salinity range of juvenile mangrove snapper in southern African estuaries is 1-35. Although *L. argentimaculatus* is frequently recorded from some of the larger subtropical estuaries, it is also capable of surviving prolonged oligohaline conditions in small temporarily closed estuaries and may even enter large rivers on the subcontinent. This fish also occurs in both clear (e.g. Kosi) and turbid (e.g. Thukela) estuaries.

The mangrove snapper is an ambush predator. In estuaries *L. argentimaculatus* feeds mainly on mugilids and sparids, although crabs and prawns are also consumed. In the marine environment a variety of reef fish and crabs are eaten (van der Elst 1988).

Family: LUTJANIDAE

Species: *Lutjanus fulviflamma* (Forsskal 1775)

Common name: Dory snapper

Illustrated specimen length: 14 cm SL

### Selected anatomical features

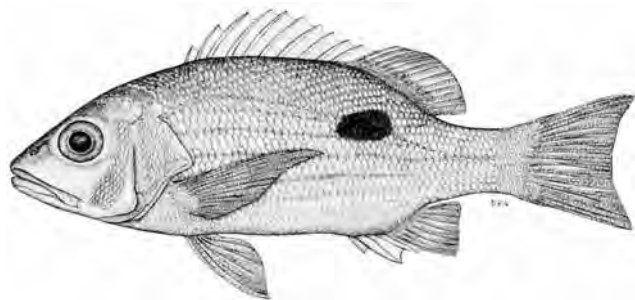
Fin elements: Dorsal X-XI, 12-14;

Anal III, 8; Pectoral 15-17

Lateral scales: 46-49

Maximum recorded length in southern

African waters:  $\pm 28$  cm SL



### Distribution

Anderson & Allen (1986) state that *L. fulviflamma* ranges from the Red Sea and tropical Indo-West Pacific region, south to approximately East London. However, recent unpublished records indicate that juveniles occur in estuaries as far south as the Swartkops Estuary in Port Elizabeth.





### Biology and ecology

This widespread species is especially common off rocky shores but is equally at home in estuaries over either muddy bottoms or in eelgrass beds (van der Elst 1988). Sexual maturity is attained between 16 cm and 17 cm TL, with spawning occurring over marine reefs from August to December. The juveniles first enter estuaries at about 20 mm TL (van der Elst 1988) and range upwards in size to about 16 cm TL (Day et al. 1981). Sexually mature individuals are absent from estuaries.

The salinity range of *L. fulviflamma* in southern African estuaries is 8-35 although, in other parts of its range, juveniles have been recorded

in the lower reaches of freshwater streams (Allen 1985). However, this species is usually associated with euhaline conditions in the lower reaches of permanently open estuaries on the subcontinent.

Although not a typical shoaling fish species, *L. fulviflamma* does congregate in groups, and the juveniles are sometimes associated with *Rhabdosargus holubi* aggregations in certain estuaries. The diet includes a variety of crustaceans, particularly crabs, isopods, amphipods, prawns, shrimps, mysids and polychaetes (Day et al. 1981, van der Elst 1988). Small fish, especially demersal species (e.g. gobies), are readily consumed when available.

Family: SPARIDAE

Species: *Acanthopagrus vagus* (Peters 1852)

Common name: Estuarine bream

Illustrated specimen length: 11 cm SL

### Selected anatomical features

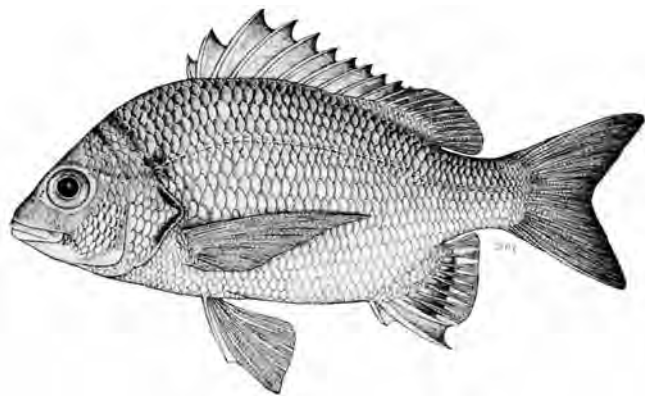
Fin elements: Dorsal XI-XII, 10-13;

Anal III, 8-9; Pectoral 14

Lateral scales: 43-47

Maximum recorded length in southern

African waters:  $\pm$  60 cm SL



### Distribution

The estuarine bream is abundant and widespread in the tropical Indo-West Pacific, extending into subtropical waters of the southeast coast of Africa (Smith & Smith 1986). This species is rare in warm-temperate estuaries but occasional specimens are found as far west as Swartvlei. It is the only sparid that has been regularly recorded in rivers (e.g. Phongolo) and associated freshwater pans (Skelton 2001).

### Biology and ecology

This important angling species is a protandrous hermaphrodite which changes sex from a male into a female. However, not all males change sex as James et al. (2003) have documented some males being present in the larger size classes (300-340 mm FL) in northern KwaZulu-Natal estuaries.

Length at 50% maturity for *A. vagus* has been estimated at 220 mm TL (Wallace 1975). This

slow-growing species is capable of reaching at least 16 years of age (James et al. 2003).

Spawning by *A. vagus* greater than 17 cm SL occurs in the KwaZulu-Natal nearshore marine environment and estuary mouths, mainly from May to August (Wallace 1975b, Garratt 1993). In the Kosi Estuary mouth region, spawning was recorded at night and timed to coincide with the ebb tidal transport of fertilised eggs out to sea (Garratt 1993).



Early larval development takes place at sea, with 0+ juveniles entering KwaZulu-Natal estuaries at approximately 10-30 mm SL, mainly between July and November (Wallace & van der Elst 1975). A monthly growth increment of 10-12 mm has been estimated for juveniles in their first year.

Population size estimates of *A. vagus* (>22 cm TL) in the Kosi lakes were undertaken by Kyle & Robertson (1997), who calculated that between 45 000 and 56 000 fish were present in the system during 1984/85 but declined considerably more recently (James et al. 2008b) due to over-exploitation.

The estuarine bream is a strong osmoregulator and has been recorded in salinities ranging from 1-72 (Whitfield 1996a). This species is associated with a wide range of water turbidities, with 42% of individuals captured in estuaries occurring in water less than 50 NTU, and 58% in water greater than 50 NTU (Cyrus & Blaber 1987c). Based on field and laboratory choice chamber experiments

(Cyrus & Blaber 1987a, 1987b), the estuarine bream can be regarded as a species that is indifferent to turbidity. This, together with a wide salinity tolerance, makes *A. vagus* ideally suited to the utilization of fluctuating estuarine environments.

Between 10 mm and 50 mm SL the juveniles feed on zooplankton, amphipods, chironomid larvae, tanaids and small crabs. From 50-100 mm SL amphipods are still consumed in large numbers but the main food is bivalve molluscs (Day et al. 1981). In Beachwood Creek (Mgeni Estuary) juvenile (<100 mm SL) *A. vagus* showed a positive selection for amphipods, tanaids and fish scales, with polychaetes, ostracods, gastropods and aquatic plants also being consumed (Harrison 1991).

The diet of adults covers a wide spectrum of prey and includes polychaetes, bivalves, sand dollars, crabs, prawns, shrimps and small fish (van der Elst 1988). This species has a reputation amongst anglers as being wary of offered bait and therefore very difficult to catch.

Family: SPARIDAE

Species: *Diplodus capensis* (Smith 1844)

Common name: Blacktail

Illustrated specimen length: 10 cm SL

#### Selected anatomical features

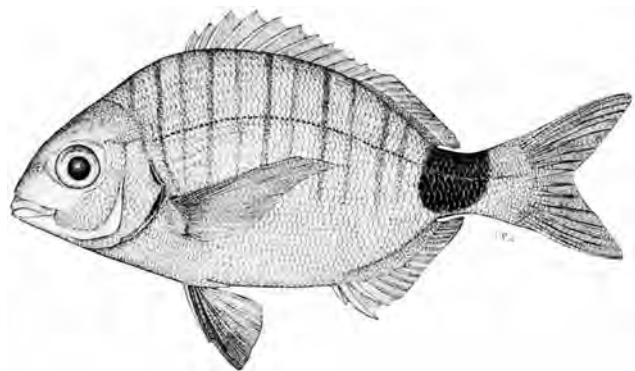
Fin elements: Dorsal XII, 14-15;

Anal III, 13-14; Pectoral 16-1

Lateral scales: 62-72

Maximum recorded length in southern

African waters:  $\pm$  32 cm SL



#### Distribution

*Diplodus capensis* ranges from Angola to Mozambique and southern Madagascar (Smith & Smith 1986). It is primarily a marine inshore species (<30 m depth), favouring turbulent seas and rocky shores. The juveniles utilize tidal pools and inshore reefs as nursery areas (Smale & Buxton 1989) but can be abundant in the lower reaches of certain open warm-temperate estuaries (Whitfield & Kok 1992).



### Biology and ecology

According to Mann & Buxton (1998) this species undergoes digynous gonadal development, with partial protandry occurring in some of the male population, i.e. only some males in the population appear to undergo a sex change. Size at 50% sexual maturity has been estimated at 21 cm FL and an age of 4 years (Mann & Buxton 1998). The breeding season is protracted, with peak spawning activity from July to September in subtropical KwaZulu-Natal (Joubert 1981) but later in the year in the warm-temperate region (Coetzee 1986).

Data from the Swartvlei Bay surf zone indicates a peak in postflexion larval abundance from October to December. Summer recruitment of juveniles into Eastern Cape intertidal pools has been documented by Beckley (1985b), and according to Smale & Buxton (1989) blacktail <40 mm TL entered subtidal gullies in the same region mainly during February and March.

Estuarine recruitment follows a similar pattern to that described for the marine inshore environment, with postlarvae 10-15 mm SL capable of entering estuaries. Early juveniles <40 mm TL were recorded in the Knysna Estuary mainly during the spring and summer months, with a peak in abundance between October and December (Whitfield & Kok 1992). In the Swartvlei Estuary recruitment was mainly from October-April with juveniles occupying eelgrass beds in the lower reaches. An influx of 0+ juveniles into the Swartkops Estuary during spring was

recorded by Beckley (1983), and Bennett (1989) documented recruitment into Western Cape estuaries during late summer /autumn.

Although this species can survive in salinities ranging from 6 to at least 42, it is usually found in the seawater dominated lower regions of open estuaries. Mortalities of blacktail were recorded in the Bot Estuary during October 1981, when salinities in this temporarily closed system declined below 6 (Bennett 1985).

The <30 mm SL size class of *D. capensis* feed mainly on harpacticoid copepods, polychaetes and amphipods in Eastern Cape intertidal pools (Christensen 1978, Mann & Buxton 1992), whereas harpacticoid copepods, chironomid larvae and ostracods were important food items of early juveniles in the Swartvlei Estuary (Whitfield 1985). Juveniles >50 mm SL are often herbivorous and closely associated with *Zostera capensis* beds in warm-temperate estuaries. Juveniles 2-3 cm in length have been observed cleaning adult blacktail in Sodwana Bay (KwaZulu-Natal) by Sikkel & Smit (2018).

In the sea *Diplodus capensis* feed mainly on rhodophytes, chlorophytes, poriferans, pelecypods and ascidiaceans, with epiphytic diatoms being digested from the leaf surfaces of macroalgae (Joubert & Hanekom 1980). The change from a predominantly carnivorous to an omnivorous diet is facilitated by changes in anatomy, such as a lengthening of the intestine to cope more efficiently with the considerable amount of plant material consumed.

Family: SPARIDAE

Species: *Diplodus hottentotus* (Smith 1844)

Common name: Zebra

Illustrated specimen length: 76 mm SL

### Selected anatomical features

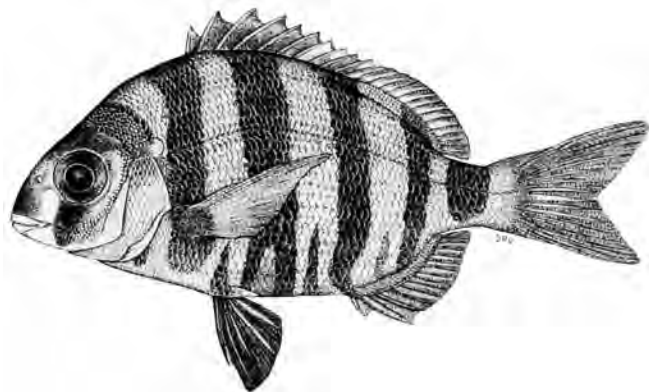
Fin elements: Dorsal XI, 12-13;

Anal III, 11; Pectoral 15

Lateral scales: 60-67

Maximum recorded length in southern

African waters:  $\pm$  46 cm SL



### Distribution

*Diplodus hottentotus* ranges from False Bay in the Western Cape Province to at least Sodwana Bay in KwaZulu-Natal (Smith & Smith 1986). This southern African endemic is primarily a marine species, ranging from inshore shallows to depths of 60 m (van der Elst 1988) but is also a regular visitor to some of the larger warm-temperate estuaries (e.g. Whitfield & Kok 1992).

### Biology and ecology

*Diplodus hottentotus* is a rudimentary hermaphrodite with no evidence of sex change (Mann & Buxton 1998). Size at 50% sexual maturity is 285 mm FL which corresponds to an age of 6 years. The breeding season is mainly during spring and early summer (October-January) in the warm-temperate region (van der Elst 1988) but recruitment of juveniles <30 mm TL into the Knysna Estuary occurred as early as September and extended into December (Whitfield & Kok 1992). A similar pattern of immigration was recorded in the Swartvlei Estuary, with the juveniles associated with the eelgrass (*Zostera capensis*) beds in the lower reaches.



The zebra is often found in the lower reaches of permanently open estuaries along the Eastern Cape coast, especially in those systems where eelgrass beds are present. Its absence from temporarily closed estuaries suggests that this species is a weak osmoregulator and cannot survive prolonged reductions in salinity.

According to van der Elst (1988) 0+ juveniles are exclusively carnivorous (e.g. polychaetes and amphipods) whereas the adults have a predominantly vegetarian diet. This is surprising as juveniles in estuaries are closely linked to aquatic macrophyte habitats; however no dietary studies have been conducted on fish in these systems.

Family: SPARIDAE

Species: *Lithognathus lithognathus*  
(Cuvier 1830)

Common name: White steenbras

Illustrated specimen length: 12 cm SL

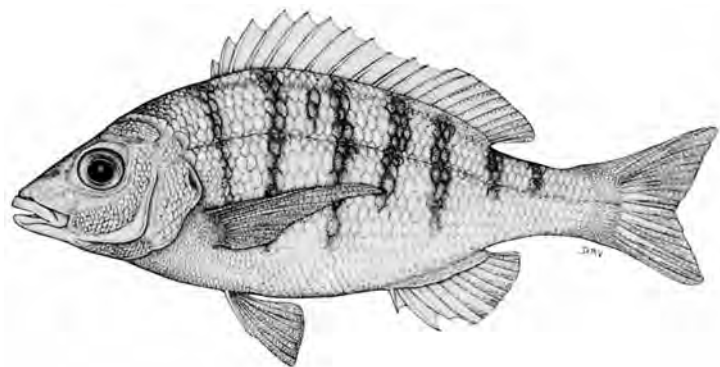
### Selected anatomical features

Fin elements: Dorsal XI, 10;

Anal III, 8; Pectoral 16-17

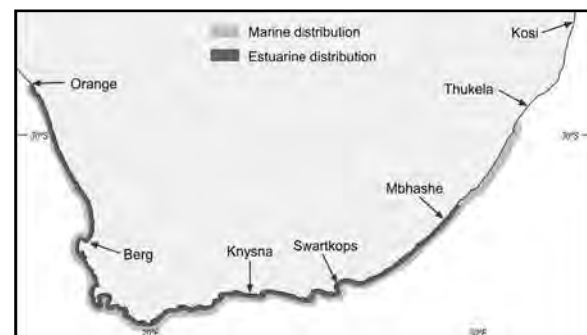
Lateral scales: 44-51

Maximum recorded length:  $\pm 89$  cm SL



### Distribution

This species ranges from the mouth of the Orange River in the west to KwaZulu-Natal in the east (Smith & Smith 1986). Juveniles are abundant in some of the larger warm-temperate estuaries but they are rare in subtropical systems along the east coast. Post-estuarine juveniles (>13 cm SL) are semi-resident in the surf zone, with the adults extending into water up to 25 m deep (Bennett 1993).



## Biology and ecology

The white steenbras is a rudimentary hermaphrodite with genetically determined sexes and, although some mature fish have approximately equal ovarian and testicular development in the gonads, individuals function only as males or females (Mehl 1973). Out of a total of 425 mature *L. lithognathus* examined, 172 were males, 233 females and 20 hermaphrodites (Bennett 1993).

Most white steenbras are mature by 54 cm SL (Bennett 1993), with late winter spawning occurring in the nearshore marine environment at multiple sites within their distributional range (Bennett et al. 2017a).

Egg and larval development occurs at sea, with late postflexion larvae <15 mm SL and 0+ juveniles (<50 mm TL) entering estuaries mainly between September and November (Bennett 1993, Whitfield & Kok 1992). A monthly growth increment of approximately 13 mm has been estimated for juvenile *L. lithognathus* (Bennett 1989, Whitfield & Kok 1992).

This species has been recorded in salinities ranging from 1-90 and is associated with both clear and turbid waters. White steenbras were recorded dying in the closed Seekoei Estuary when salinities increased above 90.

Prolonged oligohaline conditions also result in mortalities of this species (Bennett 1985), as do dissolved oxygen concentrations <1 mg l<sup>-1</sup> (Russell 1994). Oxygen consumption under different temperature and feeding regimes has been investigated by du Preez et al. (1986b) and energy loss via excretion by Cockcroft & du Preez (1989).

Early juveniles (10-30 mm SL) feed mainly on copepods and amphipods (Whitfield 1985, Wooldridge & Bailey 1982). Larger individuals in estuaries have a more diverse diet, with amphipods, anomurans, brachyurans, isopods, polychaetes and insect larvae being important prey taxa (Bennett 1993, Whitfield 1988a). A study by Schlacher & Wooldridge (1996a) has shown that male *Grandidierella lignorum* in the Gamtoos Estuary are consumed by *L. lithognathus* in significantly higher numbers than females, probably due to behavioural differences between the amphipod sexes.

The white steenbras enters extremely shallow areas, where its tail can often be seen protruding out of the water as it forages. Prawns are mostly 'blown' from their burrows by a strong jet of water which is forced through the mouth of the fish by the pumping action of the powerful gill chamber (van der Elst 1988).

Family: SPARIDAE

Species: *Lithognathus mormyrus*

(Linnaeus 1758)

Common name: Sand steenbras

Illustrated specimen length: 13 cm SL

## Selected anatomical features

Fin elements: Dorsal XI, 12-13;

Anal III, 10-11; Pectoral 15-17

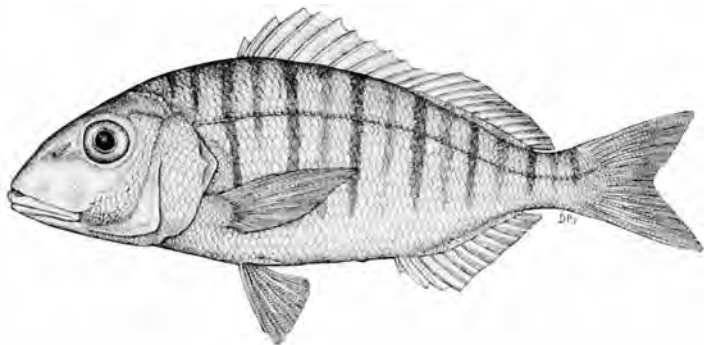
Lateral scales: 60-65

Maximum recorded length in southern

African waters: ± 46 cm SL

## Distribution

This widespread coastal shelf species occurs from the Mediterranean region to the Cape, and round the subcontinent to Mozambique (Smith & Smith 1986). Within southern African estuaries it is usually associated with the mouth region.





### Biology and ecology

Males reach sexual maturity at 16 cm and females at 19 cm (Kallianiotis et al. 2005). Spawning occurs in the marine environment, mainly during summer.

Juveniles <40 mm TL were recorded in the Knysna Estuary between September and April, and in the Swartvlei Estuary between March and May (Whitfield & Kok 1992). In contrast, the presence of *L. mormyrus* juveniles <50 mm TL were documented in Algoa Bay throughout the year (Lasiak 1983b), thus implying a very protracted spawning season.

The sand steenbras generally makes use of permanently open estuaries in the Eastern Cape and is most frequently encountered in the sandy flood tidal deltas of these systems. The silvery

coloration and darker crossbar marking on the flanks provide excellent camouflage in this low turbidity environment. Thus the sand steenbras remains inconspicuous to potential predators, even when present in moderate numbers (van der Elst 1988).

This species has not been recorded in low salinity regions of any southern African estuary or those systems that are temporarily closed, suggesting that it is intolerant of oligohaline conditions.

Juveniles prey on small invertebrates, with the adults consuming benthic invertebrates such as cracker shrimps, mole crabs and bivalve molluscs (van der Elst 1988). Similar feeding habits occur elsewhere in its range, with polychaetes and bivalve molluscs being favoured prey (Kallianiotis et al. 2005).

Family: SPARIDAE

Species: *Rhabdosargus globiceps* (Cuvier 1830)

Common name: White stumpnose

Illustrated specimen length: 82 mm SL

### Selected anatomical features

Fin elements: Dorsal XI, 11-13;

Anal III, 10-11; Pectoral 16-17

Lateral scales: 57-61

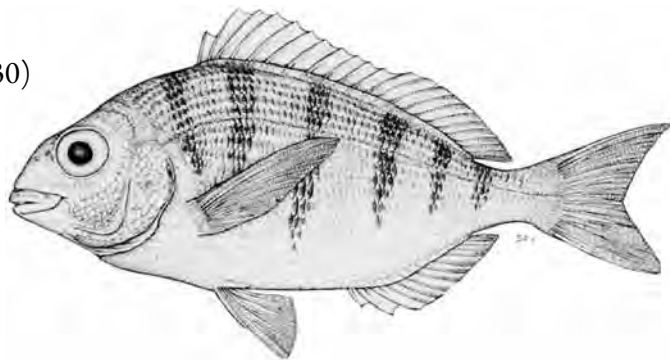
Maximum recorded length:  $\pm 45$  cm SL

### Distribution

The white stumpnose is endemic to southern African waters and has been recorded in the sea from Angola to the Eastern Cape. This temperate species is absent from subtropical KwaZulu-Natal waters and is rare in most warm-temperate estuaries of the Eastern Cape. Juveniles, up to approximately 14 cm SL, are sometimes abundant in certain of the larger estuaries along the Western Cape coast, and in sheltered areas of False Bay (Talbot 1955) and Langebaan Lagoon (Kerwath et al. 2009).

### Biology and ecology

Breeding occurs at an age of approximately three years, with female *R. globiceps* showing signs of sexual maturity at 23 cm SL and males at 27 cm



SL. In the Western Cape this species breeds in inshore marine waters between August and February, with a summer spawning peak (Talbot 1955). The fertilized eggs, which are approximately 1 mm in diameter, are buoyant and float near the water surface (van der Elst 1988).

Recruitment of white stumpnose <40 mm SL into the Klein Estuary occurred during January/February (Talbot 1955), and January-April in the Palmiet and Kleinmond systems (Bennett 1989). *Rhabdosargus globiceps* <20 mm TL were recorded in the Swartvlei Bay surf zone during September and October (Whitfield 1989b). Recruitment of <40 mm TL specimens into the Knysna and Swartvlei estuaries occurred between September and December, with a summer peak in abundance (Kok & Whitfield 1992). Juveniles remain in estuaries for approximately two years and grow at a rate of 5-10 mm per month (Talbot 1955).

Although adult fishes are invariably confined to the marine environment, often occurring in large shoals down to 70 m depth, subadult and early adults do occur in coastal systems such as Langebaan Lagoon where they are mainly confined to deep channels >4 m in depth (Attwood et al. 2007).

Very few *Rhabdosargus globiceps* are captured in the upper reaches of estuaries and none were

netted during a long-term study in Swartvlei lake (Whitfield 1986a), despite salinities in this part of the system being >10. The recorded salinity range of the white stumpnose is 3-35, with specimens dying in the temporarily closed Bot Estuary when salinities declined below 3 for a prolonged period (Bennett 1985).

The diet of newly recruited (15-25 mm SL) *Rhabdosargus globiceps* in estuaries is dominated by zooplankton and there appears to be a transition phase before they start demersal feeding on amphipods, isopods and filamentous algae. At a length of approximately 40 mm SL the juveniles start to develop molars, thus enabling them to consume a variety of molluscs, crabs, prawns and shrimps. They often feed in *Zostera* or *Ruppia* beds, and their stomachs are frequently packed with both macrophytic and filamentous algal material (Talbot 1955).

The diet of adult fish in the sea is dominated by bivalves, polychaetes, amphipods, barnacles and crabs (Day et al. 1981).

Family: SPARIDAE

Species: *Rhabdosargus holubi*

(Steindachner 1881)

Common name: Cape stumpnose

Illustrated specimen length: 97 mm SL

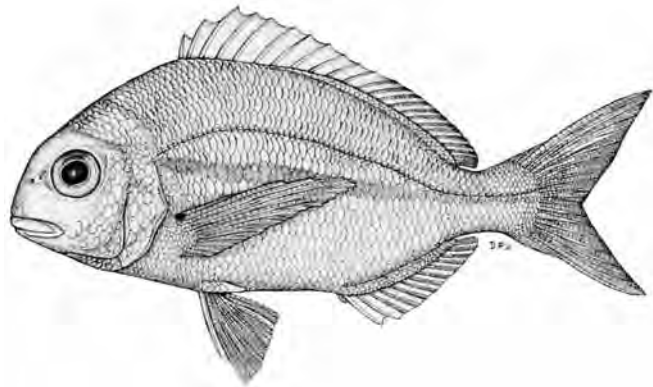
#### Selected anatomical features

Fin elements: Dorsal XI, 12-13;

Anal III, 10-11; Pectoral 14-16

Lateral scales: 55-57

Maximum recorded length:  $\pm$  30 cm SL



#### Distribution

The Cape stumpnose is endemic to southern African waters and has been recorded from the Berg Estuary in the south west to Inhaca Island in the north east. Juveniles occur almost exclusively in estuaries, and adults are found in the marine environment down to about 50 m depth (Wallace et al. 1984b). This species is abundant in all types of estuaries on the subcontinent and is distributed from the lower to the upper reaches of these systems.



### Biology and ecology

Spawning by *R. holubi* >15 cm SL occurs within the nearshore marine environment, mainly between May and August in KwaZulu-Natal (Wallace 1975b) and between July and February in the Eastern and Western Cape. The postflexion larvae first enter estuaries at a length of approximately 10 mm SL, with most recruitment occurring during summer and autumn in Eastern Cape estuaries (Kisten et al. 2015).

Growth in estuaries is rapid and the juveniles attain a length of approximately 10 cm SL in their first year. The return migration to the sea appears to occur when individuals are larger than 14 cm SL (Blaber 1974c), which implies an approximate two-year estuarine nursery phase. Growth slows down considerably in the marine environment where this species attains a maximum mass of 2.4 kg and a maximum age of 18 years (Farthing et al. 2016). An indication of the decline in growth rate at sea is the fact that individuals attain 315 mm FL by year 8 and 354 mm FL by year 18.

This species is a strong osmoregulator, tolerant of a wide range of salinities (0.7–70) and temperatures (10–30°C) (Blaber 1973b). However, blood plasma cortisol concentrations and fish behaviour deviate considerably from normal as water temperatures increase towards the upper limit (van der Vyver et al. 2013). When exposed to a new salinity the internal osmotic concentration does not change immediately, which is of considerable importance to a fish living in tidal estuaries subject to short-term changes in salinity (Blaber 1974a). *Rhabdosargus holubi* was one of the few species to survive the prolonged low salinities (<3) recorded in the temporarily closed Bot Estuary during 1981 (Bennett 1985). However, oligohaline salinities in combination with low temperatures (12°C) are lethal to this fish (Blaber & Whitfield 1976). In the temporarily closed Seekoei Estuary *R. holubi* was recorded dying in salinities above 90 (Whitfield 1998).

In Rondevlei extensive mortalities of *R. holubi* were recorded when dissolved oxygen concentrations declined below 1 mg l<sup>-1</sup> (Russell 1994). This species is associated with a wide range of water turbidities, with 65% of individuals occurring in

water less than 10 NTU (Cyrus & Blaber 1987c). Based on field and laboratory choice chamber experiments (Cyrus & Blaber 1987a, 1987b) the Cape stumpnose can be regarded as a species which prefers clear water but is tolerant of high turbidities.

Copepods were the dominant component in the diet of postlarval (10–30 mm SL) *R. holubi*, whereas juveniles larger than 30 mm feed mainly on filamentous algae, aquatic macrophytes and epibenthic invertebrates (Whitfield 1984, 1985). The fish do not appear to assimilate the macrophytic plant material due to the absence of a cellulase or a method to break down the plant tissue (de Wet & Marais 1990), but do digest the epiphytic diatoms which cover the leaves (Blaber 1974b, Sheppard et al. 2012, Nel et al. 2017).

The tricuspid teeth of juvenile *R. holubi* are specialized for grazing aquatic plants and differ from the molariform teeth of adults which consume mainly echinoderms, molluscs crustaceans and polychaetes (Buxton & Kok 1983, Schleyer & Wallace 1986). A detailed stable isotope study in conjunction with stomach content analyses in the Kowie system showed that there was a clear spatial gradient in  $\delta^{13}\text{C}$  values across the marine, estuarine and freshwater continuum (Carassou et al. 2016). The  $\delta^{13}\text{C}$  ranges of food sources and fish also overlapped within each habitat type along this continuum, thus illustrating the fidelity of *R. holubi* to specific habitats at the different life stages.

Both the condition factor and food intake of the Cape stumpnose are affected by temperature. Food intake at 15°C was approximately half that at 22°C, and the lipid content of summer specimens from the West Kleinemonde Estuary was 6.4% compared to 0.7% in winter (Blaber 1975). Daily summer and winter food consumption for juveniles in Swartvlei was calculated to be 6% and 3% of fish mass respectively (Whitfield 1984). Although juveniles are recorded in significantly higher numbers in association with aquatic plant beds, they can also survive in estuarine environments where submerged macrophytes are absent (Hanekom & Baird 1984).

The population sizes of *R. holubi* in both the West and East Kleinemonde estuaries have

been calculated by Blaber (1973a) and Cowley & Whitfield (2001a) respectively. In the West Kleinemonde the population ranged from approximately 11 000 - 55000 and in the East Kleinemonde the range was 12 000 - 107 000. Obviously both the size of the juveniles and mortalities determine the population biomass that can be supported. In addition, the export of subadult

*R. holubi* populations from estuaries into the sea each year is a significant contribution to the fish biomass of the adjacent marine environment, e.g. it was calculated that approximately 7 tonnes of Cape stumpnose biomass was exported from the Kowie Estuary into the sea each year (Carassou et al. 2016).

Family: SPARIDAE

Species: *Rhabdosargus sarba* (Forsskal 1775)

Common name: Tropical stumpnose

Illustrated specimen length: 13 cm SL

#### Selected anatomical features

Fin elements: Dorsal XI, 12-13;

Anal III, 10-11; Pectoral 14-15

Lateral scales: 56-59

Maximum recorded length in southern

African waters:  $\pm 55$  cm SL

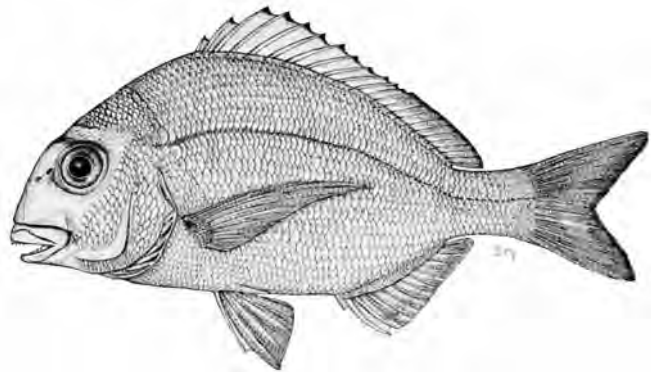
#### Distribution

This species has a mainly tropical Indo-West Pacific distribution, extending into the subtropical waters of the southeast coast of Africa. They are rare in warm-temperate estuaries but occasional juveniles have been found as far west as Knysna and the Wilderness estuarine lakes in the Western Cape Province.

#### Biology and ecology

*Rhabdosargus sarba* passes through a hermaphroditic stage with testes and ovaries present simultaneously (van der Elst 1988) and is regarded as protandrous (Yeung & Chan 1987), i.e. it functions first as a male, then later changes to a female. The tropical stumpnose is a slow growing and long-lived species, reaching a maximum age of 16+ years (Radebe et al. 2002).

Nocturnal serial spawning by adults >20 cm SL occurs in the KwaZulu-Natal nearshore marine environment, mainly from August to November (Wallace 1975b). A proportion of the spent individuals do return to estuaries but these are confined to fish <35 cm SL. According to Wallace (1975a) adults >35 cm SL are seldom recorded in estuaries and are usually confined to sandy bays and inshore reefs shallower than 50 m.



Larval *R. sarba* attain 10 mm TL within 30 days (Leu 1994) and a spring and summer monthly growth increment of 14 mm has been estimated for 0+ juveniles. Fry enter estuaries at 15-20 mm SL, mainly during August to November (Wallace & van der Elst 1975).

The tropical stumpnose is a strong osmoregulator and has been recorded in salinities ranging <1 to 80 (Whitfield 1996a). In Lake Nhlangwe this species was recorded in salinities <1 during both summer and winter. However, salinities of <3, in combination with a temperature of 12°C, are lethal to this fish (Blaber & Whitfield 1976). Similarly, mortalities of *R. sarba* under hypersaline conditions at Lake St Lucia were recorded after the sudden onset of cold weather (Wallace 1975a).

The tropical stumpnose is associated with water turbidities ranging from less than 10 NTU to greater than 80 NTU, with 74% of individuals captured in estuaries occurring in water less than 50 NTU (Cyrus & Blaber 1987c). Based on field and laboratory choice chamber experiments (Cyrus & Blaber 1987a, 1987b) *R. sarba* can be regarded as a clear to partially turbid water species in estuaries.

The diet of juveniles and subadults consists mainly of aquatic macrophytes and filamentous algae, although a considerable proportion is made

up of bivalves and amphipods. The last two taxa are positively selected for when little plant material is consumed (Blaber 1984). In Durban Bay, *R. sarba* feed mainly on brachyurans and surface-dwelling bivalves (Day & Morgans 1956).

The development of strong molariform teeth on the pharyngeal bones in adults results in an increased utilization of hard shelled molluscs on the coast (Day et al. 1981, Schleyer & Wallace 1986). Foraging occurs mainly during daylight hours, with a peak in activity during the early afternoon (Blaber 1984).

Family: SPARIDAE

Species: *Rhabdosargus thorpei* (Smith 1979)

Common name: Bigeye stumpnose

Illustrated specimen length: 95 mm SL

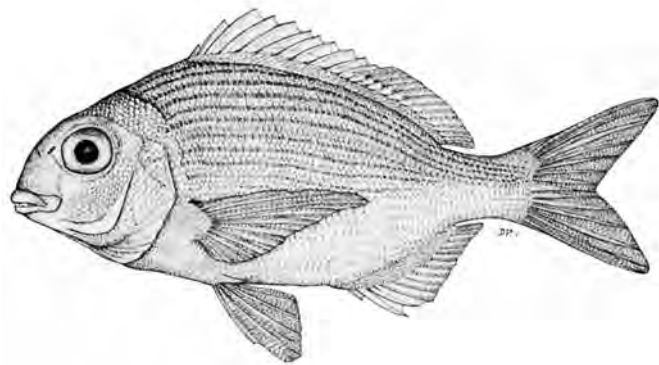
#### Selected anatomical features

Fin elements: Dorsal XI, 13;

Anal III, 12; Pectoral 14-15

Lateral scales: 55-60

Maximum recorded length:  $\pm$  32 cm SL



#### Distribution

The bigeye stumpnose is an endemic sparid that is known only from southern Mozambique to the Eastern Cape Province (Smith & Smith 1986). Adults of this probable tropical species do not enter estuaries but juveniles are sometimes common in the lower reaches of certain subtropical systems, e.g. Kosi (van der Elst 1988).



#### Biology and ecology

Very little is known about the life history of the bigeye stumpnose. It was previously confused with *R. sarba* but differs in having a larger eye, and the whole ventral area (including the pelvic and anal fins) is a bright yellow. Both sparid species have a similar southern African distribution and frequently occur together in estuaries.

Newly recruited juveniles of *R. thorpei* enter both turbid and clear estuaries and also occur in certain temporarily closed systems but are generally rare in the region. This species is euryhaline and has been found in salinities ranging from 8-38 (Whitfield 1996a).

The diet of juveniles in the Kosi Estuary consists mainly of bivalves and crustaceans (Blaber 1984), with the prey being crushed and shredded by the molars and pharyngeal bones. Although small amounts of filamentous algae were found in 37% of the specimens examined from the Kosi system, this plant material was probably consumed incidentally together with the invertebrate prey (Blaber 1984). In other estuaries aquatic macrophytes are also consumed. The remains of clams, mussels, barnacles, crabs and small rock lobsters have been found in the stomachs of specimens from the marine environment (van der Elst 1988).

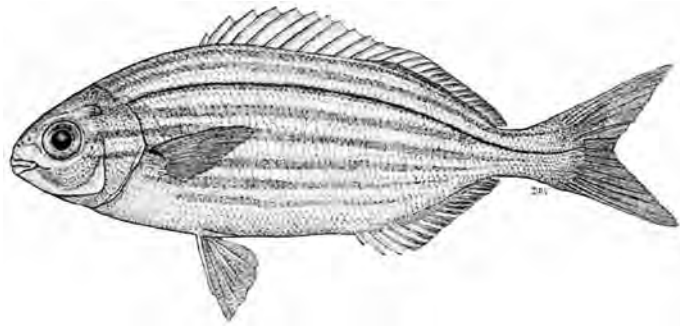


Family: SPARIDAE

Species: *Sarpa salpa* (Linnaeus 1758)

Common name: Strepie

Illustrated specimen length: 13 cm SL



### Selected anatomical features

Fin elements: Dorsal XI, 14-16;

Anal III, 13-15; Pectoral 16

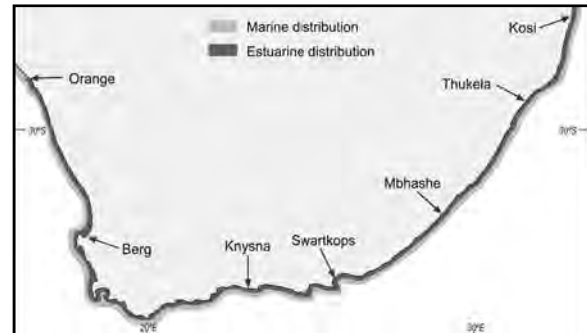
Lateral scales: 71-79

Maximum recorded length in southern

African waters:  $\pm 26$  cm SL

### Distribution

The strepie is an inshore species, with a distribution from the Mediterranean and eastern Atlantic round South Africa to southern Mozambique (Smith & Smith 1986). Although large shoals of juveniles are often found near eelgrass beds in warm-temperate estuaries, they are not dependent on these systems as nursery areas and are also common around subtidal reefs and in sandy beach surf zones. Adult fish are usually confined to the marine environment down to a depth of 20 m.



### Biology and ecology

Males mature at 14-15 cm and females 16-17 cm FL (Joubert 1981), with indications that this species undergoes a protandrous sex change (van der Walt & Mann 1998). Spawning occurs between April and September, with months of peak activity being June to August. Evidence suggests that *S. salpa* spawns off the KwaZulu-Natal coast and that the larvae drift southwards into warm-temperate waters, possibly assisted by the Agulhas Current (van der Elst 1988).

Juveniles <40 mm TL have been recorded entering Eastern and Western Cape surf zones between May and September (Lasiak 1983b, Whitfield 1989b). Recruitment of *S. salpa* <30 mm TL into Eastern Cape tide pools takes place between June and September (Christensen 1978) with peak immigration of 0+ juveniles into Western Cape estuaries occurring between September and December (Whitfield & Kok 1992). Cohort analyses from the Knysna system indicated a growth of approximately 14 cm in the first year, which was similar to the 12 mm per month estimated by Lasiak (1983b) for juveniles in Algoa

Bay. The maximum recorded age for *S. salpa* is six years and a fork length of 27 cm (van der Walt & Beckley 1997).

Although this species has been recorded in salinities ranging from 8-35 (Whitfield 1996a), it is usually found in the lower half of permanently open estuaries where salinities seldom decline below 20.

The 10-25 mm SL size classes of *S. salpa* feed mainly on harpacticoid copepods (Christensen 1978, Whitfield 1985), with fish above 50 mm SL in estuaries being almost exclusively herbivorous, feeding on *Zostera capensis* and associated epiphytic algae (Whitfield 1988a).

In the marine environment this sparid forages predominantly on rhodophytes (40 species) and hydrozoans (Joubert & Hanekom 1980). The change from a carnivorous to a herbivorous diet is facilitated by changes in anatomy. The pointed and conical teeth of the 0+ juveniles are replaced by sharp multicusped incisors, more suited to a browsing habit, and the gut lengthens considerably to cope more efficiently with the vegetarian diet (van der Elst 1988). Gerking (1984) has shown that *S. salpa* can maintain its body weight by consuming algae at a rate of approximately 6% of the body mass per day.

Family: MONODACTYLIDAE

Species: *Monodactylus argenteus*

(Linnaeus 1758)

Common name: Round moony

Illustrated specimen length: 70 mm SL

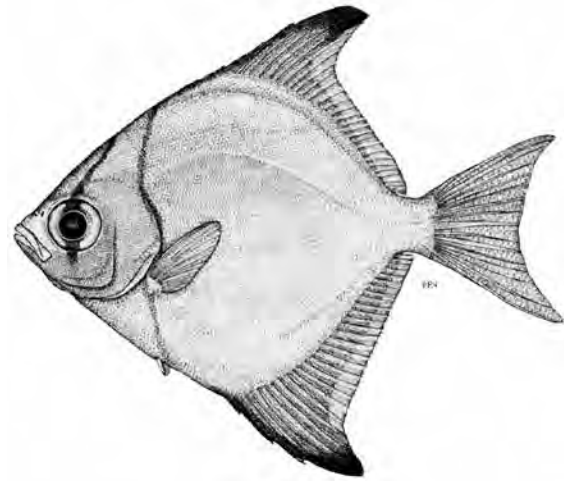
### Selected anatomical features

Fin elements: Dorsal VIII, 27-30;

Anal III, 27-30; Pectoral 16-18

Lateral scales: 52-58

Maximum recorded length:  $\pm 19$  cm SL



### Distribution

The round moony is an Indo-West Pacific fish extending into the warm-temperate waters of southern Africa. Although this is mainly a tropical species, specimens have been collected as far west as the Breede Estuary (Heemstra 1986b). Juveniles are frequently common in KwaZulu-Natal estuaries, sometimes entering freshwater areas in the vicinity of these systems. Within estuaries this species is most often associated with submerged macrophytes or rocky reef habitats near the mouth.



### Biology and ecology

Sexual maturity occurs at approximately 13 cm SL and breeding takes place at sea (Day et al. 1981). Newly recruited juveniles in estuaries tend to shelter in shallow water where emergent or submerged plants are present. Juveniles have two curved dark stripes in the head region which tend to fade and eventually disappear in adults (Heemstra 1986b).

The round moony is strongly euryhaline and can tolerate salinities ranging from fresh water to at least 48. It has also been shown that the ultrastructure of the gills of *M. argenteus* undergo morphological changes that are associated with environmental salinity changes (Fearnhead & Fabian 1971). Those individuals entering freshwater areas depart these habitats as juveniles and not adults.

Although the majority of specimens captured in Lake St Lucia were associated with water

turbidities less than 10 NTU (Cyrus & Blaber 1987c), laboratory experiments have shown that the round moony prefers intermediate turbidities between 10 and 80 NTU (Cyrus & Blaber 1987b). It is possible that *M. argenteus* seeks more turbid conditions when placed in an unfamiliar laboratory environment, since in estuaries it is most abundant in clear water areas where submerged or emergent macrophytes are present.

*Monodactylus argenteus* feed mainly on zooplankton, with individual selection of prey items from the water column being the dominant mode of foraging. They also consume epibenthic and epiphytic organisms such as amphipods and filamentous algae that are associated with submerged aquatic macrophytes (Day et al. 1981). This species was also abundant around the rocky reef inside the mouth of the Kosi Estuary where the water was clear and euhaline salinities prevailed.

Family: MONODACTYLIDAE

Species: *Monodactylus falciformis*

(Lacepède 1800)

Common name: Oval moony

Illustrated specimen length: 89 mm SL

### Selected anatomical features

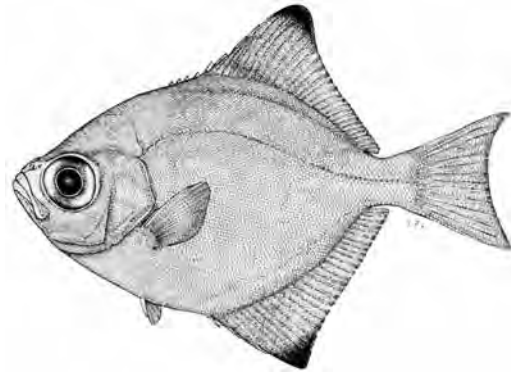
Fin elements: Dorsal VIII, 25-30;

Anal III, 25-29; Pectoral 17-18

Lateral scales: 51-58

Maximum recorded length in southern

African waters:  $\pm 24$  cm SL



### Distribution

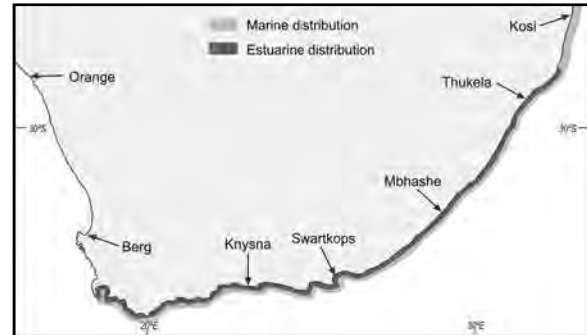
*Monodactylus falciformis* ranges from the Red Sea and northern Indian Ocean south to False Bay (Heemstra 1986b). Within southern African waters, the juveniles are often abundant in estuaries, especially in the middle and upper reaches. The adults of this species are usually confined to shallow reefs in the marine environment and seldom enter estuaries.

### Biology and ecology

Spawning by adult ( $>14$  cm SL) *M. falciformis* occurs in the nearshore marine environment, often in the vicinity of estuary mouths (van der Elst 1988). The breeding season lasts from October to February in Western Cape waters (Whitfield & Kok 1992), with evidence suggesting that this species is a serial spawner in Algoa Bay (Lasiak 1984a). The absence of adults from estuaries indicates that individuals do not return to these systems after spawning.

The postlarvae first enter southern African estuaries at a length of 5-10 mm SL, with most recruitment taking place between November and March (Melville-Smith & Baird 1980). The 0+ juveniles of *M. falciformis* have 11-12 vertical bars across the head and body, which may assist in providing camouflage since this species is often associated with submerged aquatic macrophyte beds. Small size classes ( $<15$  mm SL) of this species also have the ability to turn almost pitch black, especially when stressed.

*Monodactylus falciformis* juveniles favour the middle and upper reaches of estuaries as nursery areas (Beckley 1984a, Hanekom & Baird 1984,



Whitfield 1984), where they sometimes form large shoals. There is a tendency to remain in the estuarine environment until a length of  $\pm 12$  cm SL is attained, at which stage they return to the sea.

This species is a strong osmoregulator, tolerant of salinities ranging from 1-90. Juveniles  $<50$  mm SL are often recorded above the ebb and flow of estuarine systems and are tolerant of direct transfer to fresh water without negative effects (Day et al. 1981). Lower salinities do not appear to be the main reason for attracting juveniles to the upper reaches of estuaries since *M. falciformis* was still most abundant in this region under reversed salinity conditions in the Kariega Estuary (Ter Morshuizen & Whitfield 1994). This species was recorded dying in the temporarily closed Seekoei Estuary when salinities increased above 90 (Whitfield 1998).

Copepods were the dominant component in the diet of postlarval (19-30 mm SL) *M. falciformis*, whereas juveniles larger than 50 mm SL fed mainly on small crabs, isopods, amphipods and insects (Whitfield 1984, 1985). Foraging of this mainly midwater species occurs during both the day and night (van der Elst 1988), with daily summer food consumption for juveniles in Swartvlei calculated to be 2.5% of fish mass (Whitfield 1984).

Family: GERREIDAE

Species: *Gerres longirostris* (Lacepède 1801)

Common name: Strongspine pursemouth

Illustrated specimen length: 13 cm SL

### Selected anatomical features

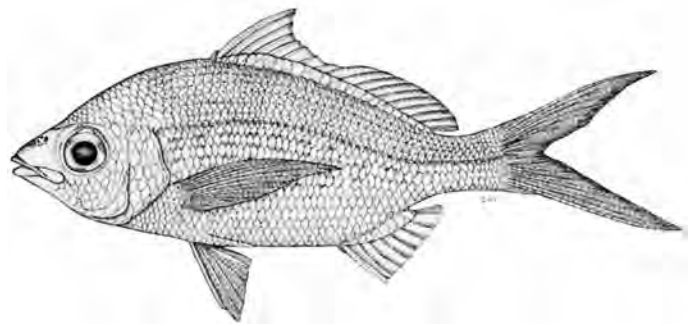
Fin elements: Dorsal IX-X, 9-11;

Anal III, 7

Lateral scales: 42-45

Maximum recorded length in southern

African waters:  $\pm 23$  cm SL



### Distribution

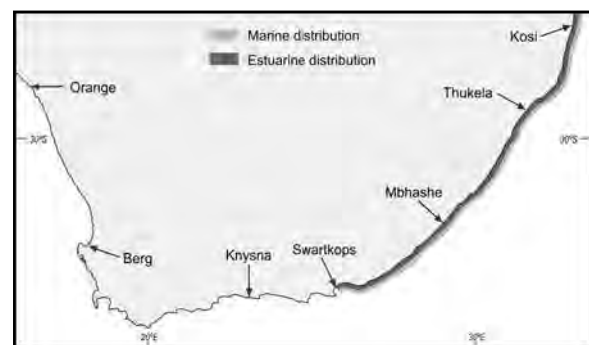
The strongspine pursemouth has a mainly tropical Indo-Pacific distribution, extending into the subtropical waters of southern Africa. This species has been recorded as far south as Algoa Bay (Woodland 1986) but is seldom found in warm-temperate estuaries.

### Biology and ecology

Sexual maturity for both males and females is attained at approximately 11 cm SL and mature or ripe gonads have been recorded throughout the year. The absence of ripe-running individuals from KwaZulu-Natal estuaries suggests that the completion of gonadal development occurs in the sea (Cyrus & Blaber 1984a). Spawning by *G. longirostris* in the KwaZulu-Natal nearshore marine environment is very protracted, with newly recruited fry (approximately 10 mm SL) being recorded during all four seasons in the Kosi Estuary (Cyrus & Blaber 1982a).

It has been suggested that juveniles remain within the estuarine environment until they reach maturity, thus benefitting from reduced predation rates. Cyrus & Blaber (1984c) have shown that predation on *Gerres* species by piscivorous fishes in the Kosi Estuary is very low (<1% of their diet), despite the abundance of gerreids within this system. These authors suggested that this may be related to the 'loose association' type of shoaling by the pursemouths, as well as the fact that they blend in well to a pale sand background.

*Gerres longirostris* is abundant in salinities from 3-35 but rare in Lake Nhlangwe where salinities were <1 (Cyrus & Blaber 1982a). Shoals of *G. longirostris* are usually more abundant in the



clearer KwaZulu-Natal estuaries, with 90% of the juveniles captured occurring in water turbidities <10 NTU (Cyrus & Blaber 1987a). This apparent abundance in clearer waters may be related to their preference for foraging in sandy habitats.

The diet of postlarvae (<20 mm SL) in the Kosi estuarine system was dominated by calanoid copepods. Larger juveniles (20-40 mm SL) consumed mainly polychaetes, bivalve siphon tips and chironomid larvae (Cyrus & Blaber 1983a). The diet of juveniles >40 mm SL and adults consisted mainly (64% of energy intake) of the siphon tips belonging to the bivalve *Hiatula lunulata* (Cyrus & Blaber 1983b). In Durban Bay this species feeds mainly on bivalves, polychaetes, amphipods and copepods (Day & Morgans 1956).

Food items are usually detected visually and the protrusible jaw mechanism (Figure 137) facilitates the capture of sedentary and motile prey (Cyrus & Blaber 1982b). Feeding occurs mainly during the day, although some foraging has been recorded during nocturnal hours (Cyrus & Blaber 1984b).

Family: GERREIDAE

Species: *Gerres methueni* (Regan 1920)

Common name: Evenfin pursemouth

Illustrated specimen length: 12 cm SL

### Selected anatomical features

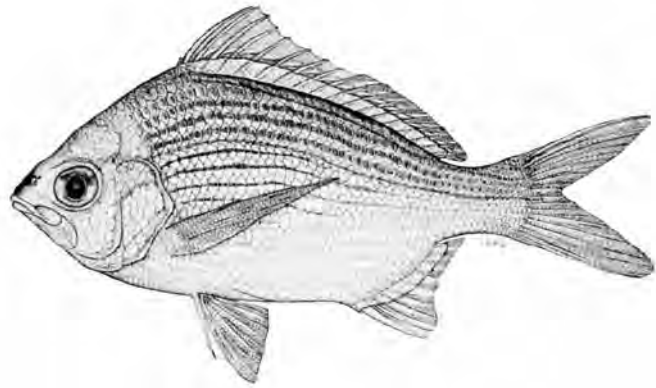
Fin elements: Dorsal IX, 10-11;

Anal III, 7

Lateral scales: 41-49

Maximum recorded length in southern

African waters:  $\pm 23$  cm SL



### Distribution

Although Woodland (1986) describes *G. rappi* (a junior synonym of *G. methueni*) as a mainly temperate species, ranging from Algoa Bay into southern Mozambique, the available evidence suggests a subtropical centre of distribution (Cyrus & Blaber 1982a). Only a few subadults and adults of the evenfin pursemouth have been recorded in warm-temperate estuaries, whereas all life stages are abundant in subtropical KwaZulu-Natal estuaries (Cyrus & Blaber 1982a).



### Biology and ecology

Males become sexually active from 11 cm SL, and females at 14 cm SL. Mature or ripe gonads have been recorded during summer, autumn and winter in the Kosi system (Cyrus & Blaber 1984a). The above authors documented large shoals of ripe adults leaving the Kosi Estuary mouth prior to spawning. The absence of ripe-running individuals in KwaZulu-Natal estuaries, and the atresion of oocytes in mature individuals isolated in the temporarily closed Fafa Estuary, supports the view that the completion of gonad development occurs at sea (Cyrus & Blaber 1984a). Spawning in the KwaZulu-Natal nearshore marine environment probably occurs during summer, autumn and winter, with newly recruited fry ( $\pm 15$  mm SL) being recorded during all seasons except summer in the Kosi Estuary (Cyrus & Blaber 1982a). It has been suggested that the juveniles of this species remain within the estuarine environment until they reach maturity (Cyrus & Blaber 1984a).

In the Kosi system *G. methueni* is abundant only in the oligohaline waters of Lake Nhlangwe (Cyrus & Blaber 1982a). This species is, however,

able to tolerate a wide range of salinity (0.5-40) and has been recorded in a number of temporarily closed KwaZulu-Natal estuaries where salinities were  $<1$ . Although the evenfin pursemouth occurs mainly in clear estuarine waters, 35% of the juveniles captured in KwaZulu-Natal systems were associated with water turbidities between 10 and 50 NTU, and 5% between 50 NTU and 80 NTU (Cyrus & Blaber 1987c).

The diet of postlarvae less than 20 mm SL is dominated by calanoid copepods (Cyrus & Blaber 1983a, Whitfield 1985). Larger juveniles (20-40 mm SL) consume mainly amphipods, polychaetes and copepods (Cyrus & Blaber 1983a). The diet of juveniles greater than 40 mm SL and adults consists mainly of bivalves (40% of energy intake), followed by chironomid larvae (32%) and crabs (17%) (Cyrus & Blaber 1983b).

Food items are usually detected visually and the jaw protrusion and retraction time when capturing prey was calculated to be 0.2 seconds (Cyrus & Blaber 1982b). Feeding occurs mainly during the day although some foraging has been recorded during nocturnal hours (Cyrus & Blaber 1984b).

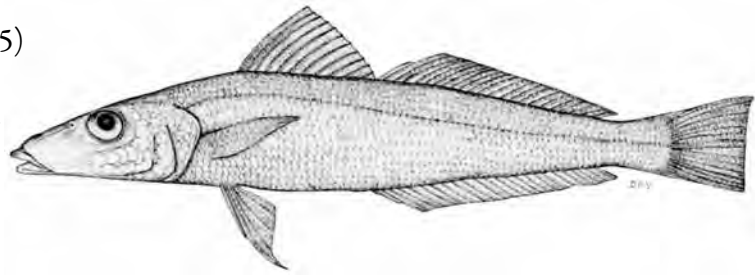


Family: SILLAGINIDAE

Species: *Sillago sihama* (Forsskal 1775)

Common name: Silver sillago

Illustrated specimen length: 16 cm SL



#### Selected anatomical features

Fin elements: Dorsal XI+I, 20-23;

Anal II, 21-23; Pectoral 16-17

Lateral scales: 62-72

Maximum recorded length in southern

African waters:  $\pm 26$  cm SL

#### Distribution

The silver sillago is a mainly tropical species that has a widespread distribution within the Indo-Pacific region, reaching as far south as Knysna (McKay 1986). It is mainly a shallow water fish of sandy bays and estuaries (van der Elst 1988).



#### Biology and ecology

*Sillago sihama* is a predominantly shoaling species that is most common in southern African waters during summer. According to van der Elst (1988) breeding occurs mainly in East African waters but Connell (1996) has recorded spawning in the subtropical St Lucia Estuary. The silver sillago is capable of considerable colour changes, usually to blend with the colour of the substratum over which it is moving. When threatened they are known to bury themselves in the sand until danger has passed (van der Elst 1988). In addition, they are sometimes known to skip along the water surface to evade pursuers.

Although this species has been recorded in salinities ranging from 3-35 (Whitfield 1996a),

it is usually found in the lower reaches of permanently open estuaries and bays where salinities seldom decline below 20. The distribution of *S. sihama* in estuaries appears to be inversely related to turbidity, with the highest densities being recorded in clearer water estuarine bays (Weerts et al. 1997).

Juveniles <60 mm SL feed predominantly on planktonic organisms, especially copepods and larvaceans, but with increasing size this species preys mainly on benthic crustaceans, polychaetes, tanaids and bivalve siphon tips (Weerts et al. 1997, Blackler 2002).

The adult diet consists mostly of marine polychaetes, shrimps, prawns and small crabs, all of which are collected from the benthos with the aid of a long, conical snout (van der Elst 1988).

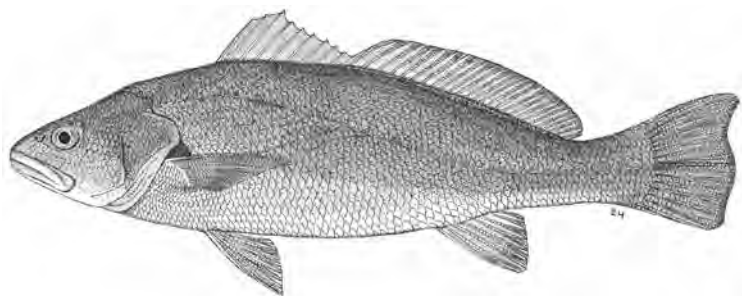
Family: SCIAENIDAE

Species: *Argyrosomus japonicus*

(Temminck & Schlegel 1843)

Common name: Dusky kob

Illustrated specimen length: 44 cm SL



#### Selected anatomical features

Fin elements: Dorsal X+I, 26-29;

Anal II, 7; Pectoral 17

Lateral scales: 48-54

Maximum recorded length in southern

African waters:  $\pm 170$  cm SL

## Distribution

The dusky kob has an African range extending from Cape Point to southern Mozambique. It also occurs in Indo-Pacific waters to Japan and Australia in the east and Pakistan in the west (Griffiths & Heemstra 1995). There is a strong possibility that cryptic taxa within the very wide geographical range of this supposed single species exist. *Argyrosomus japonicus* is a coastal species with a maximum recorded depth of 100 m in southern African waters (Griffiths 1996).

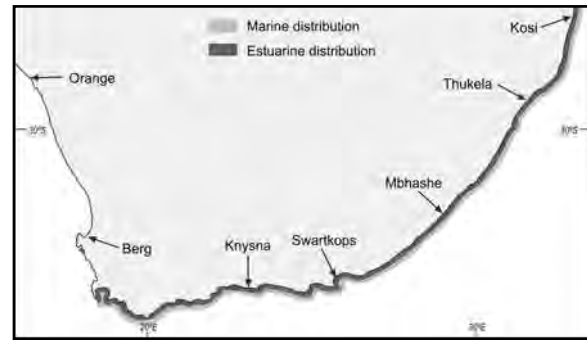
## Biology and ecology

Dusky kob become sexually active at approximately 92 cm TL for males and 107 cm TL for females. Nocturnal spawning occurs in the marine environment from August to November in KwaZulu-Natal and from October to January in the Eastern Cape. A large proportion of the adult population are reputed migrate to KwaZulu-Natal to breed, although spawning may continue once they return to the Eastern Cape (Griffiths 1996).

Newly recruited juveniles enter southern African estuaries during spring and summer, mainly between October and February (Wallace & van der Elst 1975). The early juveniles (20-30 mm TL) appear to remain in the upper reaches of large turbid estuaries, where they find suitable food and refuge from predators (Griffiths 1996). At approximately 15 cm TL they begin to occupy the middle and lower estuary reaches, with some individuals entering the sea adjacent to these systems (Cowley et al. 2008).

Juveniles do not appear to migrate great distances from their natal estuaries or coastal marine environments (Childs et al. 2015) but remain as separate localised populations until they reach sexual maturity (Griffiths 1996).

Growth is rapid, attaining approximately 35 cm TL in the first year. Using the growth models of Griffiths & Hecht (1995), all males are sexually mature by 7 years and females by 8 years. Individuals up to 42 years of age have been recorded but specimens older than 27 are rare. The maximum recorded mass is 75 kg and fish of 45 kg are common in the sea.



The salinity range of dusky kob is usually 3-66 (Wallace 1975a), although some specimens have been captured in riverine sections above the Great Fish Estuary (Ter Morshuizen et al. 1996b). Newly recruited juveniles favour oligohaline areas (<5) in certain turbid Eastern Cape systems (Griffiths 1996) where spring and summer food conversion rates are elevated in the low salinity, warmer waters (Bernatzeder & Britz 2007, Bernatzeder et al. 2010). However, subadults were recorded dying in the Bot and St Lucia estuarine systems when exposed to prolonged low salinities (<3) in conjunction with low temperatures (Blaber & Whitfield 1976, Bennett 1985).

According to van der Elst (1988) *A. japonicus* hunts mainly by combining olfactory and lateral line senses and is therefore well equipped to forage in turbid waters. This species is associated with a wide range of water clarity but is particularly abundant in turbid estuaries (>50 NTU) which may aid its method of hunting.

The diet of newly recruited 0+ juveniles is dominated by calanoid copepods and mysids (Griffiths 1996). Juveniles >17 cm SL and adults in estuaries are primarily piscivorous, with fish in the diet having a frequency of occurrence ranging between 76% and 94% (Whitfield & Blaber 1978a, Marais 1984).

*Argyrosomus japonicus* <43 cm SL tend to prey on small resident fish species in large numbers (e.g. *Gilchristella aestuaria*) or the juveniles of marine fishes. Dusky kob >43 cm SL also consume these species but are able to prey on larger fish such as the subadults of marine taxa, e.g. *Rhabdosargus holubi*.

Family: SCIAENIDAE

Species: *Johnius dorsalis* (Peters 1855)

Common name: Small kob

Illustrated specimen length: 18 cm SL

### Selected anatomical features

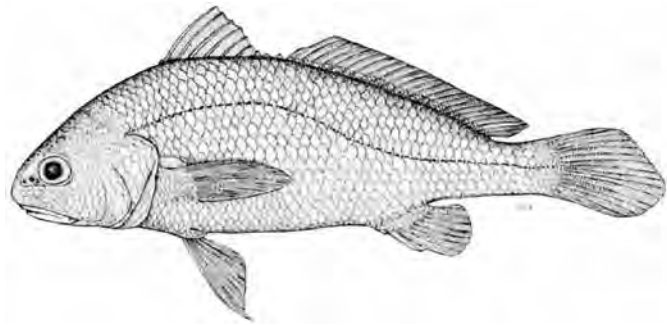
Fin elements: Dorsal IX-X/I, 27-30;

Anal II, 7-8; Pectoral 19

Lateral scales: 47-49

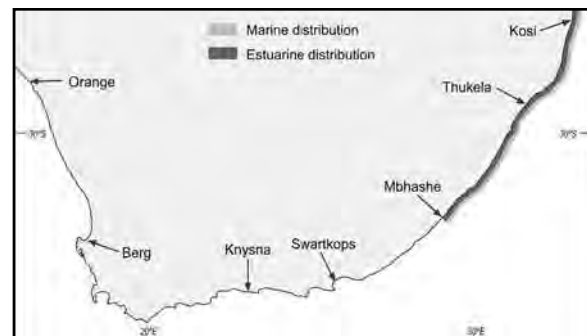
Maximum recorded length in southern

African waters:  $\pm 21$  cm SL



### Distribution

This mainly tropical Indo-West Pacific species has a distribution extending from Singapore to the Eastern Cape. As is the case with *Argyrosomus japonicus*, the possibility exists that *J. dorsalis* in southern Africa are a genetically different species from those populations in the eastern part its range. Although adults occur both in estuaries and the sea, they appear to be more abundant in the marine environment where they occur down to a depth of 40 m.



### Biology and ecology

*Johnius dorsalis* is a shoaling fish, common in certain permanently open estuaries and estuarine lakes on the northern KwaZulu-Natal coast but seldom recorded in temporarily closed estuaries. This species has a size range in estuaries from 2-28 cm TL, with the 16-26 cm TL size classes being most abundant (Wallace 1975a).

Males become sexually active at approximately 10 cm SL and females at 13 cm SL. Spawning occurs in the sea between September and February (Wallace 1975b), with spent adults recorded entering estuaries after breeding. The period of migration by juveniles into estuaries has not been quantified and they are only common in northern KwaZulu-Natal systems (van der Elst 1988).

The recorded salinity range of *J. dorsalis* is 1-55 (Whitfield 1996a) but large scale mortalities of this species were documented in Lake St Lucia under low salinity (<3) and low temperature (12°C) conditions (Blaber & Whitfield 1976). The small kob appears to favour turbid water areas, with all specimens captured in Lake St Lucia by Cyrus & Blaber (1987a) being associated with

water >50 NTU and almost 70% of the catch occurring in turbidities >80 NTU.

In estuaries, *J. dorsalis* is a benthic forager over muddy substrata, preying on both invertebrates and small fishes. Invertebrate taxa in the diet include crabs, mysids, amphipods, bivalves and gastropods, with fish such as *Glossogobius callidus*, *Gilchristella aestuaria* and *Thryssa vitrirostris* being important prey items (Whitfield & Blaber 1978a). Fish scales from large species were also found in the stomach contents of 5% of the individuals examined in Lake St Lucia. The sub-terminal mouth position of *J. dorsalis* would suggest that these scales were picked up from the substratum and not removed from living individuals (as is the case for *Terapon jarbua*).

The slow swimming small kob is frequently preyed upon by larger piscivores such as *Argyrosomus japonicus* (van der Elst 1988). This species was a major prey item of white-breasted cormorants and Caspian terns at Lake St Lucia during the mid-1970s (Whitfield & Blaber 1978d, 1979b).

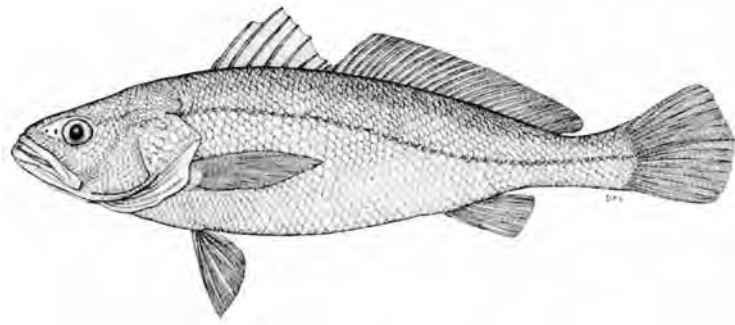
Family: SCIAENIDAE

Species: *Otolithes ruber*

(Bloch & Schneider 1801)

Common name: Snapper kob

Illustrated specimen length: 23 cm SL



### Selected anatomical features

Fin elements: Dorsal IX-X/I, 27-30;

Anal II, 7-8; Pectoral 17

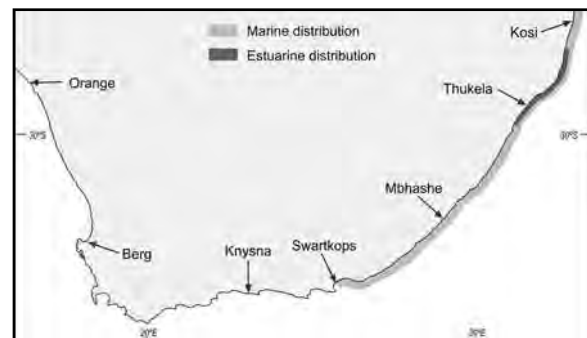
Lateral scales: 48-50

Maximum recorded length in southern

African waters:  $\pm 70$  cm SL

### Distribution

The snapper kob is a tropical and subtropical Indo-West Pacific species (Heemstra 1986c) extending as far south as Algoa Bay in the Eastern Cape (Wallace 1975a). Although adults are frequently recorded in some of the larger northern KwaZulu-Natal estuaries, juveniles have not been found in these systems (van der Elst 1988). This mainly demersal species is known to occur mainly over muddy and sandy substrata but tend to avoid areas where rocky reefs occur.



### Biology and ecology

This is a shoaling fish of coastal waters, sheltered bays and large estuarine systems (van der Elst 1988), especially those systems with a high mud content..

Sexual maturity is attained at about 23 cm SL, with breeding occurring in the nearshore marine environment during spring and summer (September-February) (Wallace 1975b). Both ripe and spent individuals have been recorded in estuaries, but the ripe-running stage only occurs in the marine environment.

The larvae and 0+ juveniles appear to use the marine environment as a nursery area because early juveniles have not been recorded in estuaries (van der Elst 1988). This species is abundant on the Thukela Banks and it would appear that adult *O. ruber* are being opportunistic by utilizing St Lucia and Richards Bay as estuarine feeding grounds.

The snapper kob is euryhaline and has been found in salinities ranging from 7-35 (Whitfield 1996a). This species appears to avoid clear-water

estuaries such as the Kosi system but is often associated with the high turbidity waters of Lake St Lucia.

According to van der Elst (1988) *O. ruber* is a rather sluggish and mainly demersal carnivore which hunts in an opportunistic manner. Whitfield & Blaber (1978a) found that adult snapper kob in Lake St Lucia preyed mainly on pelagic clupeids and engraulids, although penaeid prawns from the hyperbenthos were also consumed. In the marine environment they feed on small fish, squid and shrimps (van der Elst 1988).

Initial growth by this species is fairly rapid, with a 3-year old fish attaining 300 mm TL and then the growth rate slowing down, with an 8-year old fish measuring 485 mm TL (Brash & Fennessy 2005). *Otolithes ruber* is heavily targeted by subsistence gill nets, beach seines and line fishing in Mozambique. In South Africa this species forms part of the bycatch of prawn trawlers on the Thukela Banks and is also targeted by recreational hook and line anglers along the coast (Fennessy 1994).

Family: LEIOGNATHIDAE

Species: *Leiognathus equula* (Forsskål 1775)

Common name: Slimy

Illustrated specimen length: 16 cm SL

### Selected anatomical features

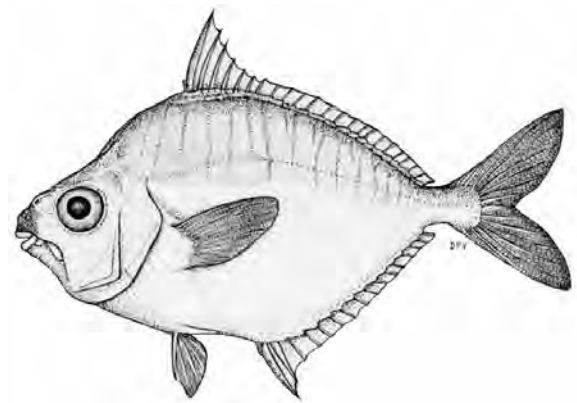
Fin elements: Dorsal VIII, 15-16;

Anal III, 14-15; Pectoral 18-20

Lateral scales: 54-63

Maximum recorded length in southern

African waters:  $\pm 20$  cm SL



### Distribution

This mainly tropical fish species has an Indo-West Pacific distribution (Smith 1986d) extending as far south as the Great Fish Estuary on the Eastern Cape coast. Shoals of *L. equula* occur in estuaries and warm coastal waters down to a depth of 40 m.

### Biology and ecology

This species is common in permanently open estuaries and bays on the KwaZulu-Natal coast but also occurs in some of the larger temporarily open /closed systems within the subtropical region. The size range of *L. equula* in estuaries is 15-240 mm TL, with the 40-80 mm TL size classes being most abundant (Wallace 1975a, Blackler 2002).

*Leiognathus equula* becomes sexually mature at approximately 13 cm SL. No ripe-running individuals have been sampled in KwaZulu-Natal estuaries but the occurrence of ripe fish suggests that spawning extends mainly from October to March (Wallace 1975b). Spent *L. equula* have been recorded in estuaries, thus confirming a strong estuary association.

Juveniles enter estuaries when <20 mm TL, with size classes between 30 mm and 80 mm TL making extensive use of estuaries as nursery areas during summer. The absence of these size classes, and preponderance of 100-150 mm SL size classes in the St Lucia system after 30 months of closure, illustrates the importance of marine-estuarine connectivity to this species (Cyrus & Vivier 2006).

The recorded salinity range of *L. equula* is from 1-37 (Whitfield 1996a), but mortalities of this species were recorded in Lake St Lucia under low salinity (<3) and low temperature (12°C)



conditions (Blaber & Whitfield 1976). The slimy is an intermediate turbidity species, with 36% of the specimens captured in Lake St Lucia by Cyrus & Blaber (1987a) being associated with water 10-50 NTU, and 56% between 50 NTU and 80 NTU.

Prey consumption may occur using either a pelagic or benthic mode of foraging, depending mainly on fish size. Newly recruited 0+ juveniles tend to feed in the midwater on planktonic crustaceans such as copepods, cumacea and crab zoeae, while larger juveniles and adults prey mainly on small crabs, prawns, amphipods, polychaetes, tan- aids and small bivalves (Whitfield 1980e, Day et al. 1981, van der Elst 1988, Blackler 2002). Demersal foraging is aided by a protrusible mouth that points downwards when fully extended.

Flexibility in foraging behaviour is epitomized by *L. equula* in the Mfolozi-Msunduzi Estuary where this species dominated the ichthyofauna between 2008 and 2010 (Nhleko et al. 2012). These authors determined that the zoobenthos in this system was impoverished but the zooplankton was rich and dominated by the copepod *Pseudodiaptomus stuhlmanni*. The diet of *L. equula*, both spatially and temporally, was also dominated by the above copepod and Nhleko et al. (2012) hypothesized that *P. stuhlmanni* was



preyed upon by *L. equula* during daylight hours when this calanoid congregates on or near the substratum.

Despite producing copious amounts of mucus and being able to lock the spines of both the

dorsal and anal fins into an upright position, this species is preyed upon by a wide range of piscivorous birds and fishes. The reason why such a large amount of mucus is used to coat the body, when compared to other fishes, has yet to be determined.

Family: LOBOTIDAE

Species: *Lobotes surinamensis* (Bloch 1790)

Common name: Tripletail

Illustrated specimen length: 89 mm SL

#### Selected anatomical features

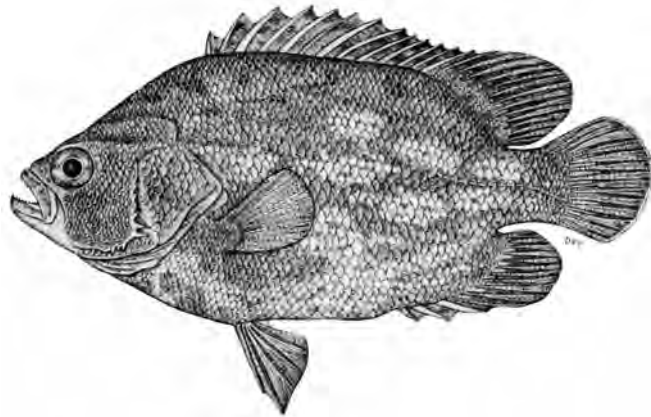
Fin elements: Dorsal XI-XII, 15-16;

Anal III, 11-12; Pectoral 17

Lateral scales: 43-45+5 on caudal

Maximum recorded length in southern

African waters:  $\pm$  87 cm SL



#### Distribution

The tripletail is found in shallow tropical and subtropical waters of all oceans, extending into the warm-temperate region of the Eastern Cape Province as far south as St Francis Bay (Heemstra 1986d). This sluggish but versatile fish predator has been recorded in the shallow waters of Lake St Lucia and, when present in river mouths or permanently open estuaries, this species is usually confined to the deeper channel areas within the lower reaches.



#### Biology and ecology

*Lobotes surinamensis* in southern African waters appear to favour muddy estuaries and large river mouths (van der Elst 1988). Spawning occurs in summer and limited numbers of 0+ juveniles are sometimes found in KwaZulu-Natal and Eastern Cape estuaries.

Early juveniles are predominantly yellow and black, while the caudal fin is translucent, giving the overall appearance of a dead mangrove leaf. Within estuaries they often mimic floating leaves by drifting slowly on their sides with the current (van der Elst 1988). In this way they may avoid the attentions of predators as well as being able to approach unsuspecting prey. Juveniles at sea are sometimes found well offshore near floating objects (Heemstra 1986d).

The documented salinity range of *L. surinamensis* is 10-35 (Whitfield 1996a) but further sampling is likely to increase these tolerance limits especially in low salinity systems. Fishermen have reported catching a wide size range of this species in the normally oligohaline Thukela Estuary that is dominated by river flow. Adults have been recorded in South Lake of the St Lucia system when salinities were 10.

The tripletail is a predominantly demersal species foraging mainly on bottom-dwelling crustaceans, including crabs, penaeid prawns, mud prawns and sometimes small fish (van der Elst 1988). Three *L. surinamensis* captured by an angler in the Thukela mouth region had been feeding on *Hilsa kelee*, *Thryssa vitrirostris* and juvenile mugilids.

Family: CARANGIDAE

Species: *Caranx ignobilis* (Forsskal 1775)

Common name: Giant kingfish

Illustrated specimen length: 93 mm SL

#### Selected anatomical features

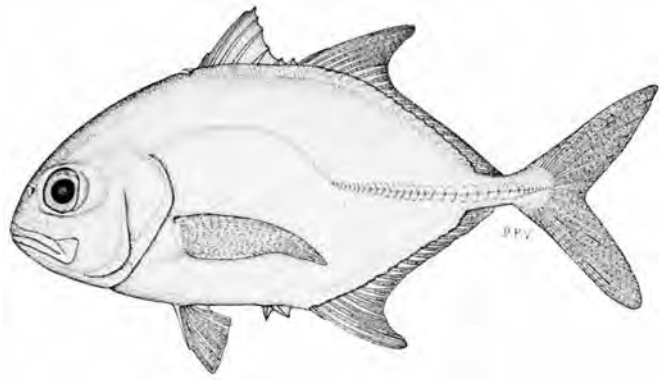
Fin elements: Dorsal VIII+I, 18-21;

Anal II+I, 15-17

Lateral line with 26-38 scutes

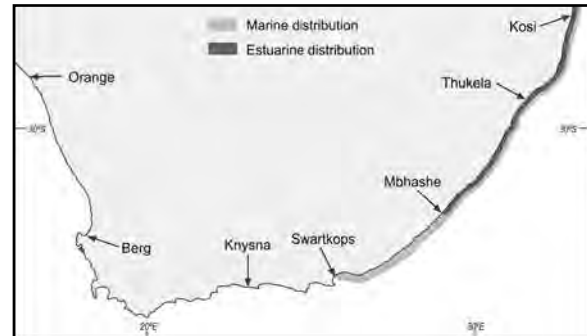
Maximum recorded length in southern

African waters:  $\pm$  140 cm SL



#### Distribution

*Caranx ignobilis* is a widespread tropical and subtropical Indo-Pacific species, extending into the Eastern Cape Province (Smith-Vaniz 1986). Although the adults are associated with coastal reefs, juveniles are frequently found in estuaries and shoals of adults are known to gather in the Mtentu Estuary each spring.



#### Biology and ecology

Sexual maturity is attained at 58 cm SL, with spawning occurring during summer in the marine environment (van der Elst 1988, Daly et al. 2018). Recruitment of 0+ juveniles into Kwa-Zulu-Natal estuaries also occurs during summer but larger fish are present throughout the year.

Giant kingfish have been recorded in salinities from 1-38 and subadults from 1-35 (Blaber & Cyrus 1981). Juveniles (<20 cm SL) occur in highly turbid waters (>50 NTU) such as St Lucia, as well as in clear waters (<5 NTU) in the Kosi Estuary. The 0+ juveniles do not form mixed shoals with other carangids (Blaber & Cyrus 1983). The diet of juveniles (40-199 mm SL) in

Kwa-Zulu-Natal estuaries is dominated by small fish together with large quantities of penaeid prawns (Blaber & Cyrus 1983). Prey is primarily located by sight and this species tends to be more active during the day, especially at dusk and dawn (van der Elst 1988). Juveniles <20 cm SL feed mainly during the day with maximum stomach fullness at 18h00 (Blaber & Cyrus 1983). Subadult fish >20 cm SL are almost entirely piscivorous, feeding particularly on *Ambassis* species in estuaries (Blaber & Cyrus 1983). In the marine environment approximately 70% of the diet of *C. ignobilis* comprises fish (van der Elst 1988).

Family: CARANGIDAE

Species: *Caranx papuensis*

(Alleyne & Macleay 1877)

Common name: Brassy kingfish

Illustrated specimen length: 16 cm SL

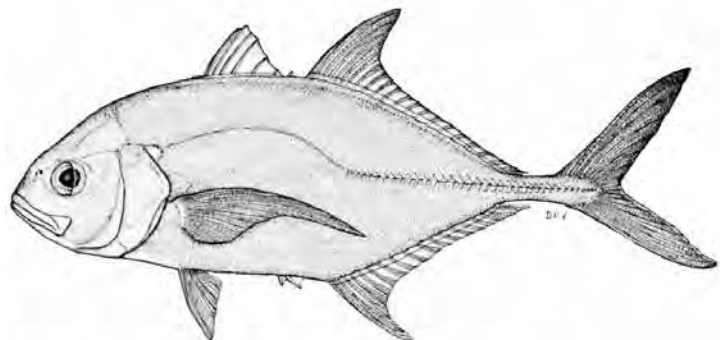
#### Selected anatomical features

Fin elements: Dorsal VIII+I, 21-23;

Anal II+I, 16-19

Lateral line with 31-39 scutes

Maximum recorded length:  $\pm$  66 cm SL



### Distribution

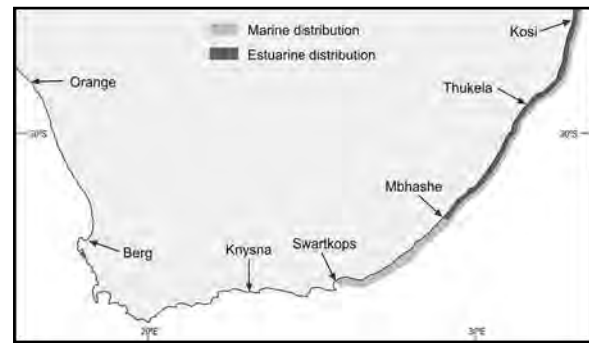
The brassy kingfish is a widespread tropical Indo-Pacific species, ranging from southern Africa northward and eastward to the Marquesas Islands. According to Smith-Vaniz (1986) this is a predominantly seaward reef species but juveniles do occur in subtropical estuaries on the subcontinent.

### Biology and ecology

*Caranx papuensis* is present in KwaZulu-Natal waters throughout the year, with a peak in abundance during summer (van der Elst 1988). Juveniles occur in certain permanently open estuaries of the subtropical region, increasing in abundance from south to north (Blaber & Cyrus 1983). Although adult fish have been captured from the Kosi and Mlalazi estuaries, no reproductively active fish have been recorded. Spawning probably occurs in tropical waters off the East African coast with early larval development occurring at sea.

In southern African estuaries, juveniles 4-12 cm SL are found in mixed shoals with *Caranx sexfasciatus* and *Caranx melampygus*, but the subadults (18-28 cm SL) usually occur in single species shoals (Blaber & Cyrus 1983).

Adult *C. papuensis* appear to be intolerant of turbid water and low salinity conditions (van der Elst 1988). Blaber & Cyrus (1983) captured adults only in the lower reaches of estuaries, usually in groups of 4-6 individuals. The recorded



salinity range of juveniles was 6-35 and of subadults 4-35. Juveniles and subadults are associated with water turbidities up to 25 NTU (Blaber & Cyrus 1983).

The diet of juveniles (4-16 cm SL) in KwaZulu-Natal estuaries consists mainly of mysids and small penaeids, with small fish also being important. The mysids are probably captured by filter feeding, since *C. papuensis* has long gill rakers with well-developed denticles (Blaber & Cyrus 1983). Foraging by both juveniles and subadults in KwaZulu-Natal estuaries occurs mainly during the day, with peak stomach fullness occurring between 12h00 and 15h00 depending on fish size.

Adult brassy kingfish in the marine environment hunt singly or in pairs, moving over reefs as well as sandy beaches between rocky outcrops (van der Elst 1988). They prey primarily on small fish, especially reef dwelling species, although squid, prawns and crabs are also consumed.

Family: CARANGIDAE

Species: *Caranx sexfasciatus* (Quoy & Gaimard 1825)

Common name: Bigeye kingfish

Illustrated specimen length: 84 mm SL

### Selected anatomical features

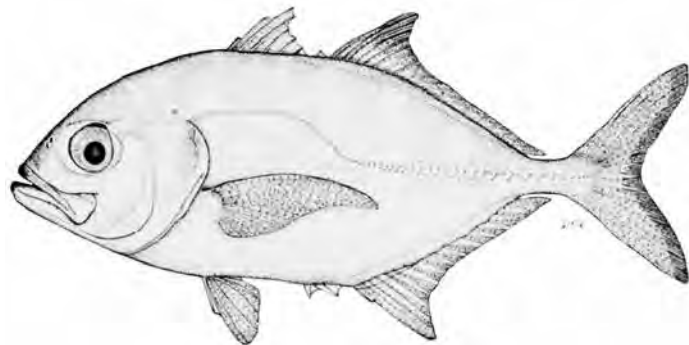
Fin elements: Dorsal VIII+I, 19-22;

Anal II+I, 14-17

Lateral line with 27-36 scutes

Maximum recorded length in southern

African waters:  $\pm 71$  cm SL



### Distribution

The bigeye kingfish is a widespread tropical Indo-Pacific species, ranging from the Eastern Cape northward and eastward to the Americas

(Smith-Vaniz 1986). Although the larger juveniles and adults are usually associated with coastal reefs, 0+ juveniles are common in certain KwaZulu-Natal estuaries, sometimes extending their distribution into permanently open warm-temperate Eastern Cape estuaries during summer.

### Biology and ecology

Sexual maturity is attained at approximately 42 cm SL (van der Elst 1988). Spawning in the marine environment probably occurs during spring and summer because newly recruited juveniles 30-60 mm SL enter KwaZulu-Natal estuaries between October and April. Modal sizes of *C. sexfasciatus* from Kosi indicate a growth of 12 cm in both the first and second years (Blaber & Cyrus 1983).

Small juveniles (30-100 mm SL) usually occur in discrete shoals, but on occasion have been recorded mixed with *Caranx melampygus* and *C. papuensis*. All sizes of *C. sexfasciatus* in estuaries are euryhaline, with a recorded salinity range from 0.5-40 (Blaber & Cyrus 1983). Juveniles 60-70 mm SL have been found in fresh water above the ebb and flow of certain Eastern Cape estuaries (e.g. Keiskamma), and in Lake Nhlangwe they are present throughout the year in a salinity <1 (Blaber & Cyrus 1981).

The bigeye kingfish is predominantly associated with clear to partially turbid waters, with 54% of the juveniles captured in KwaZulu-Natal estuaries being associated with water turbidities <10 NTU, and 37% between 10 and 50 NTU (Cyrus & Blaber 1987c). Specimens larger than 12 cm SL were only recorded from <10 NTU waters (Blaber & Cyrus 1983).

Family: CARANGIDAE

Species: *Lichia amia* (Linnaeus 1758)

Common name: Leervis, Garrick

Illustrated specimen length: 16 cm SL

### Selected anatomical features

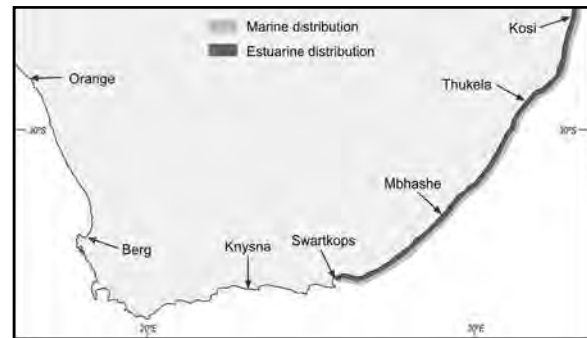
Fin elements: Dorsal VII+I, 19-21;

Anal II+I, 17-21

Lateral line sinuous

Maximum recorded length in southern

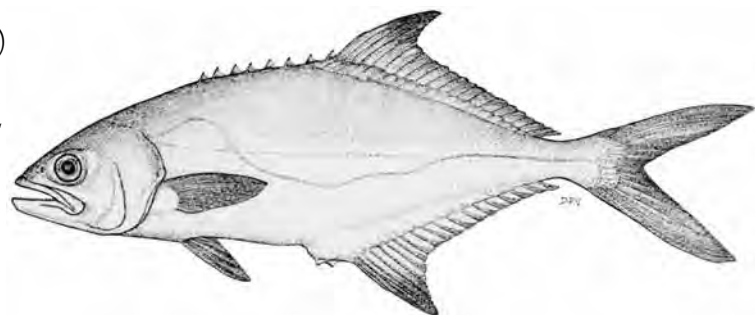
African waters:  $\pm$  110 cm SL



Adult fish seem more sensitive to changes in temperature and salinity than juveniles, with the former life stage showing a preference for clear marine waters (van der Elst 1988). The absence of adult *C. sexfasciatus* from Eastern Cape estuaries where the juveniles have been recorded suggests that the former cohort is less adapted to the cooler water temperatures of warm-temperate systems.

The diet of newly recruited juveniles (30 mm SL) in KwaZulu-Natal estuaries is dominated by calanoid copepods. Larger juveniles prey on the fry of a number of estuary-associated marine species, although a considerable proportion of the diet consists of penaeid prawns. Subadult *C. sexfasciatus* >20 cm SL are almost entirely piscivorous, feeding particularly on ambassids in estuaries. This size group forages mainly during the early morning and late evening, whereas the smaller juveniles showed a peak stomach fullness at 15h00 (Blaber & Cyrus 1983).

Adult fish hunt singly, moving from reef to reef in search of food which consists mainly of small fish. The diet is however supplemented with prawns, mantis shrimps, swimming crabs and other epibenthic or midwater organisms (van der Elst 1988).



## Distribution

The leervis has a range extending from the Mediterranean Sea, southward along the entire African coast and around Cape Point to northern KwaZulu-Natal (Smith-Vaniz 1986). Juveniles are mainly associated with estuaries, whereas the adults occur predominantly in the nearshore marine environment (van der Elst 1988).

## Biology and ecology

*Lichia amia* become sexually active at 58 cm SL (van der Elst 1988). Spawning in the marine environment probably occurs during late winter and spring, with spent individuals recorded mainly between September and November in KwaZulu-Natal waters (Wallace 1975b).

The southward transport of larvae is probable, with small juveniles being rare in KwaZulu-Natal estuaries but increasingly common towards the southwest (Wallace & van der Elst 1975). Cohorts 25-40 mm SL enter warm-temperate estuaries during summer (Beckley 1984a, Bennett 1989, Whitfield & Kok 1992). Juveniles 40-50 mm SL from the Orange Estuary indicate that breeding may also occur off the cool-temperate west coast.

The recorded salinity range for *L. amia* is 2-39 (Whitfield 1996a) and the leervis was one of the few marine species not to succumb to the prolonged low salinities (<3) in the Bot Estuary (Bennett 1985). *Lichia amia* occurs in a wide range of turbidities, but it is particularly abundant in clear to partially turbid estuaries (<50 NTU).

According to van der Elst (1988) this species undertakes seasonal migrations, moving to Kwa-Zulu-Natal in winter (June) and back to the warm-temperate region in early summer. Winter



migrations usually coincide with the annual northward movement of *Sardinops sagax* shoals and are associated with a period of increased gonad development by *L. amia*.

The diet of newly recruited leervis, which are yellow in colour with broad dark bars on the back half of the body, is dominated by mysids, shrimps and small fishes. They are voracious predators and specimens <80 mm SL and can consume prey up to 70% of their body length (Smale & Kok 1983). Growth is extremely rapid, and Blaber (1974c) recorded an 11 cm length increase within six months (January-July) in the West Kleinemonde Estuary.

Subadults are primarily piscivorous on estuarine species such as *Gilchristella aestuaria* and estuary-associated marine taxa such as *Chelon richardsonii* (Coetzee 1982b, Marais 1984). In the marine environment, adults of this species prey extensively on *Pomatomus saltatrix*, *P. olivaceus* and *Sarpa salpa* (van der Elst 1988).

Laboratory studies on oxygen consumption by *L. amia* have been conducted by du Preez (1987) and faecal and non-faecal energy losses by leervis feeding on *Chelon richardsonii* have been investigated by du Preez & Cockcroft (1988b).

Family: CARANGIDAE

Species: *Scomberoides lysan* (Forsskål 1775)

Common name: Doublespotted queenfish

Illustrated specimen length: 16 cm SL

## Selected anatomical features

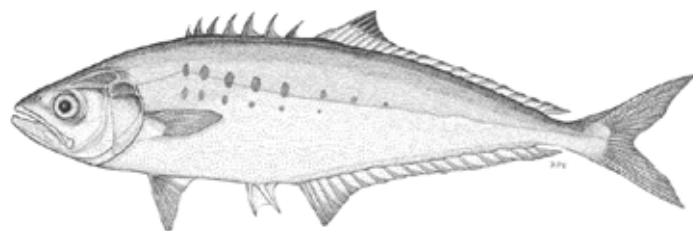
Fin elements: Dorsal VI-VII+I, 19-21;

Anal II+I, 17-19

Scales on midbody lanceolate

Maximum recorded length in southern

African waters:  $\pm$  65 cm SL





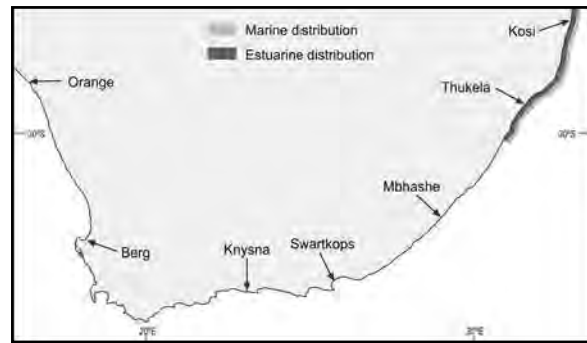
### Distribution

This queenfish is a widespread Indo-West Pacific species, ranging from southern Africa northward and eastward to the Hawaiian Islands (Smith-Vaniz 1986). It is found from estuaries to marine offshore areas, from surface waters to 100 m depth.

### Biology and ecology

Within southern African estuaries, *S. lysan* is commonly recorded in some of the larger KwaZulu-Natal systems such as Kosi, usually in single size-class shoals numbering at least 100 individuals (Blaber & Cyrus 1983). Spawning occurs in the marine environment during spring and early summer, with the juveniles entering estuaries at a length of 20-30 mm SL during late summer. A growth rate of 12 cm per annum for first and second year fish has been estimated, with a slower growth recorded in the third year (Blaber & Cyrus 1983). No mature *S. lysan* were recorded in KwaZulu-Natal estuaries, with the largest specimen measuring 42 cm SL.

This species appear to be intolerant of highly turbid water because they are absent from Lake St Lucia. According to Blaber & Cyrus (1983) the juveniles appear to be more tolerant of turbid water than the subadults. The recorded salinity range of juveniles was approximately 6-35, with



subadults found in salinities down to 1 (Blaber & Cyrus 1983).

The diet of juveniles 20-60 mm SL in KwaZulu-Natal estuaries comprises a variety of planktonic organisms and fish scales (Blaber & Cyrus 1983, Major 1973). Juveniles 7-19 cm SL feed primarily on mysids and small penaeid prawns, although the fry of a number of fish species are also taken.

The subadults (19-42 cm SL) show a switch in diet to fish although large quantities of mysids are still consumed (Blaber & Cyrus 1983). Filter feeding of the mysids is a distinct possibility since *S. lysan* have long gill rakers with well-developed denticles. Foraging occurs mainly during the day, with peak stomach fullness occurring at 15h00 for both juveniles and subadults (Blaber & Cyrus 1983).

Family: MUGILIDAE

Species: *Chelon dumerili* (Steindachner 1870)

Common name: Grooved mullet

Illustrated specimen length: 26 cm SL

### Selected anatomical features

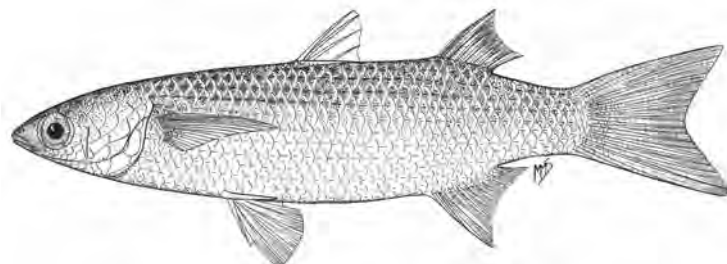
Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 16

Lateral scales: 36-39

Maximum recorded length in southern

African waters:  $\pm 32$  cm SL



### Distribution

The southern African grooved mullet has an African distribution extending from the Western Cape to Mozambique (Smith & Smith 1986b). This species occurs as far west as False Bay (Clark et al. 1994) but is absent from the cool-temperate

Western Cape coastal region. A West African population of *C. dumerili* occurs from Senegal to Namibia. The juveniles are normally abundant in estuaries, with the adults occurring in both the estuarine and marine environment (Wallace 1975a).

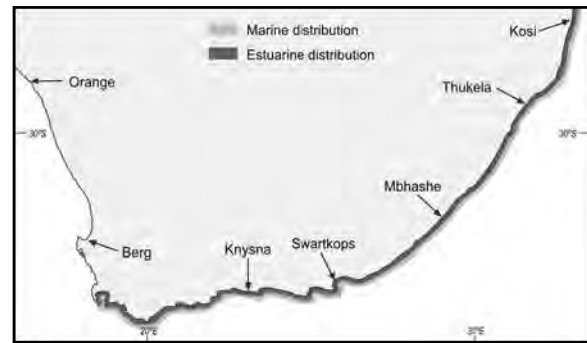
### Biology and ecology

Spawning by *C. dumerili* > 18 cm SL appears to take place in the vicinity of estuaries, with some specimens in a ripe-running condition recorded within estuary mouths (van der Horst & Erasmus 1981). In KwaZulu-Natal, breeding occurs between June and November (Wallace 1975b) but in the Eastern Cape spawning has been recorded in the summer between December and February (van der Horst & Erasmus 1978, 1981). Large numbers of spent individuals return to the estuarine environment following spawning (Wallace 1975b).

According to Wallace & van der Elst (1975) the recruitment of juvenile *C. dumerili* < 50 mm TL occurs mainly from August to February in KwaZulu-Natal estuaries, whereas in Eastern Cape systems peak immigration is from April to May (Beckley 1984a). On the southern Cape coast, recruitment of *C. dumerili* < 30 mm TL occurs throughout the year with a peak between November and June (Whitfield & Kok 1992).

*Chelon dumerili* is a highly euryhaline species and has been recorded in salinities from 1 to 90 (Whitfield 1996a). In the temporarily closed Seekoei Estuary this species did not survive salinities above 90 (Whitfield 1998). Routine oxygen consumption by this and other mugilid species has been calculated by Marais (1978).

The grooved mullet is associated with water turbidities ranging from <10-80 NTU, with more than 90% of individuals occurring in water <50 NTU (Cyrus & Blaber 1987c). Based on field and laboratory choice chamber experiments *Chelon*



*dumerili* can be regarded as a clear to partially-turbid water species, an adaptation that enables it to colonize a wide variety of estuaries.

The diet of postlarval *C. dumerili* < 20 mm SL consists mainly of ostracods, insect larvae, foraminiferans and diatoms, with a switch to a typical juvenile diet occurring at a length > 20 mm and coinciding with a switch to benthic foraging (Blaber & Whitfield 1977a).

Juveniles and adults consume mainly particulate organic matter, macrophytic plant material, diatoms, foraminiferans and small gastropods. Large amounts of sand with mean particle diameters ranging from 0.2-0.5 mm are also ingested (Masson & Marais 1975, Blaber 1976, 1977).

Feeding periodicity studies indicate that *C. dumerili* forages during the day and night, with a lower food intake during the nocturnal hours (Blaber 1976, Marais 1980). According to Marais (1978), oxygen consumption by this species displays a diel rhythm, with lowest consumption rates at midday and midnight and highest just after sunrise and sunset.

Family: MUGILIDAE

Species: *Chelon richardsonii* (Smith 1846)

Common name: Southern mullet

Illustrated specimen length: 16 cm SL

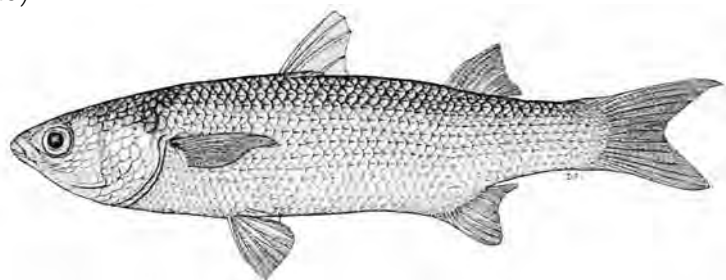
### Selected anatomical features

Fin elements: Dorsal IV+I, 8-9;

Anal III, 9; Pectoral 16-18

Lateral scales: 44-50

Maximum recorded length:  $\pm$  32 cm SL



## Distribution

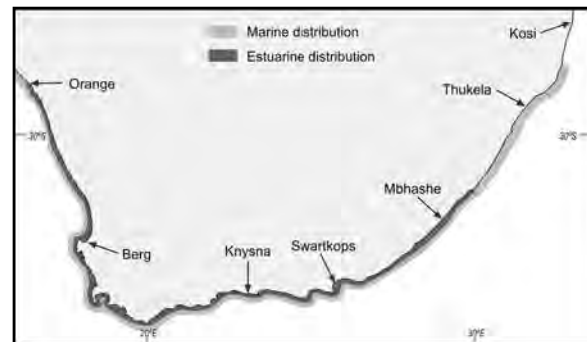
The southern mullet is an endemic species that is often abundant in temperate South African estuaries but is rarely recorded in subtropical KwaZulu-Natal systems. Although the juveniles and adults are common in Eastern and Western Cape estuaries (Bennett 1989), this species is usually more abundant in the nearshore marine environment.

## Biology and ecology

*Chelon richardsonii* matures at 18 cm SL (de Villiers 1987) and according to Lasiak (1983a) spawns in Eastern Cape waters between September and March, often close inshore (van der Horst & Erasmus 1981). The larval development of this species, which has been described by Cambray & Bok (1989), takes place in the nearshore marine environment.

Peak abundance of postflexion larvae in the Swartvlei Bay surf zone was between October and March (Whitfield 1989c), which coincided with the immigration of *C. richardsonii* <20 mm TL into the Swartvlei Estuary. It would appear, however, that juvenile recruitment into permanently open Western Cape estuaries occurs throughout the year, with peak immigration between November and May (Bennett 1989, Whitfield & Kok 1992). Cohorts 10-40 mm SL were recorded migrating up the Serpentine in the Wilderness Lakes system during February (Hall et al. 1987).

Unlike most other mugilids, which rely mainly on estuarine nursery areas (Wallace et al. 1984a), the juveniles of *C. richardsonii* are common both in estuaries (Beckley 1984a) and in the marine environment (Romer & McLachlan 1986). In the Knysna and Swartvlei estuaries, 0+ juveniles are most abundant in the lower and middle reaches (Whitfield & Kok 1992). They do, however, penetrate the upper reaches of estuaries and were common in the littoral zone of Swartvlei lake when the aquatic macrophyte beds underwent major senescence.



The southern mullet is euryhaline and has been recorded in salinities ranging from 2-90 (Branch et al. 1985, Whitfield 1996a). Limited mortalities were documented in the temporarily closed Bot Estuary when salinities remained below 3 for more than a month and coincided with low water temperatures (Bennett 1985). It would appear that *C. richardsonii* in estuaries maintains a better physiological condition (e.g. higher lipid levels) than marine populations due to more favourable feeding opportunities and the retention of energy usually lost through spawning (de Decker & Bennett 1985).

The diet of postlarval *C. richardsonii* less than 20 mm SL consists mainly of copepods and macruran larvae, with a switch to a typical juvenile diet occurring at a length greater than 20 mm SL (Whitfield 1985). Juveniles and adults consume mainly particulate organic matter, pennate diatoms, unicellular and filamentous algae, macrophytic plant material and foraminiferans derived from benthic substrata (Masson & Marais 1975, Whitfield 1988a).

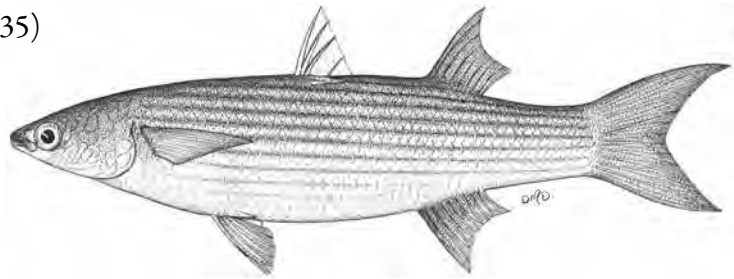
Large amounts of fine sand and silt are ingested together with food items by estuarine populations (Marais 1980) but planktonic feeding habits appear to be common in the marine environment (Romer & McLachlan 1986, de Villiers 1987). Feeding periodicity studies in the Swartkops Estuary indicate that *C. richardsonii* forages mainly during the day and have a very low food intake at night (Marais 1980).

Family: MUGILIDAE

Species: *Chelon tricuspiciens* (Smith 1935)

Common name: Striped mullet

Illustrated specimen length: 45 cm SL



### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 18

Lateral scales: 43-52

Maximum recorded length:  $\pm$  60 cm SL

### Distribution

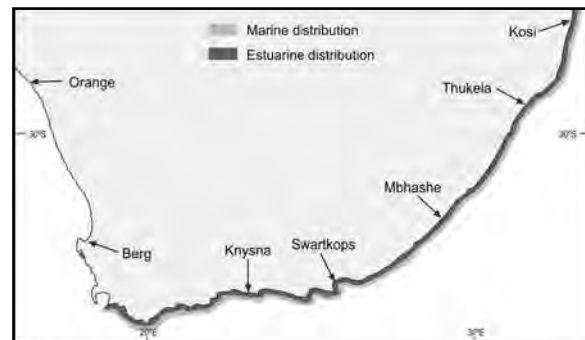
The striped mullet is an endemic southern African species which is absent from cool-temperate estuaries of the west coast (Smith & Smith 1986b). Juveniles and adults of this species occur both in estuaries and the nearshore marine environment. There is a decline in the abundance of *C. tricuspiciens* between subtropical KwaZulu-Natal and Eastern Cape estuaries (Blaber 1977), and westwards along the Western Cape coast towards the Palmiet system (Bennett 1989).

### Biology and ecology

This species matures at 38 cm SL and spawns mainly between August and November in KwaZulu-Natal waters (Wallace 1975b). Very few juveniles have been recorded in KwaZulu-Natal estuaries (Wallace & van der Elst 1975) but in the Eastern Cape, *C. tricuspiciens* < 10 cm TL have been recorded in moderate numbers from the Sundays and Swartkops systems (Beckley 1983, 1984a), as well as from tidal pools in the area (Beckley, 1985b).

Juveniles first enter estuaries at a length of 20-30 mm TL (Wallace & van der Elst 1975, Beckley 1983, 1984a) and, according to Blaber (1987), recruitment occurs between November and January. Evidence from Whitfield & Kok (1992) suggests an October-May influx of 0+ juveniles into the Knysna and Swartvlei estuaries, with peak recruitment between October and December. Cohort analyses from Knysna indicate that *Chelon tricuspiciens* may attain 14 cm TL in their first year. Large juveniles and adults of this species have great leaping powers when disturbed.

In the Knysna and Swartvlei systems, this species is most abundant in the lower half of the



estuaries, with relatively few individuals penetrating the upper reaches (Whitfield & Kok 1992, Whitfield 1993). A similar situation pertains to the nearby Wilderness system, where *C. tricuspiciens* was mainly restricted to the Wilderness lagoon (Hall et al. 1987).

Indications are that this species has a lower salinity tolerance limit of 4 (Blaber 1987), which may account for the avoidance by *C. tricuspiciens* of the upper reaches of most estuarine systems and those freshwater dominated temporarily closed estuaries where salinities often decline below 5. The striped mullet was recorded dying in the temporarily closed Seekoei Estuary when salinities increased above 90 (Whitfield 1998).

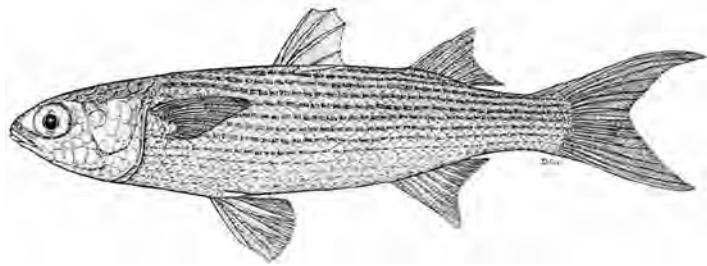
The diet of *C. tricuspiciens* in estuaries consists mainly of filamentous algae, macrophytic plant material, epiphytic diatoms and foraminiferans (Masson & Marais 1975, Blaber 1976, 1977). The tricuspid teeth of this species may aid the cropping of aquatic plants such as *Zostera* and *Ruppia* (Marais 1980). The large amounts of epiphytes consumed by *C. tricuspiciens* may account for the higher food protein and carbohydrate content when compared to other mullet species in the Swartkops Estuary (Marais & Erasmus 1977a). Small amounts of sand with mean particle diameters ranging from 0.2-0.6 mm are also ingested (Blaber 1976, 1977, Marais 1980).

Family: MUGILIDAE

Species: *Mugil cephalus* (Linnaeus 1758)

Common name: Flathead mullet

Illustrated specimen length: 17 cm SL



### Selected anatomical features

Fin elements: Dorsal IV+I, 6-8;

Anal III, 8; Pectoral 16-17

Lateral scales: 39-42

Maximum recorded length in southern

African waters:  $\pm 54$  cm SL

### Distribution

The flathead mullet has a cosmopolitan distribution, occurring in all warm and temperate seas, estuaries and rivers (Whitfield et al. 2012b). In southern Africa, this species is abundant in subtropical and warm-temperate estuaries but also occurs in cool-temperate estuaries along the west coast. The juveniles rely on estuaries and rivers as nursery areas, with the adults occurring in both estuarine and marine environments (Wallace 1975a).

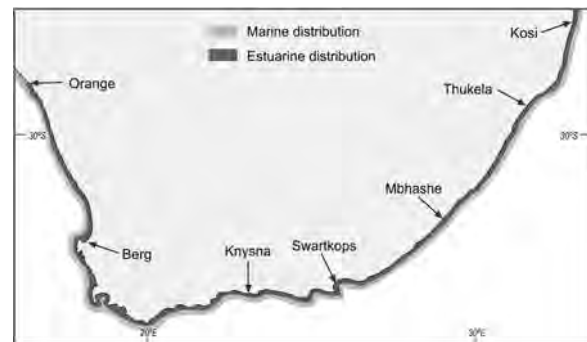
### Biology and ecology

This species spawns along the coast between May and September (Wallace 1975b) with recruitment of <30 mm TL juveniles into KwaZulu-Natal estuaries occurring between June and October (Wallace & van der Elst 1975).

In Eastern Cape estuaries, the main recruitment period is June to October (Bok 1979), with a peak during August /September (Beckley 1984a). Juveniles in the Eastern Cape sometimes penetrate riverine systems up to 100 km from the head of the estuary (Bok 1979).

Recruitment of 0+ juveniles into the Knysna Estuary occurs from August to December, with a peak during September-November (Whitfield & Kok 1992). Cohort analysis indicates that specimens <40 mm TL recruiting into the above estuary during August and may attain 16 cm TL by the end of March.

*Mugil cephalus* occurs in a wide range of salinities (0-84), temperatures (10-32°C) and turbidities (<10-80 NTU). Although it has been recorded dying in Lake St Lucia when low salinities (<2) and low temperatures occurred



simultaneously (Blaber & Whitfield 1976), the same species survived prolonged oligohaline conditions (<3) in the Bot and Kosi systems (Blaber & Cyrus 1981, Bennett 1985). In the temporarily closed Seekoei Estuary *M. cephalus* was recorded dying in salinities above 90 (Whitfield 1998). In the Eastern Cape, juveniles of this species regularly migrate into river catchment areas (Bok 1979) but there is little evidence to suggest similar large-scale movements in either the Western Cape or KwaZulu-Natal rivers.

The seaward spawning migration of *Mugil cephalus* in Lake St Lucia has been well documented, with large shoals of mature fish (+3 years of age, +34 cm SL) moving down the system in April each year (Whitfield & Blaber 1978b). Jumping activity by this species increases dramatically during the above migration, possibly as a result of increased predation by piscivorous birds and crocodiles (Whitfield & Blaber 1979b, 1979d).

The diet of postlarval *M. cephalus* <20 mm SL consists mainly of copepods, ostracods and diatoms, with a switch to the typical juvenile diet occurring at a length >20 mm SL (Blaber & Whitfield 1977a). Juveniles and adults consume mainly particulate organic matter, diatoms, macrophytic plant material, foraminiferans and small gastropods (Masson & Marais 1975, Blaber 1977).



Large amounts of sand with a mean particle diameter of 0.2-0.5 mm are also ingested and feeding periodicity studies in Lake St Lucia

indicate that *M. cephalus* forages mainly during the day, with a much lower food intake at night (Blaber 1976).

Family: MUGILIDAE

Species: *Crenimugil burchanani* (Bleeker 1853)

Common name: Bluetail mullet

Illustrated specimen length: 12 cm SL

#### Selected anatomical features

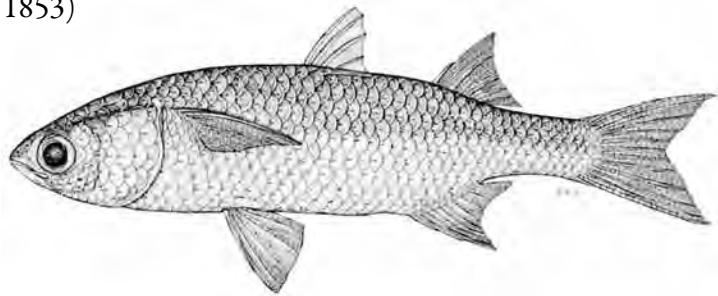
Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 17-18

Lateral scales: 33-36

Maximum recorded length in southern

African waters:  $\pm$  58 cm SL



#### Distribution

The bluetail mullet is an Indo-West Pacific species with stragglers reaching as far south as the Breede Estuary. Within southern African waters the juveniles of this species are most common in subtropical estuaries.

#### Biology and ecology

*Crenimugil burchanani* matures at approximately 36 cm SL and spawns in the inshore marine environment, mainly between October and December (Wallace 1975b). The peak immigration period of juveniles into subtropical KwaZulu-Natal estuaries ranges from May to July (Wallace & van der Elst 1975) and in warm-temperate estuaries from March to June (Whitfield & Kok 1992). Postlarvae enter estuaries from 10 mm SL upwards (Blaber 1987) and are usually most abundant in the lower reaches of these systems.

The bluetail mullet has been found in salinities ranging from 1-58 (Whitfield 1996a) but appears to avoid low salinity areas (<10). Peak abundance of juveniles occurs in permanently open estuaries, where salinities usually range between 20 and 35.

Although found in a wide range of water turbidities (<10-80 NTU), 90% of specimens



collected in Lake St Lucia avoided waters greater than 50 NTU (Cyrus & Blaber 1987c). Laboratory studies have confirmed the preference of *C. burchanani* for clear to partially-turbid waters (Cyrus & Blaber 1987b), hence the abundance of this species in the Kosi Estuary.

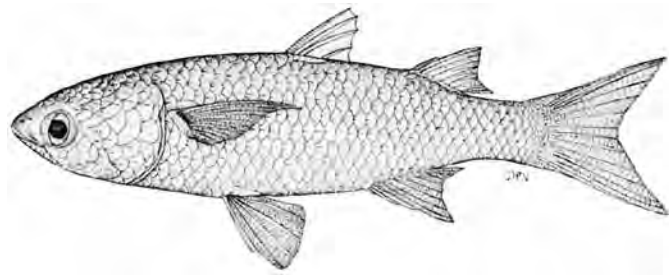
The diet of individuals <20 mm SL consists mainly of planktonic and vertically migrating crustaceans, with a switch to a typical juvenile diet occurring at a length of approximately 20 mm SL (Blaber & Whitfield 1977a). Juveniles and adults consume mainly diatoms, flagellates, particulate organic matter, terrestrial plant debris and foraminiferans (Blaber 1976, 1977). Large amounts of fine sand with a mean particle diameter of 0.1-0.2 mm are also ingested.

Family: MUGILIDAE

Species: *Moolgarda cunnesius*  
(Valenciennes 1836)

Common name: Longarm mullet

Illustrated specimen length: 12 cm SL



#### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

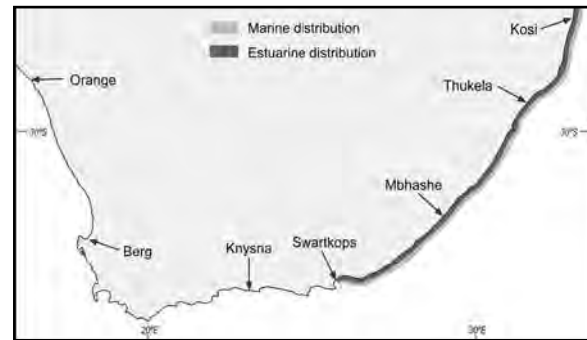
Anal III, 9; Pectoral 15

Lateral scales: 33-36

Maximum recorded length:  $\pm 27$  cm SL

#### Distribution

The longarm mullet is an Indo-West Pacific species reaching as far south as the Eastern Cape Province on the African continent (Smith & Smith 1986b). It is most common in temporarily closed subtropical estuaries along the KwaZulu-Natal coast (van der Elst 1988) and specimens have also been collected at the Save-Runde river confluence in eastern Zimbabwe.



#### Biology and ecology

This species matures at 17 cm SL and spawns inshore in the vicinity of estuary mouths between October and May (Wallace 1975b). According to Wallace & van der Elst (1975) there is no definite recruitment season, with 20-50 mm TL juveniles entering KwaZulu-Natal estuaries over a nine month period between October and June. Whitfield (1980c) recorded 10-40 mm SL *M. cunnesius* immigrating into the temporarily open Mhlabisa Estuary during summer.

The longarm mullet has been found in salinities ranging from 1-67 (Whitfield 1996a), with the juveniles particularly abundant in the low salinity waters (<10) of temporarily closed estuaries on the KwaZulu-Natal coast (Harrison & Whitfield 1994). Under oligohaline closed mouth

conditions at St Lucia, this became the dominant mullet species in the system.

Although the longarm mullet is associated with a wide range of turbidities, 86% of individuals were captured in waters ranging from 50-80 NTU (Cyrus & Blaber 1987c). *M. cunnesius* can thus be classified as an intermediate turbidity species (Cyrus & Blaber 1987a).

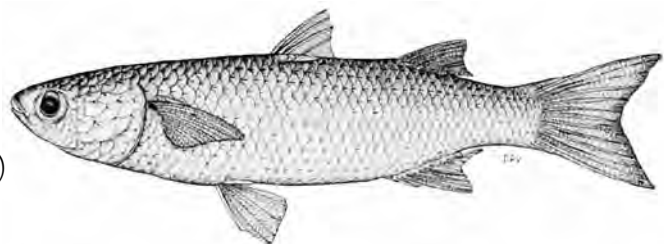
The diet of postlarvae <20 mm SL consists mainly of copepods, cladocerans and crustacean larvae, with a switch to a typical juvenile diet occurring at a length greater than 20 mm SL (Whitfield 1985). Juveniles and adults consume mainly particulate organic matter, diatoms, flagellates and foraminiferans (Blaber 1976, Whitfield 1980e). Large amounts of fine sediment with a mean particle diameter of 0.1-0.2 mm are also ingested (Blaber 1976, Whitfield 1980b), indicating that this species forages on more muddy bottoms than most other mullet species.

Family: MUGILIDAE

Species: *Osteomugil robustus* (Günther 1861)

Common name: Robust mullet

Illustrated specimen length: 12 cm SL



### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 15-16

Lateral scales: 36-39

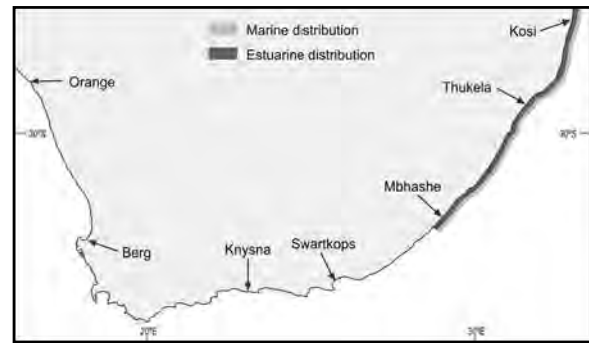
Maximum recorded length:  $\pm 25$  cm SL

### Distribution

The robust mullet is an endemic southern African species, ranging from Mozambique and Madagascar to the Eastern Cape Province (Smith & Smith 1986b). Although common within southern Mozambique estuaries, in South Africa this species is only abundant in the Kosi Estuary on the Kwa-Zulu-Natal north coast (Blaber 1977).

### Biology and ecology

*Osteomugil robustus* attains sexual maturity within the estuarine environment but breeding occurs exclusively at sea. The immigration period of juveniles into KwaZulu-Natal estuaries ranges from September to May (Blaber 1987) suggesting that spawning occurs during spring and summer.



Postlarvae enter estuaries from 10 mm SL upwards. Within estuaries the juveniles and adults occur in salinities ranging from 1-39.

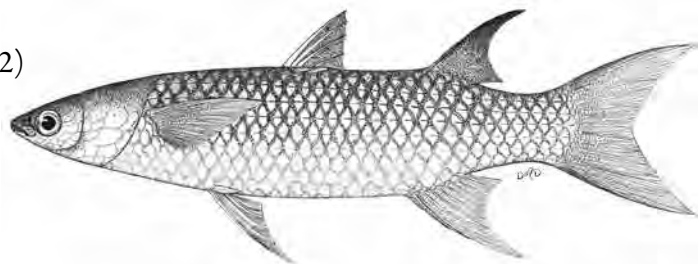
As was the case with the other mullet species, the diet of postlarval *O. robustus* <15 mm SL is dominated by vertically migrating plankton (Blaber & Whitfield 1977a). Juveniles and adults consume mainly diatoms, blue-green algae, flagellates, filamentous algae, terrestrial plant debris and particulate organic matter (Blaber 1976, 1977). Large amounts of fine sand with a mean particle diameter of 0.1-0.2 mm are also ingested.

Family: MUGILIDAE

Species: *Planiliza alata* (Steindachner 1892)

Common name: Diamond mullet

Illustrated specimen length: 45 cm SL



### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 16

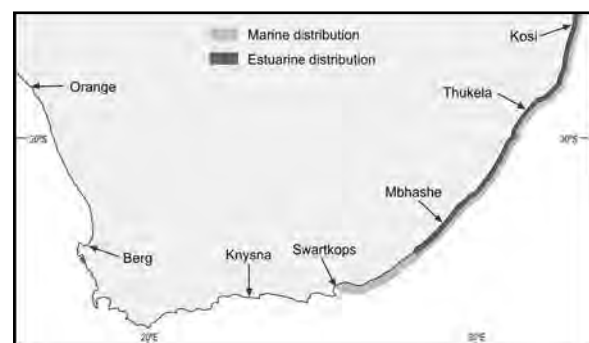
Lateral scales: 29-32

Maximum recorded length in southern

African waters:  $\pm 61$  cm SL

### Distribution

The diamond mullet is an Indo-West Pacific species which reaches as far as Algoa Bay in the south-west (Smith & Smith 1986b). Juveniles and adults of *P. alata* frequent KwaZulu-Natal and Eastern Cape estuaries but are not abundant in southern Africa (Wallace 1975a, Blaber 1977).



of 14 mm SL. Recruitment into estuaries occurs between July and January but peak immigration periods are unknown.

### Biology and ecology

According to Blaber (1987) spawning by *P. alata* occurs in the inshore marine environment and the 0+ juveniles first enter estuaries at a length

The diamond mullet is frequently captured in low salinity and low turbidity areas of estuaries, especially the middle reaches of lagoon and lake systems (Whitfield 1980b, Blaber & Cyrus

1981). This species appears to be attracted to humate-stained waters and will concentrate in areas of an estuary where such conditions are prevalent, e.g. in the St Lucia system the only area where this species was regularly recorded was where the peat-stained waters of the Nkazana Stream entered South Lake. *Planiliza alata* has a recorded salinity range of 1-35 (Whitfield 1996a).

The diet of newly recruited *P. alata* in estuaries consists mainly of vertically migrating zooplankton (e.g. copepods) and meiobenthos, with the switch to microphytobenthos occurring at approximately 20 mm SL (Blaber & Whitfield

1977a). Larger juveniles and adults feed mainly on filamentous algae, terrestrial plant debris, small gastropods, pennate diatoms and particulate organic matter (Blaber 1976, 1977). Relatively large sand particles with mean diameters 0.3-0.7 mm are also ingested.

As global warming develops along the south-east African coastline, this species is likely to extend its distribution southwards (James et al. 2016). *Planiliza alata* would be a very successful coloniser of southern Cape estuaries since many of these systems possess the humate-stained waters favoured by this species.

Family: MUGILIDAE

Species: *Planiliza macrolepis* (Smith 1846)

Common name: Largescale mullet

Illustrated specimen length: 24 cm SL

#### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 16

Lateral scales: 33-35

Maximum recorded length in southern

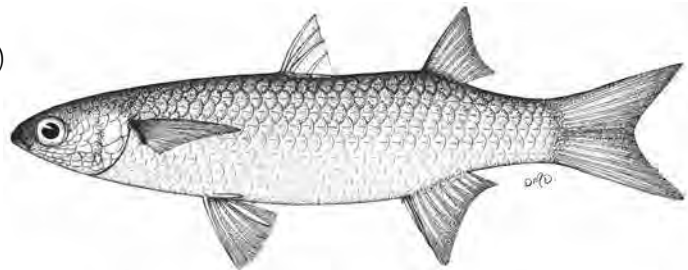
African waters:  $\pm 29$  cm SL

#### Distribution

The largescale mullet is an Indo-West Pacific species (Smith & Smith 1986b) with stragglers extending as far as the Knysna Estuary in the Western Cape Province. Juveniles are usually abundant in KwaZulu-Natal estuaries, with the adults occurring in both the estuarine and marine environment. The relative abundance of this species in subtropical estuaries increases from south to north (Blaber 1977) with few individuals entering the warm-temperate estuaries of the Eastern Cape. However, increasing numbers of this species are likely to move southwards as global warming continues (James et al. 2016).

#### Biology and ecology

Spawning by largescale mullet greater than 23 cm SL appears to take place in the vicinity of estuaries, with the gonads of some specimens in a ripe-running condition recorded within estuary mouths (Wallace 1975b). Garratt (1993) found large quantities of *P. macrolepis* eggs leaving the Kosi



Estuary on the ebb tide, i.e. spawning had taken place in the lower reaches of this system. Breeding occurs mainly during winter and spring, i.e. between May and November (Wallace 1975b, Garratt 1993). In KwaZulu-Natal estuaries, ripe and spent fish constitute the bulk of the adult population, with ripe specimens outnumbering post-spawners in Lake St Lucia (Wallace 1975b).

According to Wallace & van der Elst (1975) postlarvae 10-20 mm TL first start entering KwaZulu-Natal estuaries in winter and continue to do so until spring. Larger 0+ juveniles (20-40 mm TL) are abundant in subtropical estuaries from September to December and may represent older recruits. Overall, the most intense recruitment period for this species is between July and December.

Recruitment by *P. macrolepis* was recently recorded in the East Kleinemonde Estuary (James et al. 2008c).

*Planiliza macrolepis* occurs in salinities ranging from less than 1 to 75 (Whitfield 1996a, Blaber 1987) and is also associated with a wide range of water turbidities. Cyrus & Blaber (1987c) found that 49% of individuals were captured in less than 10 NTU and 28% in 10-50 NTU. Data from Cyrus & Blaber (1987a, 1987b) shows that this fish can be regarded as a clear to partially-turbid water species.

The diet of postlarvae less than 20 mm SL consists mainly of copepods, cladocerans, insect

larvae, fish eggs and diatoms (Whitfield 1985), with a switch to a typical juvenile diet occurring at a length greater than 25 mm SL (Blaber & Whitfield 1977a).

Juveniles and adults consume mainly particulate organic matter, diatoms, flagellates, filamentous algae, macrophytic plant debris, foraminiferans and small gastropods. Large amounts of sand with mean particle diameters ranging from 0.1-0.3 mm are ingested together with the food items and aid in the digestive process (Blaber 1977, Whitfield 1980b). Feeding periodicity studies indicate that *P. macrolepis* forages during the day and ceases feeding at night (Blaber 1976).

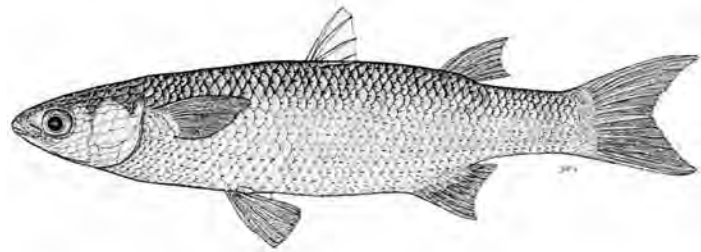
Family: MUGILIDAE

Species: *Pseudomyxus capensis*

(Valenciennes 1836)

Common name: Freshwater mullet

Illustrated specimen length: 23 cm SL



#### Selected anatomical features

Fin elements: Dorsal IV+I, 8;

Anal III, 9; Pectoral 17

Lateral scales: 43-45

Maximum recorded length:  $\pm 37$  cm SL

#### Distribution

The freshwater mullet is an endemic species which ranges from subtropical estuarine systems in the north (Blaber 1978) to cool-temperate estuaries in the southwest (Bennett 1989). Juveniles and adults frequently occur both in estuaries and rivers, particularly in the Eastern Cape where specimens are often captured more than 10 km from the head of an estuary and sometimes as far inland as 135 km from the mouth (Bok 1979). This species is usually most abundant in the estuarine reaches and not the river catchment of most systems.

#### Biology and ecology

The breeding season of the freshwater mullet extends from March to November, and Bok (1979) recorded ripe-running *P. capensis* in the sea adjacent to the Great Fish Estuary in April. The main recruitment period of juveniles (<20 mm SL) occurs in the late winter and early summer

months in the Kowie Estuary (Bok 1979). Data from the heads of other Eastern Cape Province estuaries indicate a September-November peak in recruitment although *P. capensis* fry less than 30 mm FL were present in the upper reaches of these systems during most months (Bok 1984).

In KwaZulu-Natal estuaries, immigration of 20-50 mm TL juveniles occurs from August to December (Wallace & van der Elst 1975), whereas recruitment of *P. capensis* <30 mm TL into Western Cape estuaries was recorded throughout the year. The main immigration period extends from July to November, with a spring peak (October/November) for the above size classes (Whitfield & Kok 1992).





Cohort analysis in the Knysna Estuary between November and January indicates an early juvenile growth rate of approximately 10 mm per month (Whitfield & Kok 1992). *Pseudomyxus capensis* attain 10 cm SL by the end of year one and 19 cm SL after year two (Bok 1984). Male fish mature at approximately 19 cm SL and females at 23 cm SL (Bok 1983).

The salinity range of freshwater mullet is 0-49 and it frequents both turbid (>100 NTU) and clear estuaries (<10 NTU) on the Eastern Cape coast. *P. capensis* is a facultative catadromous species in the Eastern Cape and survived prolonged low salinities and low temperatures in the temporarily closed Bot Estuary when other marine fish taxa were dying (Bennett 1985). The reason for the attractiveness of rivers to freshwater mullet could be the opportunity for reduced

competition with the other mugilid species in estuaries, as well as the abundance of infalling insect prey from the adjacent riparian vegetation (Carassou et al. 2017).

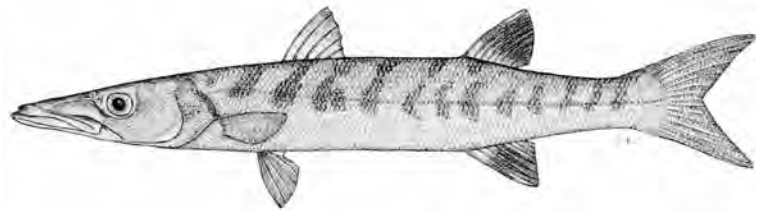
The diet of postlarval *P. capensis* <30 mm SL consists mainly of copepods, crustacean larvae and cumaceans, with a switch to a typical juvenile diet occurring at a length >30 mm SL (Blaber & Whitfield 1977a). Juveniles and adults consume mainly particulate organic matter, pennate diatoms, terrestrial plant debris and filamentous algae in estuaries (Blaber 1976, 1977). The diet in river catchments is different and insects, both aerial and semi-aquatic, are often a major dietary component in these areas (Carassou et al. 2017). Sand particles with a mean diameter of 0.2-0.3 mm are also ingested (Blaber 1977, Whitfield 1980b).

Family: SPHYRAENIDAE

Species: *Sphyraena barracuda*  
(Walbaum 1792)

Common name: Great barracuda

Illustrated specimen length: 22 cm SL



### Selected anatomical features

Fin elements: Dorsal V+I, 9; Anal I, 10

Lateral scales: 77-85

Maximum recorded length in southern African waters:  $\pm 140$  cm SL

### Distribution

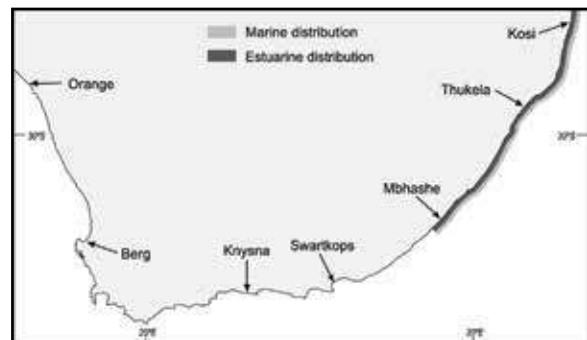
The great barracuda is a widespread species, known from KwaZulu-Natal and all tropical seas except the eastern Pacific (de Sylva & Williams 1986). Although adults usually show a preference for reef environments, the choice of habitat is also linked to age and size, with juveniles being more common in tropical mangrove areas and estuaries (van der Elst 1988).

### Biology and ecology

*Sphyraena barracuda* reaches a length of almost 50 cm SL after only 2 years, and sexual maturity is attained between 54 cm and 67 cm SL (Blaber 1982a). According to Kadison et al. (2010) males mature between 1 and 2 years of age and females

between 2 and 4 years of age. Spawning occurs during summer in the tropical waters of East Africa and the Seychelles. The larvae and postlarvae are pelagic and particularly sensitive to sudden changes in water temperature (van der Elst 1988).

Immigration of postlarvae 20 mm SL was recorded in the Kosi estuarine system between October and April. Juveniles 20-79 mm SL frequented shallow (<0.5 m deep) submerged plant beds within 3 m of the shore, specimens 8-30 cm SL were found among mangrove root systems <2 m deep, while fish of 30-50 cm SL occurred in open-water areas (Blaber 1982a).



*Sphyraena barracuda* in Florida are seldom recorded in salinities less than 24 (de Sylva 1963) but within southern Africa it has been found in low salinity systems such as Lake Nhlangwe (Blaber 1982a). The great barracuda has also been recorded in Lake St Lucia under mesohaline conditions. This species is generally associated with clear waters (<3 NTU), the early juveniles occurring in water temperatures ranging from 20-37°C during summer, with larger fish being found in temperatures from 14-28°C (Blaber 1982a).

The diets of all three size groups found in the Kosi Estuary consisted almost entirely of fish. The first group (20-79 mm SL) consumed mainly post-larval mugilids and cichlids which are abundant in and adjacent to littoral *Stuckenia pectinata* beds. *Sphyraena barracuda* 8-30 cm SL preyed on a wide variety of fish taxa which occur in *Phragmites* and mangrove areas. The diet of fish larger than 30 cm SL was dominated by *Gerres* and *Rhabdosargus*

species that were captured on the shallow sandy shelf areas. Foraging occurred mainly during the day, especially during dawn and dusk (Blaber 1982a).

In the marine environment the juveniles feed on anchovies and other small shoaling teleosts, whereas the adults consume either sluggish reef fish, or faster swimming surface species such as mullet and needlefish (van der Elst 1988).

A detailed study of the diet of *S. barracuda* in the tropical western Atlantic by de Sylva (1963) showed that Atherinidae, Clupeidae and Gobidae were important prey fish groups for great barracuda <400 mm FL, and that Tetraodontidae, Carangidae, Scombridae, Belonidae and Mugilidae were major prey for specimens >400 mm FL. *Sphyraena barracuda* has also been recorded attacking humans at various tropical coastal localities around the world although the reasons for such attacks have not been determined.

Family: BOTHIDAE

Species: *Pseudorhombus arsius*  
(Hamilton 1822)

Common name: Largetooth flounder

Illustrated specimen length: 11 cm SL

#### Selected anatomical features

Fin elements: Dorsal 72-78;

Anal 54-60; Pectoral 11-13

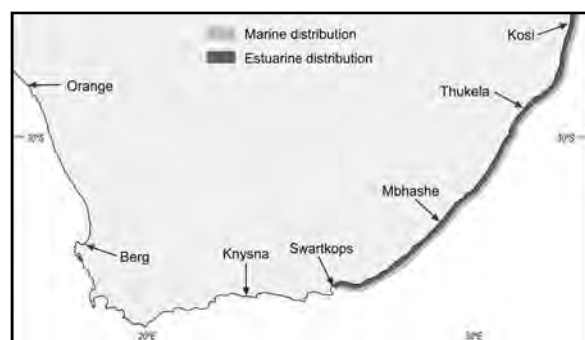
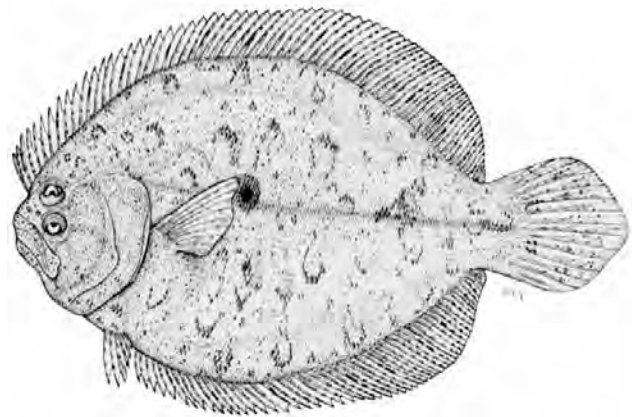
Body depth 1.7-2.0 in SL

Maximum recorded length in southern

African waters:  $\pm$  38 cm SL

#### Distribution

The largetooth flounder is an Indo-West Pacific species ranging south to Algoa Bay (Hensley 1986). This species frequents sandy, muddy or gravel bottoms and has a depth distribution ranging from shallow estuaries to 100 m in the marine environment. The closely related leopard flounder *Bothus pantherinus* also occurs in South African estuaries, from the Bushmans in the south to the Kosi system in the north (Cyrus & Martin 1991).



#### Biology and ecology

Reproductive maturity is attained at about 20 cm SL (Cyrus & Martin 1991). Records from the northern Indian Ocean show that this species spawns at sea during late spring (Bawazeer 1987).

The larvae look very similar to other teleost larvae after hatching but with the onset of the juvenile phase they swim with the left side facing upwards and the right eye begins to migrate towards the left side of the head (van der Elst 1988).

Recruitment into southern African estuaries occurs at a standard length > 50 mm. Indications are that *P. arsius* is not dependent on estuaries as nursery areas but is present in the lower parts of some of the larger KwaZulu-Natal systems in low numbers throughout the year. Juveniles

attain between 8 cm and 16 cm in their first year of growth (Bawazeer 1987).

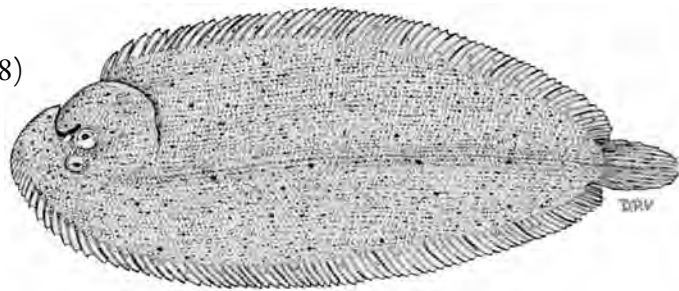
Juveniles in KwaZulu-Natal estuaries feed mainly on benthic crustaceans whereas adults in the sea prey mainly on fish, prawns, crabs and polychaetes (Cyrus & Martin 1991). According to van der Elst (1988) this species uses its excellent camouflage when lying on the seabed and then pounces on unsuspecting prey. It can also move surprisingly quickly by undulating the dorsal and anal fins, while using the pectorals for steering.

Family: SOLEIDAE

Species: *Heteromycteris capensis* (Kaup 1858)

Common name: Cape sole

Illustrated specimen length: 80 mm SL



#### Selected anatomical features

Fin elements: Dorsal 95-102;

Anal 64-75

Body depth 2.5-2.8 in SL

Maximum recorded length:  $\pm 17$  cm SL

#### Distribution

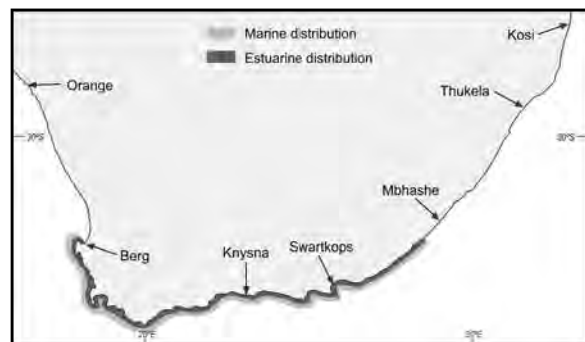
The Cape sole is a southern African endemic species, confined to shallow, sandy habitats between Walvis Bay in the west and the Kei Estuary in the east. This sole frequents water between 1 m and 25 m in depth (Heemstra & Gon 1986) and is most common in the lower reaches of permanently open estuaries (Richardson et al. 2006).

#### Biology and ecology

*Heteromycteris capensis* attains sexual maturity at approximately 80 mm SL (Cyrus & Martin 1991). Spawning occurs in the nearshore marine environment throughout the year, with a peak between October and February (Brownell 1979).

Larvae have been recorded in False Bay and Algoa Bay throughout the year (Beckley 1986), with post-flexion larvae present in the Swartvlei Bay surf zone from September to March (Whitfield 1989c). Recruitment of larvae and postlarvae into warm-temperate estuaries occurs mainly between October and March at a length of 5-15 mm BL (Whitfield & Kok 1992).

This species has a recorded salinity range



of 5-35 (Whitfield 1996a) but is usually confined to the lower reaches of permanently open estuaries where salinities seldom decline below 30. However, sediment characteristics and not salinity appear to be the main factor influencing longitudinal distribution within an estuary. In the Kariega system *H. capensis* was common in the sandy lower reaches but did not extend its distribution into the muddy reaches, despite the absence of a salinity gradient within this estuary at the time of sampling (Richardson et al. 2006).

The diet of Cape sole in estuaries consists mainly of small benthic invertebrates. The habits and cryptic colouration of both juveniles and adults on a sandy background provide excellent protection from pelagic predatory fishes and wading piscivorous birds.

Family: SOLEIDAE

Species: *Solea turbynei* (Gilchrist 1904)

Common name: Blackhand sole

Illustrated specimen length: 77 mm SL

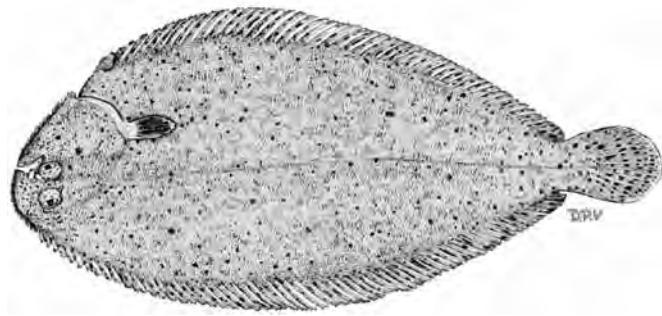
### Selected anatomical features

Fin elements: Dorsal 61-74;

Anal 46-59; Pectoral 7-8

Body depth 1.9-2.7 in SL

Maximum recorded length:  $\pm 13$  cm SL



### Distribution

The blackhand sole is a southern African endemic species, ranging from the Olifants Estuary on the South African west coast to Tanzania on the African east coast. The localised distribution of *S. turbynei* in estuaries is governed primarily by a preference for muddy rather than sandy substrata and it is therefore more abundant in the middle and upper reaches of most permanently open estuaries in this region (Richardson et al. 2006).

### Biology and ecology

*Solea turbynei* attains sexual maturity at about 60 mm SL (Cyrus 1991a). Breeding takes place both in the sea and in certain large estuarine systems when conditions are suitable (Cyrus 1991b). Spawning occurs between June and December in KwaZulu-Natal waters, with a peak in reproductive activity during early summer (Cyrus 1991a).

The abundance of larvae (<5 mm BL) in near-shore marine waters between November and March (Beckley 1986, Whitfield 1989b) suggests that spawning in the warm-temperate region is also a mainly summer phenomenon. Flexion occurs early (3-4 mm BL) at which stage the post-flexion larvae utilize the surf zone to settle and undergo metamorphosis into juveniles (Strydom et al. 2015). Migration of juveniles into Eastern Cape estuaries occurs between November and March (Melville-Smith & Baird 1980) and sexual maturity is attained within the estuarine environment.

*Solea turbynei* has a recorded salinity range of 1-42 (Whitfield 1996a) and this species occurs mainly in the middle and upper reaches of permanently open estuaries as adults (Richardson et al. 2006). Larval growth and survival has been closely linked to warm water and Strydom et al. (2015)



have also shown a positive relationship with turbidity in terms of recruitment into estuaries. This view is supported by Cyrus & Blaber (1987c) who categorized *S. turbynei* as a turbid water species because it occurred in greatest numbers in areas where turbidities exceeded 80 NTU. The absence of this species from the clear Kosi Estuary (Blaber & Cyrus 1981) supports the view that this sole prefers systems that provide turbid water habitats.

Where both *S. turbynei* and *Heteromyceteris capensis* occur together in the same estuary, the former occupies the muddier sediments of the middle reaches whereas the latter is usually most abundant in the sandier lower reaches (Richardson et al. 2006).

The diet of both juvenile and adult *S. turbynei* in estuaries consists mainly of benthic crustaceans (Cyrus & Martin 1991), with bivalve siphons being consumed in large quantities by adult fish (Cyrus 1988b).

According to van der Elst (1988) this is a sluggish species which only moves from its position if disturbed or to snatch prey. Despite its cryptic colouration and occupation of turbid water areas, the blackhand sole is preyed upon by the reed cormorant *Phalacrocorax africanus* in Lake St Lucia (Whitfield & Blaber 1979b).

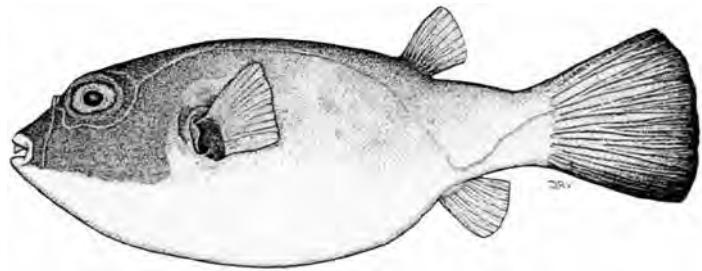
Family: TETRAODONTIDAE

Species: *Arothron immaculatus*

(Bloch & Schneider 1801)

Common name: Blackedged pufferfish

Illustrated specimen length: 10 cm SL



### Selected anatomical features

Fin elements: Dorsal 9-10;

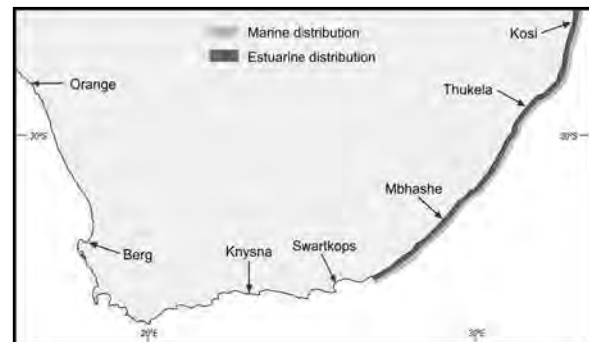
Anal 9-10; Pectoral 16-17

Maximum recorded length in southern

African waters:  $\pm 25$  cm SL

### Distribution

The blackedged pufferfish is a tropical Indo-West Pacific pufferfish, ranging as far south as the Bushmans Estuary in southern African waters (Smith & Heemstra 1986b). This pufferfish is sometimes common in submerged plant beds of subtropical estuaries in KwaZulu-Natal and the Eastern Cape. The related whitespotted pufferfish *Arothron hispidus*, a species that also enters estuaries, has a distribution which overlaps with that of *A. immaculatus* in the subtropical region.



### Biology and ecology

*Arothron immaculatus* attains sexual maturity at approximately 12 cm TL and females with ripening ovaries have been found in estuaries during spring (Day et al. 1981). Breeding probably takes place in the sea during early summer, with the larvae utilizing the marine environment for the early developmental stages. Juveniles first enter estuaries at a length of approximately 20 mm TL and individuals up to 16 cm TL are often associated with aquatic plant beds in these systems.

This euryhaline pufferfish has been recorded in estuaries where salinities have ranged between 8 and 38. *Arothron immaculatus* is usually found in the lower reaches of permanently open estuaries where salinities are usually euhaline.

Newly recruited blackedged pufferfish feed mainly on copepods when first entering an estuary, but larger juveniles and adults prey on bivalves, gastropods and crabs (Day et al. 1981). *Zostera*

*capensis* is also incidentally consumed when foraging in eelgrass beds.

The liver, gonads and even skin of *A. immaculatus*, like that of many other pufferfishes, contains tetrodotoxin that is a sodium channel blocking compound and can cause respiratory paralysis if consumed by humans. The tetrodotoxin is bioaccumulated by pufferfish via the marine food chain and has antimicrobial but not antifungal properties (Kumaravel et al. 2011). Although protection against predation and consumption by mammals appears to have some validity, consumption of tetrodotoxin by other teleosts does not appear to induce the same adverse effects (Saha et al. 2015). It is therefore uncertain whether the possession of tetrodotoxin does confer some sort of protection for pufferfish from their natural predators but perhaps the antimicrobial properties in the gonads are of value to the fertilised eggs of *A. immaculatus* in the aquatic environment.

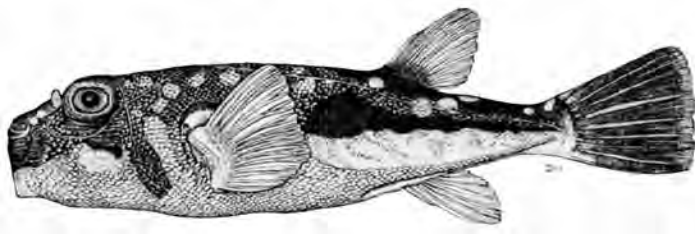


Family: TETRAODONTIDAE

Species: *Geneion honckenii* (Bloch 1785)

Common name: Evileye pufferfish

Illustrated specimen length: 78 mm SL



### Selected anatomical features

Fin elements: Dorsal 9-10;

Anal 8; Pectoral 14-16

About 42 spinules across belly between pectoral bases

Maximum recorded length:  $\pm 25$  cm SL

### Distribution

The evileye pufferfish has a wide distribution, ranging from South Africa to China. This mainly tropical Indo-West Pacific species is found in tide pools, estuaries and in the sea down to depths of 400 m (Smith & Heemstra 1986b). Within southern African subtropical, warm-temperate and cool-temperate estuaries it is frequently associated with eelgrass beds in the lower reaches of some of the larger systems.



### Biology and ecology

*Geneion honckenii* attains sexual maturity at approximately 80 mm SL and is ready to spawn towards the end of winter (Day et al. 1981). Details of the early life-history are unknown, but van der Elst (1988) has suggested that the juveniles are dispersed by sheltering beneath floating objects borne along by ocean currents. Although the juveniles do not appear to be closely associated with estuaries, adults are sometimes common in the lower reaches of permanently open systems.

This species, which has an extremely wide temperature tolerance range, is usually recorded in euhaline waters but has also been found at a salinity of 14.

The evileye pufferfish is both a scavenger and a predator, feeding on small crustacea (mainly isopods) and bivalves, with eelgrass also being incidentally consumed (Day et al. 1981).

According to van der Elst (1988) *G. honckenii* is a predominantly demersal species and often buries itself beneath the sand with only its eyes protruding. From such a position it may dart out to snatch unsuspecting prey, including small crabs, slow-swimming fishes and various benthic invertebrates.

*Geneion honckenii* is poisonous to mammals and, if threatened, can inflate its body to act as a further deterrent to predators.

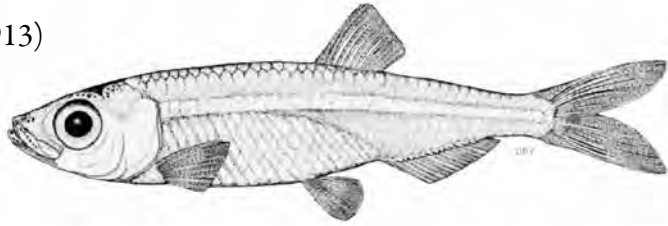
### 3.3 ESTUARINE GUILD

Family: CLUPEIDAE

Species: *Gilchristella aestuaria* (Gilchrist 1913)

Common name: Estuarine roundherring

Illustrated specimen length: 59 mm SL



#### Selected anatomical features

Fin elements: Dorsal 14-15;

Anal 20; Pectoral 11-12

Lateral scales: 39-42

Maximum recorded length:  $\pm 90$  mm SL

#### Distribution

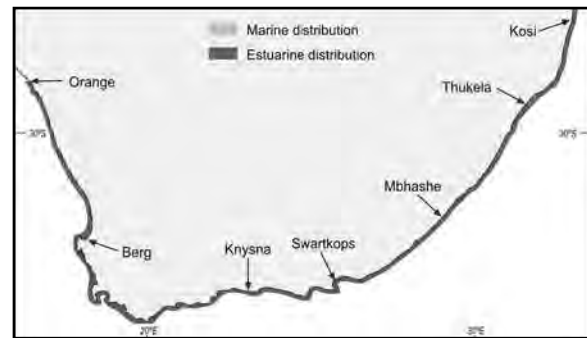
*Gilchristella aestuaria* is a southern African endemic species, ranging from Lagoa Piti (Mozambique) in the northeast to the Orange Estuary in the southwest. This shoaling fish is usually abundant in all types of estuaries and is also common in certain freshwater coastal lakes and lagoons.

#### Biology and ecology

The estuarine roundherring matures within 7 months at approximately 28 mm SL (Talbot 1982). Although this species has been reported breeding throughout the year, spawning peaks usually occur during spring and summer, with very little activity during winter (Blaber 1979, Cyrus et al. 1993). The eggs are approximately 1 mm in diameter (Connell 1996) and are usually found within the water column of the upper and middle reaches of permanently open estuaries (Wooldridge & Bailey 1982).

*Gilchristella aestuaria* larvae are most abundant between September and April (Whitfield 1989a), sometimes reaching densities in excess of 800 fish per 10 m<sup>3</sup> (Harrison & Whitfield 1990). In the Sundays Estuary, the larvae avoid ebb-tide surface currents in order to maintain their position in the middle and upper reaches (Melville-Smith et al. 1981). A similar horizontal larval distribution pattern was recorded in the Swartkops Estuary (Melville-Smith & Baird 1980).

The estuarine roundherring has been recorded in coastal water bodies where salinities range from zero to 53. This species was recorded dying in the hypersaline Seekoei Estuary at concentrations above 90 (Whitfield 1998). The salinity tolerance



of the egg and larval stages ranges from 0-48 (Day et al. 1981). This fish species is common in both clear and turbid water systems.

The diet of *G. aestuaria* has been studied in a variety of estuarine and freshwater systems, with copepods, ostracods, mysids, macruran larvae, amphipods, chironomid larvae and diatoms all recorded as important food items (Coetzee 1982a, Talbot & Baird 1985a, Whitfield 1988a, Cyrus et al. 1993). Mucus-secreting cells within the epithelial layer of the hyoid arch, branchial arches and gill rakers trap the plankton which accumulates in boluses that are then swallowed (White & Bruton 1983).

In turbid Lake St Lucia this species was a non-selective zooplankton filter feeder (Blaber 1979), whereas a predominantly visual mode of foraging is used in clear estuarine systems with poor zooplankton food resources (Blaber et al. 1981). *Gilchristella aestuaria* forages mainly during daylight hours (Blaber 1979, Bennett & Branch 1990), with approximately 37 kg dry mass of food per day being consumed in the Sundays Estuary during summer and only 1 kg per day during winter (Whitfield & Harrison 1996).

This small clupeid is preyed upon by a wide range of piscivorous birds (Whitfield 1986b) and fishes (Marais 1984), especially *Elops machnata*, *Argyrosomus japonicus* and *Lichia amia*.

The numbers of *E. machnata* captured in different parts of Lake St Lucia were closely related to the abundance of *G. aestuaria* in these areas (Whitfield & Blaber 1978a). In the Swartkops Estuary 99%

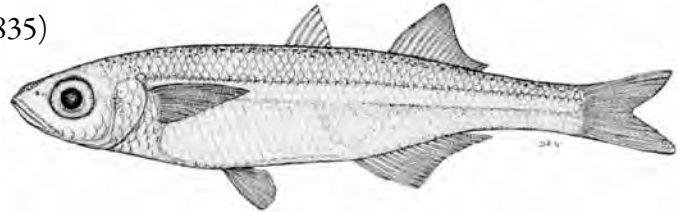
of the estuarine roundherring population were less than 2 years old (Talbot 1982), thus indicating that less than 1% of the population attains 3 years of age, probably due to high mortality rates.

Family: ATHERINIDAE

Species: *Atherina breviceps* (Valenciennes 1835)

Common name: Cape silverside

Illustrated specimen length: 64 mm SL



### Selected anatomical features

Fin elements: Dorsal V-VIII+I, 11-15;

Anal I, 15-18; Pectoral 13-16

Lateral scales: 44-50

Maximum recorded length:  $\pm 11$  cm SL

### Distribution

The Cape silverside is a southern African endemic species from northern KwaZulu-Natal to southern Namibia (Ivantsoff 1986). This shoaling fish is often associated with submerged aquatic macrophytes in estuaries. It is also common in certain freshwater and brackish coastal lakes that are isolated from the sea. Large populations occur in the nearshore marine environment, particularly the relatively sheltered bays of the Eastern and Western Cape Province (Lasiak 1984b, Clark 1997).



### Biology and ecology

This species reaches sexual maturity within eight months, at a standard length of 40 mm SL (Ratte 1989). It breeds mainly during spring and summer, with a September-January peak. The eggs are approximately 1.5 mm in diameter, and are usually attached to submerged plants and other objects by 6-12 chorionic filaments (Neira et al. 1988). *Atherina breviceps* larvae (5-8 mm BL) are most abundant in surface waters between September and March (Melville-Smith & Baird 1980, Whitfield 1989c).

The Cape silverside has been recorded in coastal water bodies where salinities range from 0-42 (Whitfield 1996a) but is replaced from the Kosi system northwards by the more tropical hardyhead silverside *Atherinomorus lacunosus* (Harman et al. 1982). Although *A. breviceps* species is found in both clear and turbid estuaries, it is more abundant in the former type of system, possibly due

to increased feeding efficiency associated with clearer waters. According to Hecht & van der Lingen (1992) the reactive distance of foraging *A. breviceps* is substantially reduced by increased turbidity levels.

The diet has been studied in a wide variety of estuarine systems (e.g. Blaber 1979, Coetzee 1982a, Bennett & Branch 1990, Hecht & van der Lingen 1992) and includes copepods, amphipods, isopods, gastropods, ostracods, decapods and insect larvae. Juveniles in the Swartvlei and Groenvlei systems feed mainly on small organisms such as rotifers, copepod nauplii, molluscan veligers and phytoplankton, whereas adults prey on larger ostracods, copepods, isopods, amphipods, insects and molluscs (Coetzee 1982a, Whitfield 1988a). Most feeding takes place during twilight and nocturnal hours (Bennett & Branch 1990).

A detailed study of the potential competition for zooplankton food resources in the Kariega Estuary (Mbandzi et al. 2018) indicated that both *A. breviceps* and *Gilchristella aestuaria* were abundant and preyed mainly on the calanoid copepod *Pseudodiaptomus hessei*. Densities of this copepod were highest in the middle reaches of

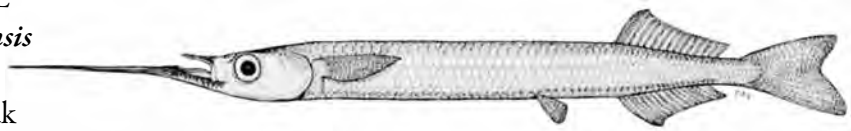
the estuary which was also the region where both zooplanktivorous fish species overlapped and were most abundant. A collapse of the zooplankton community following river flooding resulted in a collapse in the stocks of both *A. breviceps* and *G. aestuaria* within this estuary (Mbandzi et al. 2018).

Family: HEMIRAMPHIDAE

Species: *Hyporhamphus capensis*  
(Thomiot 1886)

Common name: Cape halfbeak

Illustrated specimen length: 11 cm SL



### Selected anatomical features

Fin elements: Dorsal 14-17;

Anal 15-16; Pectoral 10-12

Predorsal scales: 31-38

Maximum recorded length:  $\pm 16$  cm SL

### Distribution

The Cape halfbeak is a southern African endemic confined to estuarine and coastal waters from False Bay to Lake Piti in southern Mozambique (Collette 1986b). Although this littoral species is often abundant in estuarine lakes, some of which have tenuous links to the sea, it is absent from coastal lakes that have been isolated from the marine environment (Bruton & Kok 1980). This fish is usually found just below the water surface, especially at night.

### Biology and ecology

*Hyporhamphus capensis* mature between 80 mm and 100 mm TL. The breeding season covers the period October to March, with ripe-running and partially spawned specimens recorded in KwaZulu-Natal estuaries during October, December and March (Wallace 1975b).

The eggs of this species are 1.6 mm in diameter and densely covered with glutinous hair-like filaments which are considerably longer than the diameter of the egg (Smith 1933). *Hyporhamphus capensis* larvae less than 10 mm BL have been recorded in Swartvlei during summer (Whitfield 1989c) and are most abundant in other Western Cape estuaries during November and December.

The Cape halfbeak occupies those estuaries,

*Atherina breviceps* represents an important link in the food web, as it is extensively preyed upon by a wide variety of gamefish and piscivorous birds (van der Elst 1988). In the Swartvlei estuarine system, <1% of the Cape silversides reach 2+ years of age (Ratte 1989), probably due to high predation rates (Whitfield 1986b).



or parts of systems, where salinities range from 1-42 (Whitfield 1996a), especially in the vicinity of submerged aquatic macrophytes. According to Smith (1933), this species is present in tidal estuaries throughout the year, occasionally extending into fresh water. The absence of *H. capensis* from isolated freshwater coastal lakes may be linked to long-term salinity requirements of adult fish, or freshwater tolerance limitations of egg and larval stages.

The diet of *H. capensis* in Rondevlei has been studied by Coetzee (1981a), who found that the gut contents of juveniles 50-90 mm TL were dominated by amphipods, isopods, ostracods and insects. Between 90 mm and 190 mm TL they consumed submerged aquatic macrophytes and small bivalves which were attached to the plants.

Coetzee (1981a) determined that the annual cycle in the occurrence of *Ruppia cirrhosa* and *Stuckenia pectinata* directly influenced the feeding of the Cape halfbeak, with considerably more plant material being consumed in summer than in winter. The diet of this species and dorsal position of the mouth suggests that it feeds mainly amongst submerged plant canopies. The role of

the extended lower jaw (beak) in foraging is unknown but may be related to invertebrate prey detection in surface waters (Smith 1933).

*Hyporhamphus capensis* are preyed upon by a wide range of piscivorous fishes, especially the near surface swimming needlefish *Strongylura leiura* in Lake St Lucia (Whitfield & Blaber 1978a). This

Family: SYNGNATHIDAE

Species: *Hippichthys heptagonus* (Bleeker 1849)

Common name: Belly pipefish

Illustrated specimen length: 12 cm SL

#### Selected anatomical features

Fin elements: Dorsal 23-30; Pectoral 13-16.

Ring count: Trunk 14-15; Tail 36-42

Maximum recorded length in southern

African waters:  $\pm 15$  cm SL

#### Distribution

The belly pipefish is a tropical species ranging from the Solomon Islands in the western Pacific to KwaZulu-Natal (Dawson 1986).

#### Biology and ecology

*Hippichthys heptagonus* is the most common pipefish in subtropical southern African estuaries. This species usually shelters in *Zostera capensis* and *Halodule uninervis* beds (Day et al. 1981) but the mainly brownish colouration and general lack of distinctive markings also provides excellent camouflage in the turbid waters of KwaZulu-Natal estuaries. It usually occurs in the larger rather than smaller estuaries in the subtropics and has a recorded salinity range of 1-38.

Family: SYNGNATHIDAE

Species: *Hippocampus capensis*  
(Boulenger 1900)

Common name: Knysna seahorse

Illustrated specimen length: 70 mm TL

#### Selected anatomical features

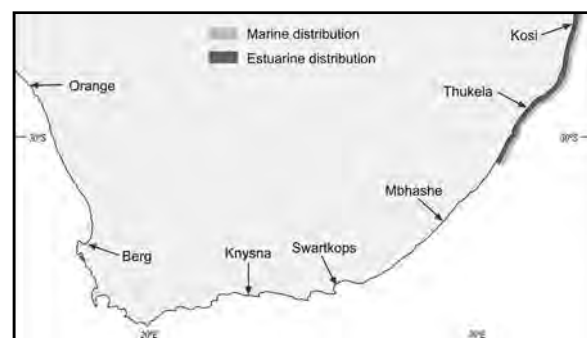
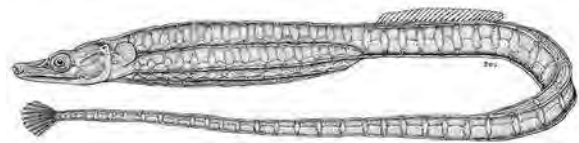
Fin elements: Dorsal 16-18;

Anal 3; Pectoral 15-17

Ring count: Trunk 10-11; Tail 32-34

Maximum recorded length:  $\pm 12$  cm SL

halfbeak is also the probable intermediate host of the cestode *Ptychobothrium belones*, which has *S. leiura* as the apparent final host (Whitfield & Heeg 1977). One of the methods of escape by *H. capensis* when being pursued by large piscivorous fish is to leap or skip along the water surface (Day et al. 1981).



The length at sexual maturity for males is 75-80 mm SL (Dawson 1985). Breeding occurs in estuaries, with the male retaining the developing embryos in a brood pouch. Relatively high densities of juveniles, with a mean length of 23 mm SL, were recorded in the St Lucia Estuary plankton by Harris & Cyrus (1995).

As is the case with most pipefishes, the diet of *H. heptagonus* is dominated by zooplankton, particularly copepods and amphipods (Day et al. 1981).





## Distribution

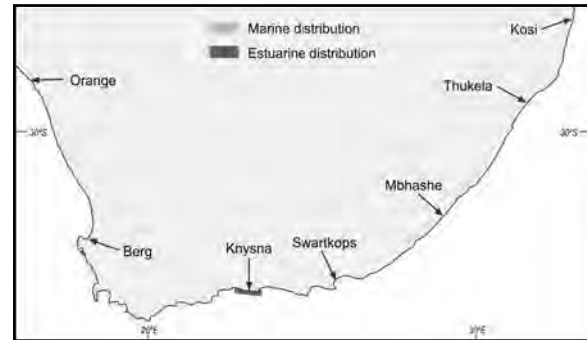
The Knysna seahorse has only been recorded from estuaries along the eastern portion of the Western Cape coast between the Klein Brak and Keurbooms systems. The centre of distribution comprises the Knysna Estuary and, to a lesser extent, the adjacent Swartvlei Estuary in the west and Keurbooms in the east (Bell et al. 2003).

## Biology and ecology

The Knysna seahorse is the most endangered seahorse in the world due to its very limited distribution and small population size (Lockyear et al. 2006). This species is usually associated with submerged eelgrass beds or macro-algae in the Knysna, Swartvlei and Keurbooms estuarine systems (Whitfield 1995b). The sometimes slightly mottled greenish or brownish colouration of *Hippocampus capensis* provides excellent camouflage in submerged plant beds and it has the ability to coil its tail around submerged objects to prevent it from being washed away by tidal currents (Teske et al. 2007). Although not a strong swimmer, this species can move in a vertical or slightly angled position, using both the dorsal and pectoral fins for propulsion. The eyes can move independently of one another (Smith 1981).

Sexual maturity is attained within one year at a length of approximately 65 mm TL. Breeding occurs in summer when water temperatures reach about 20°C. The lower abdomen of the male becomes silvery and an orange fringe develops along the dorsal fin (Grange & Cretchley 1995). The male indicates his intention to mate by grasping the female with his prehensile tail and attempting to move into the 'face to face' position. The female is courted until she is ready to deposit her eggs into his inflated brood pouch, a process that sometimes lasts several hours (Grange & Cretchley 1995). Fertilisation occurs within the pouch which swells as the embryos develop. After an approximately 2-4 week development period (depending upon water temperature) the juveniles (9-10 mm TL), which may number between 30 and 120, emerge singly from the pouch while the male experiences contractions to help expel them (Grange & Cretchley 1995).

The newly released young tend to swim in the



horizontal position and some are carried by ebb tidal currents into the sea where their chances of survival are unknown. Up until a length of 20 mm is attained, juveniles have an almost uniform black colouration. Thereafter the colour of individuals can change according to the immediate environment, from greyish white to green, brown, black or speckled (Smith 1981, Genade & Hirst 1986).

Evidence suggests that this species has the ability to survive salinities ranging from 1-59, including direct transfer from 32 to 1 and 32 to 59. The Knysna seahorse cannot survive in fresh water or at salinities greater than 59 (Riley 1986) but hypersaline conditions are unlikely to occur in the natural environment. A mass mortality of this species was recorded in the Swartvlei Estuary when water temperatures approached 32°C (Russell 1994).

The diet of juvenile *H. capensis* consists exclusively of zooplanktonic organisms up to 0.75 mm in size whereas adults feed predominantly on small crustaceans and fish larvae that are sucked from submerged leaf surfaces or from the water column. Adults can swallow individual prey items up to 12 mm in length, provided the width is not greater than 2 mm (Genade & Hirst 1986).

The Knysna seahorse is preyed upon by egrets and herons (Smith 1981). Development around the few estuaries where this species does occur poses a threat to its continued existence (Bell et al. 2003) but recent research shows that this fish has successfully colonised the Thesen Island Marina canals (Claassens 2016). In particular, *H. capensis* adults show a preference for submerged Reno mattress structures (horizontal wire cages filled with rocks), which provide ideal holdfasts for the seahorses when compared to their natural eelgrass habitat (Claassens et al. 2018).

Family: SYNGNATHIDAE

Species: *Syngnathus temminckii*

(Kaup 1856)

Common name: Longsnout pipefish

Illustrated specimen length: 19 cm SL



### Selected anatomical features

Fin elements: Dorsal 33-42;

Anal 3; Pectoral 10-14

Ring count: Trunk 18-21; Tail 36-43

Maximum recorded length in southern

African waters:  $\pm 30$  cm SL

### Distribution

*Syngnathus temminckii* occurs in both the Mediterranean and eastern Atlantic regions. Locally it is most abundant in the warm-temperate estuaries of southern Africa but extends into both the subtropical east coast and cool-temperate west coast waters. This species also occurs offshore to depths of at least 110 m (Dawson 1986).

Prior to the taxonomic and genetic study on southern African *S. temminckii* by Mwale et al. (2013), this species was synonymised with *Syngnathus acus*. However, morphological and genetic divergence between the two *Syngnathus* species were highlighted by Mwale et al. (2013) which confirmed that southern African *S. acus* were indeed *S. temminckii*.

### Biology and ecology

The longsnout pipefish is the most common pipefish in southern African estuaries (Dawson 1986) and is often associated with submerged aquatic vegetation such as *Zostera capensis*. The body shape and light greenish to dark brown colouration of this species provides excellent camouflage in estuarine eelgrass beds. According to Smith (1965) the colour of the fish shows variability according to that of the sheltering aquatic plants, further enhancing its ability to avoid predators.

Sexual maturity is attained at approximately 12 cm SL (Bennett 1989). The observed sex ratio for *S. temminckii* in southern African waters was 0.5:1.0, M:F which was significantly different to the expected 1:1 ratio (Mwale et al. 2014). The mean number of mature oocytes in the females ( $n = 379$ ) was not significantly different from



the mean number of eggs/embryos in the male brood pouch ( $n = 451$ ). In addition, the relationship between brood pouch carrying capacity and pipefish size was linear and positively correlated, implying that reproductive efficiency increases with the size of individual fish (Mwale et al. 2014).

Breeding occurs both in estuaries and the sea between November and March, with the male retaining the developing embryos in a brood pouch (Day et al. 1981). Males accept eggs from more than one female (Vincent et al. 1995) and the total number of developing eggs can reach 486 for a single male (Mwale et al. 2014).

Densities of these pipefish are usually low, with 0.008 individuals per square metre being recorded in the Bot Estuary (Bennett & Branch 1990) which is not the optimal habitat for this species. The longsnout pipefish has been recorded in salinities ranging from 3-42 (Whitfield 1996a) and a mass mortality was recorded in the Swartvlei Estuary when water temperatures approached 32°C (Russell 1994).

*Syngnathus temminckii* is an active predator that feeds on zooplankton, particularly copepods, which are sucked in individually. It also captures amphipods from the surfaces of submerged aquatic plants (Day et al. 1981). In the Bot Estuary 57% of the diet (dry mass) consisted of copepods, 24% amphipods, 15% isopods and 3% aquatic insect larvae. Feeding in the above system occurred mainly during the day between 10h00 and 18h00 (Bennett & Branch 1990) when prey items would be visible.

Family: SYNGNATHIDAE

Species: *Syngnathus watermeyeri* (Smith 1963)

Common name: Estuarine pipefish

Illustrated specimen length: 12 cm SL



### Selected anatomical features

Fin elements: Dorsal 28-32;

Anal 3; Pectoral 6-8

Ring count: Trunk 16-18; Tail 37-40

Maximum recorded length:  $\pm 13$  cm SL

### Distribution

*Syngnathus watermeyeri* is only known from a few estuaries along the Eastern Cape coast (Dawson 1986). Latest indications are that it has disappeared from the Kasouga and Kleinemonde systems, with only small populations surviving in the lower reaches of the Bushmans and Kariega estuaries. Possible recolonisation of the former estuaries following river flood events cannot be ruled out.

### Biology and ecology

This critically endangered pipefish is usually found in association with submerged plants, especially *Zostera capensis* which forms extensive beds in both the Bushmans and Kariega estuaries. The longsnout pipefish *Syngnathus temminckii* occurs sympatrically with the estuarine pipefish in eelgrass beds, with the former species still common in these areas (Whitfield & Ter Morshuizen 1992, Whitfield et al. 2017a). Within the East Kleinemonde Estuary this species was found in association with submerged *Ruppia cirrhosa* beds and, until recently, was also found in similar habitats within the West Kleinemonde system.

A recent comparison of the life-history styles of both *S. watermeyeri* and *S. temminckii* provides strong evidence for the greater success of the latter species (Whitfield et al. 2017a). Some of the main reasons for the higher numbers of *S. temminckii* include a much wider geographic distribution, higher fecundity, and alternative ecosystem selection (marine and estuarine habitats) when compared to *S. watermeyeri*.

Sexual maturity is attained at approximately 10 cm SL, with breeding occurring within the estuarine environment. Reproductively active



specimens were collected in the Kariega Estuary during September 1963, with males of 10-11 cm SL retaining up to 44 developing embryos in the brood pouch (Whitfield 1995c).

The temporary disappearance of the estuarine pipefish from the Kariega system (Whitfield & Bruton 1996) suggests that this species is very vulnerable to human perturbations of the aquatic environment. Catchment mismanagement within the Bushmans and Kariega systems, particularly the absence of environmental freshwater allocations from major impoundments, has resulted in the estuaries becoming deprived of essential freshwater pulses (Whitfield & Wooldridge 1994). These pulses provide nutrients that facilitate phytoplankton development within estuaries and, together with particulate organic material brought down by the rivers, support the zooplankton community on which pipefish depend for food. The prolonged absence of river inflow, together with frequently recorded hypersaline conditions ( $>40$ ) in both estuaries during recent decades (Ter Morshuizen & Whitfield 1994), may be indirectly responsible for the rarity of this fish.

The recolonization of estuaries that have lost their *S. watermeyeri* population are dependent on river floods that wash individuals into the sea from nearby systems. Thus the recolonization of the Kariega Estuary following river flooding during 2006 (Vorwerk et al. 2007) was almost certainly facilitated by individuals that had been washed out of the East Kleinemonde Estuary.

Family: AMBASSIDAE

Species: *Ambassis ambassis* (Lacepède 1802)

Common name: Longspine glassy

Illustrated specimen length: 66 mm SL

#### Selected anatomical features

Fin elements: Dorsal VII/I, 9-10;

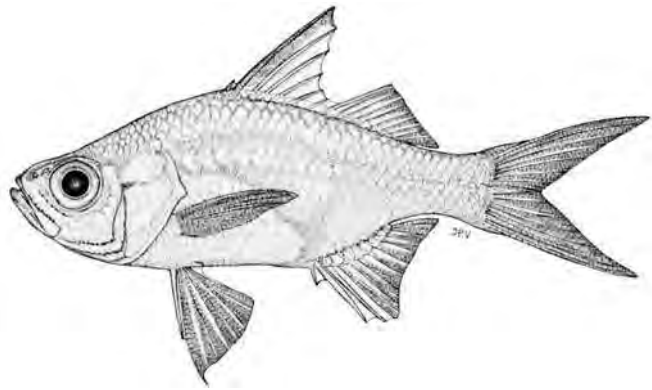
Anal III, 9-11; Pectoral 14-15

Lateral scales: 28-29

Predorsal scales: 14-18

Maximum recorded length in southern

African waters:  $\pm 14$  cm SL



#### Distribution

*Ambassis ambassis* has been reported from East Africa southwards to the Mtata Estuary (Martin & Heemstra 1988). This species is most abundant in temporarily open /closed estuaries along the KwaZulu-Natal coast.



#### Biology and ecology

Sexual maturity is attained at a length of approximately 50 mm SL. Very little is known about the breeding biology of *A. ambassis* but spawning does occur within estuarine systems (van der Elst 1988). Larval development probably occurs at sea and in estuaries, with the juveniles and adults occupying the estuarine environment for most or all of their life cycle.

The longspine glassy is a very efficient osmoregulator in oligohaline salinities but is unable to maintain its internal body fluid concentration as efficiently as the other two *Ambassis* species in salinities above that of sea water (Martin 1990). The inability to osmoregulate efficiently in hypersaline waters may be one of the factors restricting *A. ambassis* to mainly low salinity areas (<10) within KwaZulu-Natal estuaries (Martin 1988).

This species was present throughout the year in Lake Nhlangwe where salinities were <1 (Blaber & Cyrus 1981). In Lake St Lucia, *A. ambassis* numbers were low compared to the other two ambassid species when the salinity was >15 (Martin 1983) but showed increased abundance under oligohaline conditions.

The longspine glassy has a diet comprising mainly zooplanktonic and benthic crustaceans. In addition pelagic fish larvae and even juvenile fish, together with insects, are consumed. The relatively large size of adult *A. ambassis* when compared to other ambassids may be due to the fact that this predatory species derives a large proportion of its energy from fish (Martin & Blaber 1983). Feeding occurs mainly during the night and early morning (Martin 1989).

Family: AMBASSIDAE

Species: *Ambassis dussumieri* (Cuvier 1828)

Common name: Bald glassy

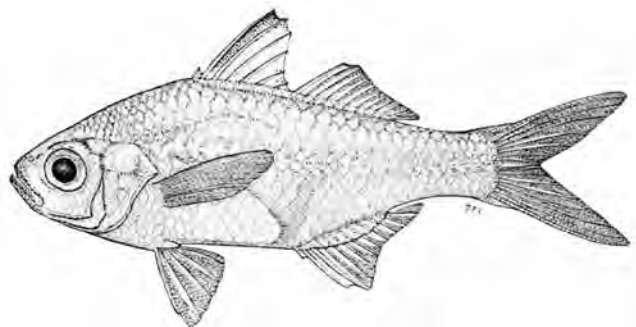
Illustrated specimen length: 46 mm SL

#### Selected anatomical features

Fin elements: Dorsal VI-VII/I, 8-10;

Anal III, 8-10; Pectoral 14-15

Lateral scales: 27-29 interrupted



Predorsal scales: 13-16

Maximum recorded length in southern

African waters:  $\pm 70$  mm SL

### Distribution

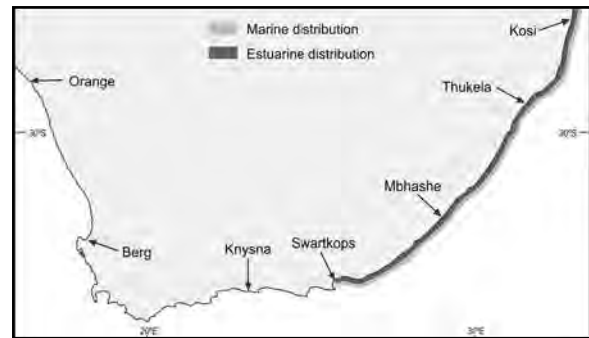
The bald glassy occurs mainly in the tropical and subtropical waters of the Indian Ocean, Indonesia and Philippines (Heemstra & Martin 1986). It extends south into the warm-temperate region of southern Africa and is most abundant in the mouth region of KwaZulu-Natal estuaries (Martin 1989).

### Biology and ecology

Ripe running *A. dussumieri* between 30 mm and 40 mm SL have been recorded from Durban Bay (Blackler 2002). It has been suggested that this species may spawn under estuarine conditions (Wallace 1975b), with confirmed eggs and larvae having been collected from Durban Bay from September to February, especially in the mouth region of this system (Connell 1996) which exhibits mainly marine conditions.

Ambassid eggs, tentatively identified as *A. dussumieri*, have also been found in the St Lucia Estuary and postflexion larvae in certain Eastern Cape estuaries (Strydom et al. 2003). The scarcity of larvae of this species in southern African estuaries, and the abundance of this life stage in the nearshore marine environment (Harris & Cyrus 1996), points to a marine larval phase for most *A. dussumieri*.

Although laboratory tests have shown that *A. dussumieri* can survive extended periods (21



days) in fresh water (Martin 1988), the large change (42%) in blood osmolality after transfer from sea water into fresh water suggests that it is the least euryhaline of the ambassids in the region (Martin 1990) and was generally absent from Lake St Lucia under oligohaline conditions. Nevertheless, this species is likely to tolerate much wider salinities under natural conditions compared to the laboratory, especially when such changes allow for long periods of acclimation.

All three *Ambassis* species from southern Africa have well developed dentition and pharyngeal teeth which, together with a relatively short gut in relation to body length, suggest a mainly carnivorous habit (Martin & Blaber 1984).

The diet of *A. dussumieri* in KwaZulu-Natal estuaries is dominated by zooplanktonic crustaceans, with fish eggs and fish larvae of secondary and tertiary importance respectively (Martin & Blaber 1983). This species feeds during both the day and night, with peak stomach fullness recorded at night.

Family: AMBASSIDAE

Species: *Ambassis natalensis*

(Gilchrist & Thompson 1908)

Common name: Slender glassy

Illustrated specimen length: 54 mm SL

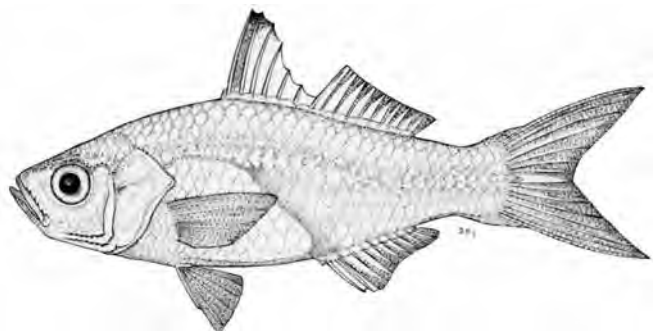
### Selected anatomical features

Fin elements: Dorsal VII/I, 9-11;

Anal III, 9-11; Pectoral 14-15

Lateral scales: 27-29

Predorsal scales: 9-11





Maximum recorded length in southern African waters:  $\pm 10$  cm SL

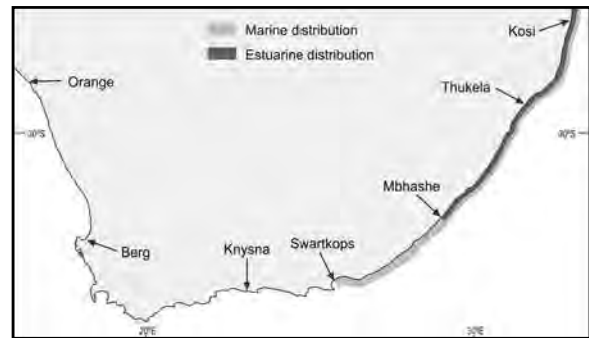
### Distribution

The slender glassy occurs from Inhaca Island southwards to Algoa Bay but it is most abundant in the subtropical region of southern Africa. There are unconfirmed records of this species occurring in the coastal waters of East Africa (Martin & Heemstra 1988).

### Biology and ecology

Sexual maturity is attained at a length of approximately 35 mm SL, with spawning recorded in estuaries between August and November (Wallace 1975b). Large numbers of ambassid larvae (probably *A. natalensis*) 3-8 mm in length have been documented from St Lucia lake and estuary (Wallace 1975b). High densities of postflexion larvae (probably *A. natalensis*) have also been recorded in the Kosi Estuary (Harris et al. 1995).

The slender glassy is euryhaline but is incapable of maintaining a constant blood osmolality in salinities above 52 (Martin 1990) and below 7 (Martin 1989). Direct transfer from sea water to fresh water results in an internal osmotic concentration change of only 20% (Martin 1990).



Both juveniles and adults were present in Lake Nhlanga at salinities  $< 1$  (Blaber & Cyrus 1981). The euryhalinity of *A. natalensis* has facilitated its colonisation of all types of estuaries, but the greatest numbers occur in the middle reaches of subtropical systems where the salinity range is 8-28 (Martin 1989).

The slender glassy has a diverse diet, foraging mainly during the morning and evening on zooplanktonic crustaceans and insects at the water surface. In addition, smaller quantities of fish larvae, polychaete larvae, bivalve spat and filamentous algae are also consumed (Martin & Blaber 1983). This species is the least piscivorous of the three ambassids occurring in southern African estuaries.

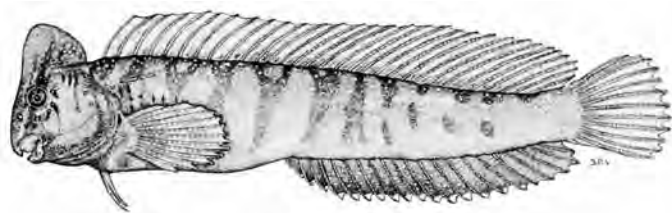
Family: BLENNIIDAE

Species: *Omobranchus woodi*

(Gilchrist & Thompson 1908)

Common name: Kappie blenny

Illustrated specimen length: 72 mm SL



### Selected anatomical features

Fin elements: Dorsal XI-XIII, 19-21;

Anal II, 20-22; Pectoral 13

Lateral line tubes on body: 2-6

Maximum recorded length:  $\pm 80$  mm SL

### Distribution

This endemic species has been recorded in estuaries from Mlalazi in KwaZulu-Natal to the Berg Estuary in the Western Cape (Montoya-Maya & Strydom 2009a), and is especially associated with permanently open systems that have extensive reef or rocky habitats in the lower reaches.



### Biology and ecology

*Omobranchus woodi* breeding occurs mainly during summer and the nest in which the eggs are laid is guarded by the male. Newly hatched larvae (2-4 mm BL) are carried out to sea on the ebb tide, only to return several weeks later when the postlarval stage has been attained (Whitfield 1989b). Densities of these larvae in some estuaries are very high, such that they can even dominate the ichthyoplankton in the lower reaches at certain times of the year (Melville-Smith & Baird 1980). The mean length of *O. woodi* in Algoa Bay

was 5.1 mm (Beckley 1986), thus confirming that the larval stages are present as part of the marine ichthyoplankton.

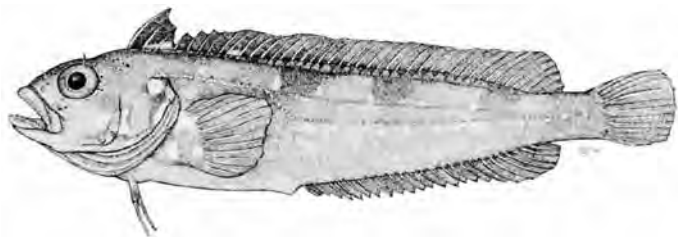
Very little is known about the kappie blenny, probably because it is a shy species, often living in burrows under stones and therefore seldom captured by conventional sampling gear in estuaries (Beckley 1983). It has well developed teeth and exceptionally large canines with which it will bite any intruder. The nuchal crest on top of the head of large males (>40 mm SL) probably has some territorial or reproductive display function.

Family: CLINIDAE

Species: *Clinus spatulatus* (Bennett 1983)

Common name: Estuary klipfish

Illustrated specimen length: 73 mm SL



### Selected anatomical features

Fin elements: Dorsal XXXII-XXXV, 6-8;

Anal II, 23-25; Pectoral 13-15

Supraorbital tentacle usually with a spatulate tip

Maximum recorded length:  $\pm 15$  cm SL

### Distribution

The estuary klipfish has only been reported from two adjacent Western Cape estuaries, namely the Bot and Kleinmond systems (Whitfield 1996c).

### Biology and ecology

Females of this viviparous species mature in their first year at a length of 75-80 mm TL (Bennett 1983). The sex ratio appears skewed, with seine net catches revealing one male to approximately 15 females.

Embryos in an advanced stage of development (>15 mm BL) were present in the Bot Estuary between March and September and grew from 25 mm to 90 mm TL in one year (Bennett 1983). Few fish appear to survive for more than 18 months. Genetic evidence suggests that this species is in a population decline (von der Heyden et al. 2015).



*Clinus spatulatus* has been recorded in salinity and temperature ranges of 2-15 and 14-25°C respectively (Bennett 1983). In the Bot Estuary this species had a density of 0.03 fish m<sup>-2</sup> (Bennett & Branch 1990), a value that is likely to fluctuate widely according to mouth state.

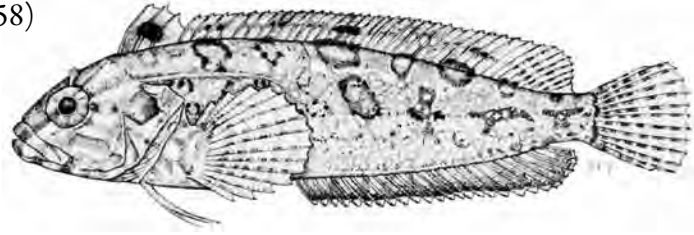
The estuarine klipfish feeds mainly on gastropods, isopods, amphipods, insect larvae and small fish (Bennett & Branch 1990). The dominant prey items were the small gastropod *Tomichia* sp., isopod *Exosphaeroma* sp. and amphipod *Melita zeylanica*.

Family: CLINIDAE

Species: *Clinus superciliosus* (Linnaeus 1758)

Common name: Super klipfish

Illustrated specimen length: 78 mm SL



### Selected anatomical features

Fin elements: Dorsal XXXI-XLII, 5-10;

Anal II, 21-30; Pectoral 15-18

Supraorbital tentacle mostly with a branching tip

Maximum recorded length in southern

African waters:  $\pm 27$  cm SL

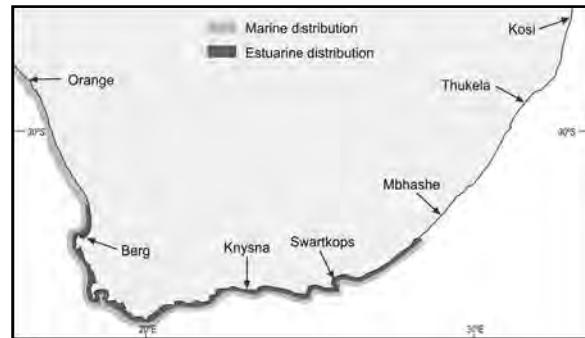
### Distribution

*Clinus superciliosus* occurs in coastal waters from approximately 19°S on the west coast to the Kei Estuary on the east coast (Smith 1986e). This species is most common among stones and submerged aquatic plants in the lower reaches of selected Cape estuaries, as well as tide pools on the open coast.

### Biology and ecology

The viviparous super klipfish matures at a length of approximately 55 mm TL (Prochazka 1994), with breeding occurring both in estuaries and the sea (Day et al. 1981). Gestation is intrafollicular, with autoradiographic studies indicating that the embryos absorb nutrients through the epidermis, fins and gut. These structures have become extensively modified in order to act as absorptive tissue (Veith 1978).

Breeding appears to occur mainly during winter and early summer but gravid females can be captured in all seasons (Veith 1979). The reduction in embryo numbers normally associated with viviparity is therefore partially overcome by *C. superciliosus* in that it breeds throughout the year, thus increasing the number of fish spawned per annum. In addition, through super-embryonation the embryos are not all spawned at the same time, and this possibly decreases the chance of detection by predators (Veith 1979), as well as facilitating larval release during optimum environmental



conditions. In contrast to the estuarine klipfish, *C. superciliosus* has undergone population expansion during the Holocene (von der Heyden et al. 2015).

The super klipfish has been recorded in a salinity range of 8-42 (Ter Morshuizen & Whitfield 1994, Whitfield 1996a) but can probably survive in lower salinity water when river floods pass through estuarine systems. This species is also adapted to a wide temperature range and the body colouration can vary according to its surroundings (Smith 1965).

In estuaries *C. superciliosus* feeds mainly on amphipods, brachyurans, isopods, gastropods and insect larvae (Day et al. 1981, Whitfield 1988a). Large adults also prey on gobies and hermit crabs. In the marine intertidal zone this species consumes mainly amphipods, decapods, molluscs, polychaetes and isopods (Bennett et al. 1984).

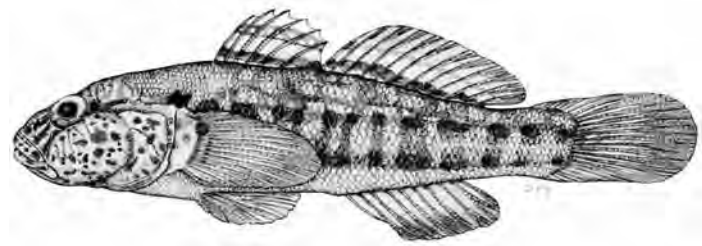
Indications are that the super klipfish consumes between 2.5% and 9.1% of its body mass per day, with smaller individuals eating proportionately more food than larger ones (Bennett 1984).

Family: GOBIIDAE

Species: *Caffrogobius gilchristi*  
(Boulenger 1900)

Common name: Prison goby

Illustrated specimen length: 59 mm SL



#### Selected anatomical features

Fin elements: Dorsal VI+I, 11-12;

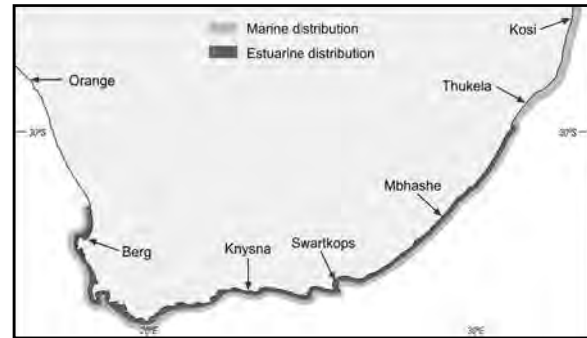
Anal I, 9-10; Pectoral 17-19

Lateral scales: 43-53

Maximum recorded length:  $\pm 13$  cm SL

#### Distribution

*Caffrogobius gilchristi* is endemic to southern African waters, with an estuarine distribution from the Olifants system on the west coast to Durban Bay in the north east. This fish is also common in marine tidal pools within its distributional range and is particularly abundant in the middle reaches of certain warm-temperate estuaries, especially those that are permanently open to the sea. It is often associated with submerged macrophyte beds but can also occur on bare substrata.



#### Biology and ecology

The prison goby matures at a length of approximately 50 mm SL (Bennett 1989), with breeding occurring mainly during the spring and early summer (September-January). Clusters of eggs are attached to shells, stones and other submerged objects. The mass hatching of larvae usually coincides with the nocturnal high tide. The larvae, which are mostly 3-4 mm BL, are then carried passively out of the estuary by the ebb tide (Beckley 1985).

Following completion of larval development in the marine environment, the postlarvae enter adjacent estuaries as permanent residents (Whitfield 1989a). In the permanently open Sundays and Swartkops estuaries, large numbers of *C. gilchristi* postflexion larvae and juveniles were recorded entering these systems via shallow littoral waters on the ebb tide (Patrick & Strydom 2014). However, large numbers of preflexion and

postflexion larvae have been recorded in certain TOCEs (Strydom et al. 2003) so the possibility exists that this species has a flexible life cycle, with larval development occurring in both the marine and estuarine environments.

*Caffrogobius gilchristi* has been recorded in a salinity range of 1 to 42, thus enabling it to survive the low estuarine salinities which prevail during river flooding. This goby is also common in certain temporarily closed systems where salinities often decline below 5 for prolonged periods. In the Swartvlei lake littoral zone this species had a mean biomass of  $0.4 \text{ g m}^{-2}$  (Whitfield 1993) and in the Bot system the value was  $0.01 \text{ g m}^{-2}$  (Bennett & Branch 1990).

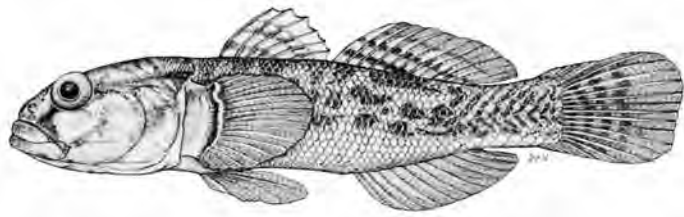
The diet of *Caffrogobius gilchristi* in the Swartvlei and Bot estuaries has been studied by Whitfield (1988a) and Bennett & Branch (1990) respectively. These authors found that this goby feeds primarily on amphipods, isopods, brachyurans, chironomid larvae, anomurans, macrurans, polychaetes and small fishes. It forages mainly at dawn and dusk, with an estimated daily food consumption of 3.5% of body mass (Bennett & Branch 1990).

Family: GOBIIDAE

Species: *Caffrogobius nudiceps*  
(Valenciennes 1827)

Common name: Barehead goby

Illustrated specimen length: 68 mm SL



#### Selected anatomical features

Fin elements: Dorsal VI+I, 11-12;

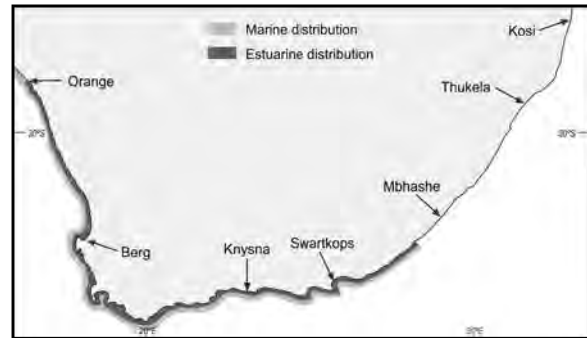
Anal I, 10-11; Pectoral 19-23

Lateral scales: 33-50

Maximum recorded length:  $\pm 12$  cm SL

#### Distribution

The barehead goby is endemic to southern African waters, ranging from East London in the warm-temperate region to Walvis Bay on the cool-temperate west coast (Hoese 1986a). Within Eastern Cape estuaries it is most abundant in the lower reaches, although specimens are also regularly captured in the middle reaches of certain systems.



#### Biology and ecology

*Caffrogobius nudiceps* matures at  $\pm 45$  mm SL. Although little is known about the breeding biology of this goby, it is likely to follow a similar life-history style to that of the closely related *Caffrogobius gilchristi*, i.e. estuarine spawning followed by a marine larval phase and postlarvae entering nearby estuaries. *Caffrogobius nudiceps* is not as dependent on estuaries as *C. gilchristi*, with

the former species often recorded in the littoral marine zone.

Despite its mainly tidal pool occurrence, the barehead goby has been recorded in a salinity range of 1-42, and is usually associated with submerged *Zostera capensis* beds in the lower half of permanently open estuaries (Ter Morshuizen & Whitfield 1994). In the warm-temperate region, the closely related *Caffrogobius natalensis* also occurs mainly in the lower reaches of estuaries but, in contrast to *C. nudiceps*, most specimens are located in the channel rather than littoral plant beds.

Family: GOBIIDAE

Species: *Croilia mossambica* (Smith 1955)

Common name: Naked goby

Illustrated specimen length: 33 mm SL



#### Selected anatomical features

Fin elements: Dorsal VI, 11-12;

Anal 12; Pectoral 13-15

Sides of body with 6-10 vertical lines

Maximum recorded length:  $\pm 55$  mm SL



#### Distribution

The naked goby ranges from Madagascar and Mozambique to KwaZulu-Natal (Hoese 1986a), occurring in estuarine and coastal lakes 1-27 m deep (Blaber & Whitfield 1977b). This species



also occurs in sandy areas of certain small estuaries as far south as the Sandlundlu.

### Biology and ecology

*Croilia mossambica* occurs in both estuaries and freshwater coastal lakes. Sexual maturity occurs at a length of approximately 30 mm SL, at which stage the fish constructs burrows up to 9 cm deep and 1 cm in diameter in fine to medium grained sand areas that are sheltered from heavy wave action (Blaber & Whitfield 1977b). When disturbed the fish always enter the burrow head first and despite its relatively narrow width, turn round within it, and position the head at the entrance to the burrow. Respiratory currents within the burrow are maintained by opercular movement and lateral undulations of the body.

The naked goby is a summer breeder with a protracted spawning season. Male gonads begin ripening in July whereas large numbers of ripe females are only present from October onwards. Males are territorial, and about 50 bright yellow adhesive eggs, 0.7-0.8 mm diameter, are laid (Blaber & Whitfield 1977b).

Large numbers of planktonic postflexion larvae (9-13 mm BL) were recorded in the Kosi Estuary during January (Harris et al. 1995). Little is known about the early juvenile stages but evidence from Lake Sibaya suggests that they inhabit littoral plant beds. In Lake Sibaya the population density

of adults varied from one individual per 10 m<sup>2</sup> to one per 70 m<sup>2</sup> (Blaber & Whitfield 1977b).

*Croilia mossambica* has been recorded in a salinity range of 1 to 35 and experimental evidence has shown that this species can tolerate major salinity fluctuations (Blaber & Whitfield 1977b). This is particularly important in the lower reaches of some of the temporarily open KwaZulu-Natal estuaries where salinities often range between fresh water and 35 within a single tidal cycle. The abundance of the naked goby in Lake Sibaya suggests that it is also well adapted to permanent freshwater conditions. The upper temperature tolerance lies between 32°C and 35°C.

When foraging *C. mossambica* holds the anterior part of the body off the substratum using the well-developed fraenum. In order to capture moving prey it moves rapidly forward by means of a tail flick and swallows the organism whole (Blaber & Whitfield 1977b). All feeding apparently takes place outside the burrow and no prey is removed from below the sediment surface. Sight is the primary sense used in locating food and all foraging occurs during the day.

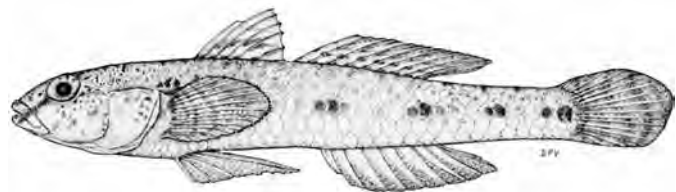
The diet of *C. mossambica* consists of slow moving benthic invertebrates such as chironomid larvae, gastropods, bivalves, ostracods and amphipods. The relative importance of each depends upon prey item abundance within the environment (Blaber & Whitfield 1977b).

Family: GOBIIDAE

Species: *Favonigobius reichei* (Bleeker 1853)

Common name: Spotted sandgoby

Illustrated specimen length: 43 mm SL



### Selected anatomical features

Fin elements: Dorsal VI+I, 8;

Anal I, 7-8; Pectoral 16-17

Lateral scales: 25-26

Maximum recorded length in southern

African waters: ± 65 mm SL

### Distribution

The spotted sandgoby is a tropical Indo-West Pacific species reaching as far south as the Mngazana



Estuary. Both this species and the closely related blackthroat goby *Favonigobius melanobranchus* have been recorded in the Mgeni Estuary (Begg 1984a).

### Biology and ecology

Little is known about the life-history of *Favonigobius reichei* in southern African waters, possibly due to its rarity, small size and excellent camouflage. This species is at the southern extremity

of its distribution and is known from only four estuaries in KwaZulu-Natal and one in the Eastern Cape Province.

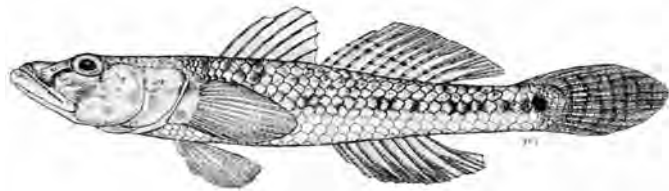
The recorded salinity range of this goby is 3-28 but it can probably also survive in seawater. Specimens captured in KwaZulu-Natal estuaries occur over substrata ranging from silt to muddy sand, and it relies on camouflage to avoid piscivorous fishes in both vegetated and bare sediment areas (Nanjo et al. 2011).

Family: GOBIIDAE

Species: *Glossogobius callidus* (Smith 1937)

Common name: River goby

Illustrated specimen length: 56 mm SL



### Selected anatomical features

Fin elements: Dorsal VI+I, 8-10;

Anal I, 7-9; Pectoral 14-19

Lateral scales: 28-32

Maximum recorded length:  $\pm 85$  mm SL

### Distribution

The endemic *G. callidus* is abundant and widespread in coastal plain rivers and estuaries of southern Africa, ranging from Mozambique to the Swartvlei region of the Western Cape. Specimens have also been recorded from the northwestern lowveld region (Greenwood 1994).

### Biology and ecology

The river goby is abundant in both freshwater and estuarine systems of southern Africa, and appears tolerant of both flowing and still water conditions. The colouration of this species provides excellent benthic camouflage in both clear and turbid systems. Furthermore, individual fish usually remain motionless on the bottom unless feeding or fleeing predators (Boullé 1989).

Sexual maturity is attained at approximately 35 mm SL, with breeding occurring mainly during spring (October-November) in the Eastern Cape. Females are speleophilic nesters and, depending on size, deposit up to 350 oval eggs (Boullé 1989) under rocks and other hard structures. The male then guards the nest for the duration of the

incubation, fanning the eggs intermittently until hatching (Wasserman et al. 2015b).

In the St Lucia Estuary, the densities of *Glossogobius callidus* larvae in the water column are greatest during November ( $>800$  individuals per  $100\text{ m}^3$ ), declining gradually over the summer (Harris & Cyrus 1995). Although the larvae are dominant in the lower St Lucia Estuary the juveniles and adults have been collected mainly from the middle reaches of most estuaries.

The river goby has been found in a salinity range of 1-42, the upper value being recorded during a reversed salinity gradient situation in the Kariega Estuary (Ter Morshuizen & Whitfield 1994). The highest goby densities were documented in the upper reaches of this estuary, despite the fact that salinities were lower towards the mouth. It would appear, therefore, that salinity is not the major factor governing the distribution of this species within estuaries.



The diet of *Glossogobius callidus* in freshwater pans of the Phongola floodplain is dominated by insect larvae, although copepods, ostracods and branchiopods are also consumed (P. la Hausse de Lalouvière, unpublished data). In Eastern Cape

Province rivers this species feeds mainly on chironomid, trichopteran and ephemeropteran larvae, and in the estuaries of this region amphipods and chironomid larvae are the dominant food items.

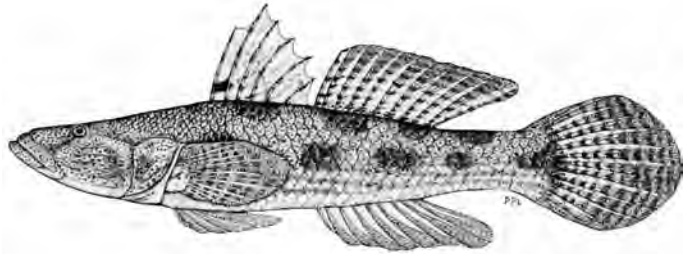
Family: GOBIIDAE

Species: *Glossogobius giuris*

(Hamilton-Buchanan 1822)

Common name: Tank goby

Illustrated specimen length: 252 mm SL



#### Selected anatomical features

Fin elements: Dorsal VI+I, 8-9;

Anal I, 8-9; Pectoral 19-20

Lateral scales: 29-33

Maximum recorded length in southern

African waters:  $\pm 30$  cm SL



#### Distribution

*Glossobius giuris* is a tropical Indo-West Pacific species reaching as far south as the Mpande Estuary in the subtropical zone (Harrison unpublished data). This goby is rare in warm-temperate estuaries of the Eastern Cape Province.

#### Biology and ecology

Although *G. giuris* appears to be a mainly freshwater species, the largest specimens occur in estuaries. The reason why the tank goby grows so large when compared to *G. callidus* has not been determined. This species normally occurs singly in shallow water where its drab colouration and sedentary habits make it cryptic and inconspicuous (van der Elst 1988).

Sexual maturity is attained at approximately 55 mm SL, with breeding occurring mainly during summer (Skelton 2001). According to van der Elst (1988) the elongated eggs adhere to submerged objects and are probably guarded by the male.

Juveniles in freshwater habitats feed on benthic invertebrates whereas larger individuals also prey on fish and tadpoles (Skelton 2001). In estuaries they feed on amphipods, decapods, tanaids, chironomid larvae and small fishes, becoming increasingly piscivorous as large adults (Day et al. 1981, van der Elst 1988).

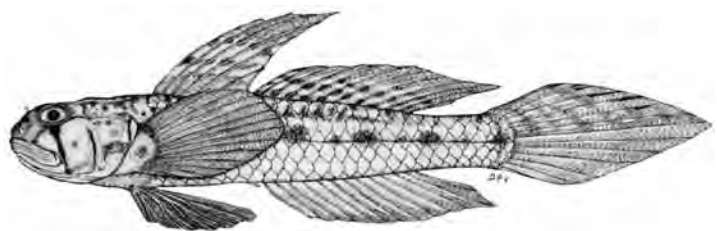
Family: GOBIIDAE

Species: *Oligolepis acutipennis*

(Valenciennes 1837)

Common name: Sharptail goby

Illustrated specimen length: 48 mm SL



#### Selected anatomical features

Fin elements: Dorsal VI+I, 10;

Anal I, 11; Pectoral 20-21

Lateral scales: 25-27

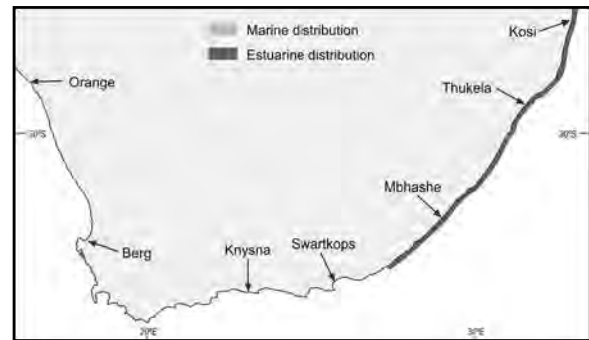
Maximum recorded length in southern African waters:  $\pm 95$  mm SL

### Distribution

*Oligolepis acutipennis* is a tropical Indo-West Pacific species reaching as far south as the Great Fish Estuary (Hoese 1986a). This goby is frequently encountered in the subtropical estuaries of Kwa-Zulu-Natal.

### Biology and ecology

As is the case with other species belonging to this genus little is known about the life-history of *O. acutipennis*. According to Day et al. (1981) this species is confined to estuaries on the subcontinent, remaining in these systems even during river flooding. The recorded salinity range of the sharp-tail goby is 1-35.



Breeding *O. acutipennis* occurs within estuaries and the eggs are guarded (Day et al. 1981). Larvae and postlarvae between 9 mm and 21 mm BL have been recorded in the St Lucia Estuary (Harris & Cyrus 1995), with juveniles present in the lake system even when a marine connection is absent.

Family: GOBIIDAE

Species: *Oxyurichthys keiensis* (Smith 1938)

Common name: Speartail goby

Illustrated specimen length: 43 mm SL

### Selected anatomical features

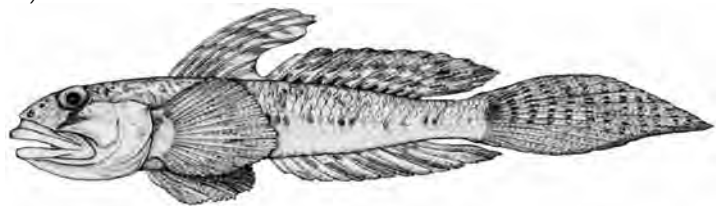
Fin elements: Dorsal VI+I, 11-12;

Anal I, 12; Pectoral 20-22

Lateral scales: 26-28

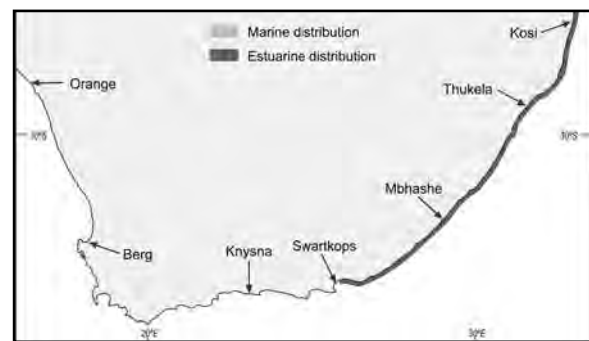
Maximum recorded length in southern

African waters:  $\pm 50$  mm SL



### Distribution

The speartail goby is a western Indian Ocean species ranging from the coastal areas of eastern Africa, including Seychelles and Madagascar, southwards to the Sundays Estuary in the Eastern Cape Province.



### Biology and ecology

Very little is known about the life-history of *O. keiensis*. Within the subtropical and warm-temperate regions of southern Africa this species appears to be exclusively estuarine, since it has not been found in either the marine or freshwater environments. Within estuaries it is usually confined to the upper reaches.

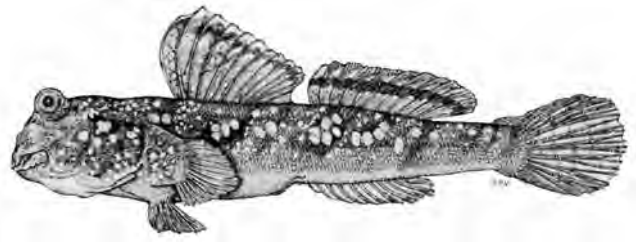
Breeding probably takes place within estuaries and no information is available on the length at sexual maturity, fecundity or the areas occupied by the larvae and postlarvae. The recorded salinity range of the speartail goby is 1-35 and the diet is dominated by small crustaceans and polychaetes.

Family: GOBIIDAE

Species: *Periophthalmus argentilineatus*  
(Valenciennes 1837)

Common name: Bigfin mudskipper

Illustrated specimen length: 81 mm SL



### Selected anatomical features

Fin elements: Dorsal XIV-XVII+I, 10;

Anal I, 9-10; Pectoral 12-13

Dorsals with white margin and black stripe  
below

Maximum recorded length in southern  
African waters:  $\pm 90$  mm SL

### Distribution

*Periophthalmus argentilineatus* has a range extending from the Indo-West Pacific to the subtropical region of southern Africa. Bigfin mudskippers spend much time out of water, and are most common along the banks of mangrove creeks from just below the lowest trees to almost the high tide mark (Macnae 1968).

### Biology and ecology

The muscular pectoral fins of *P. argentilineatus* are used for crawling over the muddy substratum, dragging the tail behind. A hopping action is employed when rapid movement is required (van Dijk 1959). Once the fish has landed after a skip, which can be over a metre in length and up to 30 cm in height, the body is immediately flexed in preparation for another possible hop. When swimming this species has a sinuous motion with the top of the head usually kept above the water surface (Macnae & Kalk 1958).

*Periophthalmus argentilineatus* is territorial, especially during the breeding season, and the males raise their striped dorsal fins when proclaiming their domains (Brillet 1975). Sexual maturity occurs at approximately 60 mm TL (Stebbins & Kalk 1961). This species breeds in estuaries, the male digging a hole in the mud with its mouth and constructing underground chambers (Macnae 1958). These chambers are interconnected by tunnels with external turrets that are 3-8 cm high and 8-10 cm apart (Stebbins & Kalk 1961). The male then attracts a female to his chambers by a courtship display. The eggs are attached to the walls of



the burrow and guarded (Day et al. 1981). After hatching the young escape from the nest at high tide and spend some time confined to the water before adopting an amphibious existence (Macnae & Kalk 1958).

The bigfin mudskipper tolerates a wide range of salinities and can survive in a freshwater environment for several weeks (Day et al. 1981). Its ability to withstand prolonged periods out of water is made possible by virtue of its capacity to retain oxygenated water in the gill chamber, and because of the superficial blood vessels that are able to absorb oxygen directly from the air (van der Elst 1988). According to Teal & Carey (1967) *P. argentilineatus* obtain as much as 60% of their oxygen requirements through the skin, which is maintained in a moist condition for diffusion by frequent body wetting. The bulbous eyes on the top of the head are able to be retracted into their sockets. As the eye is depressed it moves so that the eyelid sweeps over the eyeball, thus cleaning and moistening the eye (Stebbins & Kalk 1961).

The diet of *P. argentilineatus* is usually dominated by insects, polychaetes, amphipods, nematodes, copepods, tanaids, small crabs, prawns, shrimps and fish (Stebbins & Kalk 1961, Day et al. 1981, van der Elst 1988). When watching for prey, the head is held high and the fish adopts an attentive, immobile attitude before leaping at the prey. The act of feeding is accompanied by expulsion of the air and water from the branchial chambers (Stebbins & Kalk 1961).



Family: GOBIIDAE

Species: *Psammogobius knysnaensis*  
(Smith 1936)

Common name: Speckled sandgoby

Illustrated specimen length: 46 mm SL

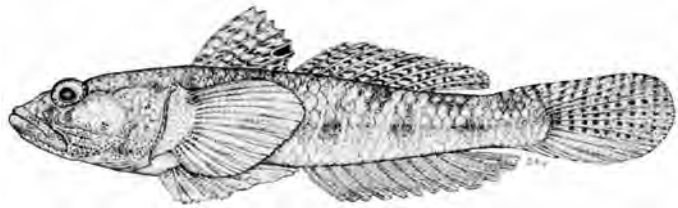
#### Selected anatomical features

Fin elements: Dorsal VI+I, 9-10;

Anal I, 9-11; Pectoral 17-18

Lateral scales: 27-30

Maximum recorded length:  $\pm 60$  mm SL



#### Distribution

*Psammogobius knysnaensis* is a southern African endemic, ranging from Port Nolloth to KwaZulu-Natal. This species is particularly abundant in the lower reaches of permanently open Western and Eastern Cape estuaries, occupying the sandy shallows less than 1 m in depth. It also occurs in intertidal rocky pools along the coast, especially those with sand at the bottom.



#### Biology and ecology

The speckled sandgoby matures at a length of approximately 30 mm SL (Bennett 1989), with the dominant lengths in estuaries ranging between 15 mm and 30 mm SL. Breeding occurs predominantly during spring and summer (October-March), with clusters of elongated eggs being laid on the underside of rocks and other benthic hard objects (Wasserman et al. 2017).

In permanently open estuaries the mass hatching of *P. knysnaensis* larvae usually coincides with the nocturnal high tide. The larvae, which are 2-3 mm BL, are then carried passively out of the estuary by the ebb tide, only to return to these systems as postlarvae (Whitfield 1989b). In the Sundays and Swartkops estuaries, large numbers of postflexion larvae and early juveniles were recorded recruiting into these systems via shallow littoral waters on the ebb tide (Patrick & Strydom 2014).

Hatching of eggs also occurs in temporarily closed estuarine, thus implying that larval development takes place within such systems (Wasserman et al. 2017). These authors postulated that the relatively low numbers of adult *P. knysnaensis* recorded in TOCEs may be a function of the

lack of hard substrata suitable for nesting in these sand-dominated ecosystems. In contrast, rocky reefs and other hard objects are more readily available in permanently open estuaries where adults of this goby are more abundant.

The speckled sandgoby has been recorded in a salinity range of 2-35 (Whitfield 1996a, Bennett 1985), thus enabling it to survive the low salinities that prevail in the lower reaches of estuaries during river flooding. This species also occurs in temporarily closed systems where salinities often decline below 5 for prolonged periods.

The diet of *P. knysnaensis* in the Swartvlei and Bot estuaries has been studied by Whitfield (1988a) and Bennett & Branch (1990) respectively. They found that it feeds mainly at night on amphipods, isopods, polychaetes, insect larvae, cumaceans, decapods, copepods and ostracods.

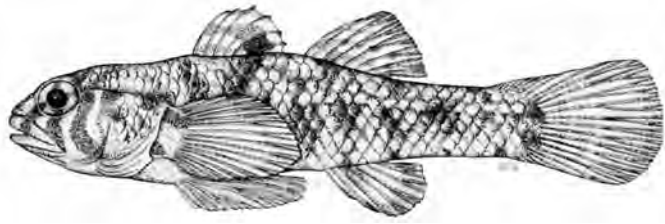
During the day this species is particularly vulnerable to predation by wading birds, and uses crab and prawn holes as temporary refuges, or relies on its mottled sandy colouration for camouflage. When disturbed it moves by short zigzag dashes, finally burying itself in the sand (Hoesé 1986a).

Family: GOBIIDAE

Species: *Redigobius dewaali* (Weber 1897)

Common name: Checked goby

Illustrated specimen length: 27 mm SL



### Selected anatomical features

Fin elements: Dorsal VI+I, 7-8;

Anal I, 5-7; Pectoral 16-18

Lateral scales: 25-29

Maximum recorded length:  $\pm 40$  mm SL

### Distribution

The endemic *Redigobius dewaali* ranges from southern Mozambique to the southern Cape (Hoesé 1986a). According to Skelton (2001) this small species occurs in clear, vegetated littoral habitats in floodplain pans, lakes and estuaries. The more recent discovery of populations in warm-temperate estuaries as far west as the Breede (James et al. 2018) suggests that global warming is benefitting this subtropical species.

### Biology and ecology

The checked goby matures within one year at approximately 20 mm SL, with breeding occurring mainly during spring and summer. Spawning in the freshwater pans of the Phongolo floodplain coincides with the summer flooding of these water bodies. Depending on size, females usually release between 700 and 1 200 spherical eggs 0.5-0.6 mm in diameter (P. la Hausse de Lalouvière, unpublished data).

Settlement of juveniles 10 mm SL occurs within a few weeks of spawning. More than 90% of individuals in freshwater areas are <30 mm SL (P. la Hausse de Lalouvière, unpublished data). The scarcity of adult *R. dewaali* >40 mm SL captured in estuaries may be due to these individuals preferentially occupying crab burrows during all states of the tide (Kramer et al. 2015). Indeed it has even been suggested that there is commensalism between the checked goby and the mud crab



*Scylla serrata* (Wasserman & Mostert 2014), a trait that may also occur with other burrow forming estuarine invertebrates.

*Redigobius dewaali* has been recorded in salinities ranging from 1-42 (Ter Morshuizen & Whitfield 1994). Despite the lower salinities in the middle and lower reaches of the Kariega Estuary, this species was confined to the upper part of the system where the salinity was >40.

The diet of the checked goby in freshwater pans of the Phongolo floodplain is dominated by dipteran larvae, copepods, ostracods and branchiopods. In estuaries this fish species feeds mainly on small crustaceans such as amphipods and copepods, as well as ostracods, chironomid larvae, small arachnids and insects (Wasserman 2012, Kramer et al. 2015).

Males have considerably larger mouths than females of an equivalent size, thus facilitating the consumption of larger prey items by the males. Ontogenetic dietary shifts also occur with regard to both prey items and prey size, with adults consuming a broader size range of organisms when compared to the juveniles (Wasserman 2012).

Family: GOBIIDAE

Species: *Silhouettea sibayi* (Farquharson 1970)

Common name: Barebreast goby

Illustrated specimen length: 25 mm SL

#### Selected anatomical features

Fin elements: Dorsal VI+I, 11;

Anal I, 13; Pectoral 14-15

Lateral scales: 24-25

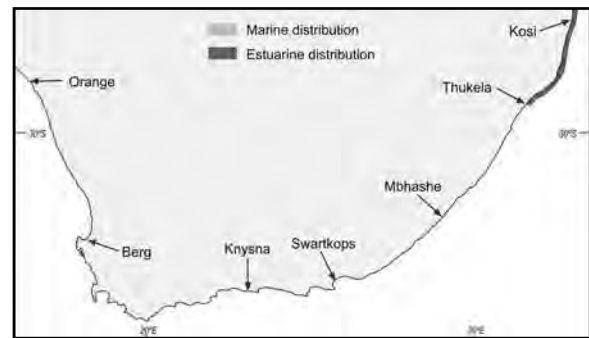
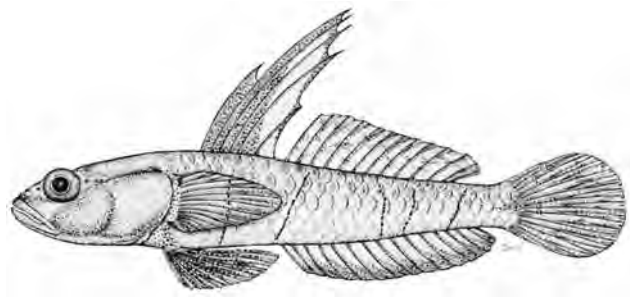
Maximum recorded length:  $\pm 40$  mm SL

#### Distribution

*Silhouettea sibayi* is a southern African endemic, known only from the estuaries and coastal lakes of KwaZulu-Natal and southern Mozambique (Hoese 1986a, Harris & Cyrus 1995).

#### Biology and ecology

The barebreast goby is a small, cryptic species which occurs over sand, mainly in shallow littoral areas where vegetation may be present or absent (Skelton 2001). This species often buries itself in the sand leaving only the eyes uncovered. The long dorsal fin is erected above the sand either for intraspecific communication or as a lure to attract prey (Bruton 1979a).



*Silhouettea sibayi* has been recorded in a salinity range of 1-35 and breeds both in freshwater and estuarine environments. Juveniles have been observed in the littoral plant beds of Lake Sibaya (Bruton 1979a) and Harris & Cyrus (1995) recorded planktonic postlarvae of this species 11-19 mm SL in the St Lucia Estuary.

Family: ELEOTRIDAE

Species: *Eleotris fusca*

(Bloch & Schneider 1801)

Common name: Dusky sleeper

Illustrated specimen length: 75 mm SL

#### Selected anatomical features

Fin elements: Dorsal VI+I, 8;

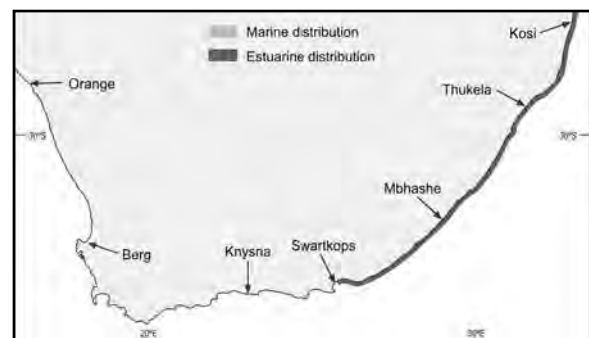
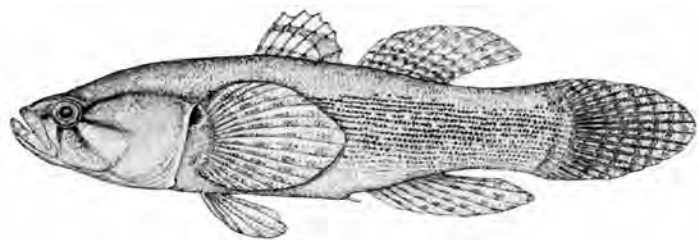
Anal I, 8; Pectoral 17-19

Lateral scales: 57-65

Maximum recorded length in southern African waters:  $\pm 22$  cm SL

#### Distribution

*Eleotris fusca* is a tropical Indo-West Pacific species (Hoese 1986b) extending into the subtropical region of southern Africa. Isolated individuals have been recorded in several warm-temperate estuaries as far south as the Sundays system in



the Eastern Cape. The closely related widehead sleeper *Eleotris mauritanus* and broadhead sleeper *Eleotris melanosoma* also occur in southern African estuaries but are rarely encountered.

### Biology and ecology

Virtually no life-history information is available on the dusky sleeper, probably because it is uncommon in most systems and is secretive and often solitary by nature. This relatively inactive fish is found under logs, stones and rootstocks in the muddy reaches of estuaries and mangrove swamps (Skelton 2001).

*Eleotris fusca* also occurs in freshwater streams leading into coastal lagoons, as well as submerged and emergent macrophyte beds surrounding these systems. Indications from tagging experiments are that the adults of this species are territorial.

Adult males have a well-developed genital papilla, the function of which is unknown. According to Day et al. (1981) this species breeds in estuaries and nektonic *E. fusca* larvae and post-larvae 11-22 mm BL have been recorded in the St Lucia Estuary (Harris & Cyrus 1995). Breeding may also take place in fresh water, since juveniles have been found in semi-isolated coastal systems such as Lake Zilonde, which is rarely linked to the Kosi Estuary. However, the absence of *E. fusca*

from Lake Sibaya and isolated KwaZulu-Natal coastal lagoons suggests intermittent connections with the estuarine environment are necessary for the completion of the life cycle and long-term survival of this species in freshwater areas. Where this species occurs on islands in both the Indian and Pacific oceans, the otolith microchemistry (especially Sr:Ca ratios) suggests that *E. fusca* is amphidromous, with the adults occurring in rivers and the larvae having a marine pelagic phase (Mennesson et al. 2015).

The largest *E. fusca* in southern Africa (16-22 cm SL) have been collected from brackish and freshwater coastal lakes in northern KwaZulu-Natal, e.g. Nhlangwe, Mgobozeleni and Nhlabane. Juveniles are frequently captured in the ebb and flow region of permanently open estuaries, often in fresh water. Studies conducted in the headwaters of the Keiskamma Estuary suggest that an upstream migration of 0+ juveniles into the river takes place.

Based on the available information, *E. fusca* occurs in a salinity range of 1-35, with most specimens collected in water <5. According to Crass (1964) the food consists of "any small aquatic creatures which come within reach of this rather sluggish little predator". The relatively wide mouth enables this fish to consume large food items for its size.

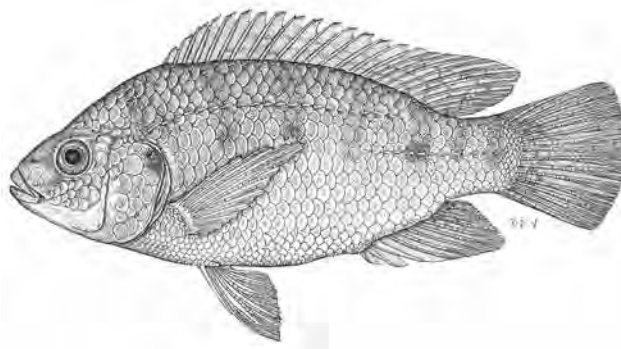
### 3.4 FRESHWATER GUILD

Family: CICHLIDAE

Species: *Oreochromis mossambicus*  
(Peters 1852)

Common name: Mozambique tilapia

Illustrated specimen length: 11 cm SL



#### Selected anatomical features

Fin elements: Dorsal XV-XVII, 10-13;

Anal III, 7-10; Pectoral 13-14

Lateral scales: 30-32

Maximum recorded length:  $\pm$  40 cm SL

#### Distribution

The Mozambique tilapia is endemic to southern Africa, from the lower Zambezi system in the north to the Bushmans River in the south (Skelton 2001). This species has been artificially introduced to many southern and western southern African river systems, is sometimes abundant in coastal lakes and temporarily closed estuaries, but is usually absent from the lower and middle reaches of permanently open estuaries (Whitfield & Blaber 1979c).

#### Biology and ecology

Sexual maturity is usually attained within one year (Bruton & Allanson 1974) at a length of 80-120 mm SL (Bruton & Kok 1980). Breeding commences in spring when nests, 30-100 cm diameter, are excavated by males in the littoral zone of lagoons, lakes, vleis, pans and estuaries (Cooper & Harrison 1992, James & Bruton 1992). After a brief courtship the female leaves the nest and mouth broods the eggs and larvae for 14-22 days (Bruton & Bolt 1975). The fry (9-10 mm SL) are then released into the shallows where they form large shoals. A single female may produce several broods in a season, which lasts from September to February (Bruton & Bolt 1975).

The Mozambique tilapia is strongly euryhaline and has been recorded in salinities ranging from 1 to more than 100. It is also associated with a wide range of water turbidities from <10 NTU to >80 NTU.

*Oreochromis mossambicus* is eurythermal but mass mortalities occurred in freshwater Lake



Bhangazi at temperatures of between 10°C and 13°C (Bruton & Taylor 1979). However, equally low water temperatures were tolerated by populations in the nearby estuarine Lake St Lucia (Blaber & Whitfield 1976) and Allanson et al. (1971) have shown that brackish water increases the tolerance of *O. mossambicus* to low water temperatures. Adults appear to be more susceptible to low temperatures than juveniles (Jubb 1979) and the optimum temperature range for this species is 20-35°C, depending on previous thermal history (Bruton & Taylor 1979). Indeed, shoals of 10-18 mm juveniles have been recorded in eulittoral pools where the temperature reached 42°C (Kyle 1984).

Juvenile *Oreochromis mossambicus* feed predominantly on zooplankton and benthic microfauna, whereas adults are mainly detritivorous but may also take advantage of planktonic organisms (Whitfield & Blaber 1978b). The detritus on which they feed is mainly a mixture of diatoms, bacteria and benthic floc (Bowen 1976, 1978). This cichlid is an opportunistic forager and may also feed on filamentous algae, aquatic



macrophytes, insects, foramaniferans, bivalves, gastropods and planktonic crustacea (Bruton & Bolt 1975, Whitfield & Blaber 1978b). It sometimes consumes other fish and has also been recorded swallowing its own young.

Family: CICHLIDAE

Species: *Pseudocrenilabrus philander*  
(Weber 1897)

Common name: Southern mouthbrooder

Illustrated specimen length: 58 mm SL

#### Selected anatomical features

Fin elements: Dorsal XIII-XVI, 9-11;

Anal III, 7-9; Pectoral 13-14

Lateral scales: 27-30

Maximum recorded length:  $\pm 10$  cm SL

#### Distribution

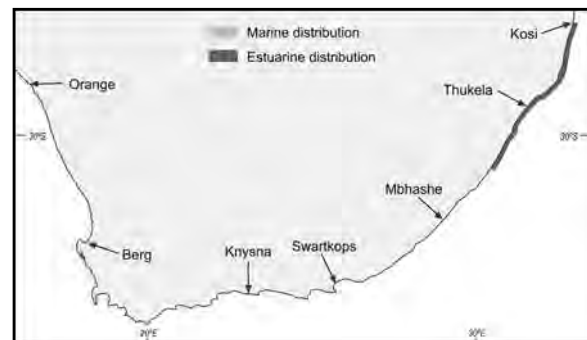
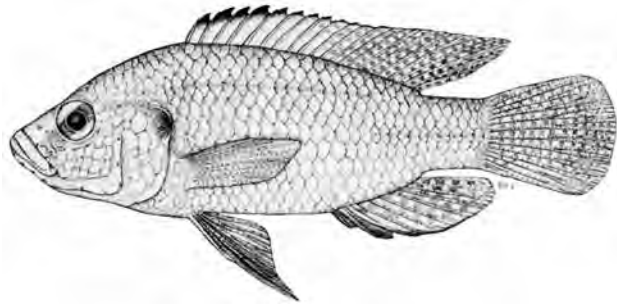
*Pseudocrenilabrus philander* extends from the Orange River and southern KwaZulu-Natal northwards to the southern Zaire tributaries and Lake Malawi (Skelton 2001). Within estuarine systems it has been recorded from the Mzumbe to the Kosi system in KwaZulu-Natal (Begg 1984a, Bruton & Kok 1980).

#### Biology and ecology

The southern mouthbrooder reaches sexual maturity at approximately 25 mm SL. In Lake Sibaya this species occurs to a depth of at least 30 m and breeds to a depth of 24 m (Bruton & Kok 1980).

Breeding occurs in fresh water during spring and summer, with several broods sometimes being raised in a single season. The males establish and defend a territory, construct a simple cleared nest and attract ripe females by means of a courtship display (Ribbink 1971). Eggs are laid in the nest, fertilised by the male and collected by the female. She then withdraws to a quiet nursery area and broods the eggs (14 days), larvae and juveniles until they are able to fend for themselves (Skelton 2001). *Pseudocrenilabrus philander* has

The Mozambique tilapia is preyed upon by a wide range of piscivores, including fishes, egrets, herons, cormorants, pelicans, kingfishers, fish eagles and crocodiles (Bruton 1979a, Whitfield & Blaber 1979b, 1979c).



not been recorded breeding in estuarine systems.

The southern mouthbrooder occurs in a wide variety of habitats from flowing streams to estuarine lakes, usually favouring vegetated zones (Skelton 2001). In the St Lucia system this species was most abundant in shallow areas, particularly oligohaline eulittoral pools when the lake level was high. The salinity tolerance of this fish is unknown, but it has been recorded in estuarine waters where salinities were as high as 21 (Millard & Broekhuysen 1970).

*Pseudocrenilabrus philander* in freshwater areas is a predator on small crustaceans and insects as well as small fishes, and in turn falls prey to predatory fishes and birds (Bruton & Kok 1980). In Lake St Lucia it has been recorded feeding on invertebrates associated with aquatic plant beds (Millard & Broekhuysen 1970).

Family: CICHLIDAE

Species: *Coptodon rendalli*

(Dunz & Schliewen 2013)

Common name: Redbreast tilapia

Illustrated specimen length: 73 mm SL

#### Selected anatomical features

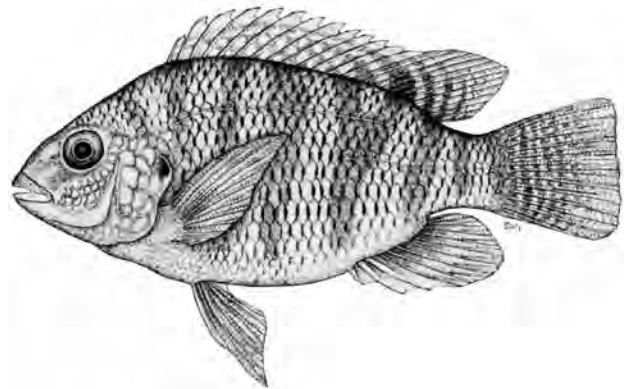
Fin elements: Dorsal XIV-XVI, 12-13;

Anal III, 9-10; Pectoral 12-14

Lateral scales: 28-32

Maximum recorded length in southern

African waters:  $\pm 33$  cm SL



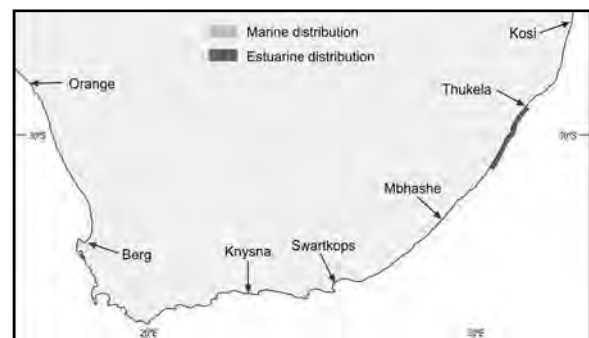
#### Distribution

*Coptodon rendalli* is a mainly tropical African freshwater cichlid, occurring naturally in eastern coastal rivers as far south as the Phongolo system (Skelton 2001). This species has been recorded in estuarine systems on the Mozambique coast (Hill et al. 1975) and has recently colonised several KwaZulu-Natal estuaries (Begg 1984a).

#### Biology and ecology

The redbreast tilapia reaches sexual maturity at 11-13 cm SL. Breeding pairs clear the littoral vegetation to form a nest about 50-120 cm across and excavate several tunnel-like brood chambers in which the eggs and larvae are protected (Skelton 2001). Juveniles up to about 15 mm SL are confined to the protective holes, and parental care occurs up to a length of approximately 40 mm SL (Ribbink et al. 1981). Breeding takes place between October and March (Bruton & Kok 1980), and several broods may be raised each summer. Parental behaviour in protecting their broods in the Kosi Estuary is described by Kyle (1996).

*Coptodon rendalli* has been recorded in estuarine lakes where salinities ranged from 1-8 (Hill et al. 1975) but this species does have the ability to tolerate salinities up to 19 (Whitfield & Blaber 1976). The maximum salinity tolerance is at temperatures 20-28°C but the temperature preference of adults and sub-adults is 35-37°C, with fry found in water up to 41°C (Caulton 1975).



Diel movements of juvenile *C. rendalli* between warm ( $>30^{\circ}\text{C}$ ) shallow water during the day and cooler ( $<20^{\circ}\text{C}$ ) deeper water at night have been shown to enhance fish growth (Caulton 1978).

The redbreast tilapia feeds mainly on water plants and filamentous algae, but also takes aquatic invertebrates and even small fish (Skelton 2001). The release of nutrients from consumed aquatic macrophytes is largely due to an efficient shredding and partial trituration of the ingested plants by well adapted pharyngeal teeth (Caulton 1976).

This tilapia appears to be particularly vulnerable to bird predation. Density dependent mortality which could be attributed to piscivorous birds, especially the reed cormorant *Phalacrocorax africanus* and whitebreasted cormorant *Phalacrocorax carbo*, was documented by Batchelor (1978).

Family: CLARIIDAE

Species: *Clarias gariepinus* (Burchell 1822)

Common name: Sharptooth catfish

Illustrated specimen length: 19 cm SL

### Selected anatomical features

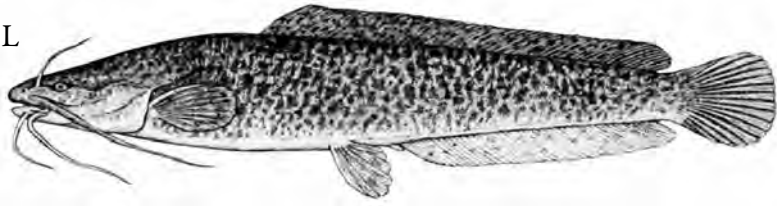
Fin elements: Dorsal 61-75;

Anal 45-60; Pectoral I, 10-11

Four pairs of long filamentous barbels

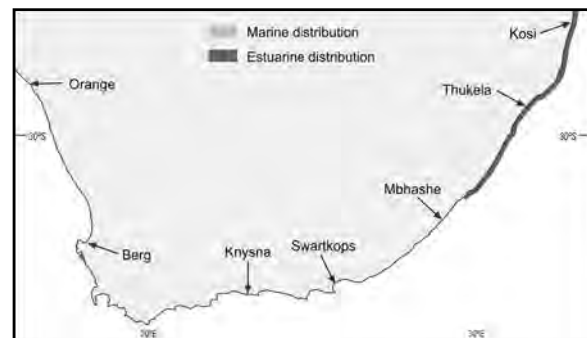
Maximum recorded length in southern

African waters:  $\pm 140$  cm SL



### Distribution

The natural distribution of *Clarias gariepinus* in Africa ranges from the Nile River in the north to the Orange system in the south (Skelton 2001). Along the southern African coast this species originally occurred as far south as the Mtamvuna River but has now been translocated into the Eastern and Western Cape.



### Biology and ecology

The sharptooth catfish occurs in almost any freshwater habitat but favours floodplains, large sluggish rivers and lakes. Although this species is seldom found in estuaries, it has been recorded in systems ranging from the Mvoti to Kosi (Begg 1984a). In Lake St Lucia this fish becomes an important predator during the oligohaline lake phase (Whitfield & Blaber 1978a).

Breeding takes place during summer (September-April) after rains, when large numbers of mature fishes migrate to flooded grassy verges to spawn. The eggs, which are adhesive, are laid on submerged vegetation and hatch within about 25-40 hours (Bruton 1979b). Larvae are free-swimming and feed within two or three days.

Although this species can endure harsh conditions such as high turbidity or desiccation, it is uncommon in salinities above 9 (Whitfield et al. 1981). In Lake St Lucia this fish retreats up inflowing rivers when salinities in the lake approach 10, and it is usually absent from the system when salinities reach 12. A mass mortality of *C. gariepinus* in the mouth region of the

Mkhuze River was attributed to polyhaline water from Lake St Lucia entering this system during a wind induced seiche (Blaber 1981b).

*Clarias gariepinus* is a versatile predator and scavenger, feeding on crustaceans, molluscs, insects and small fishes (Bruton & Kok 1980). Most foraging takes place at night on active benthic organisms, but they may also feed during the day and at the water surface (Bruton 1979c). Individual bottom foraging is the normal mode of feeding, although social hunting by groups in shallow waters has been recorded in a wide variety of habitats, including St Lucia.

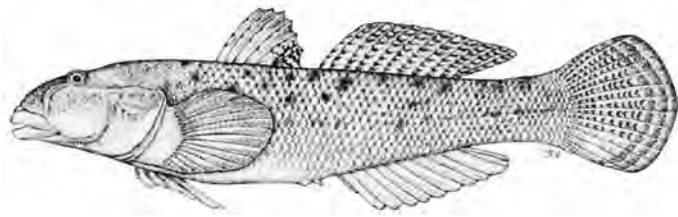
The diet of the sharptooth catfish (33-65 cm TL) in Lake St Lucia was dominated by small demersal fish species (e.g. gobies) but also included molluscs and crustaceans (Whitfield & Blaber 1978a). *Clarias gariepinus* is a favoured prey item of the fish eagle *Haliaeetus vocifer* in both freshwater and estuarine systems (Whitfield & Blaber 1978c), probably because it frequents the littoral zone and rises to the surface at frequent intervals when air breathing.

Family: GOBIIDAE

Species: *Awaous aeneofuscus* (Peters 1852)

Common name: Freshwater goby

Illustrated specimen length: 16 cm SL



### Selected anatomical features

Fin elements: Dorsal VI+I, 9-11;

Anal I, 10-11; Pectoral 15-17

Lateral scales: 50-62

Maximum recorded length in southern

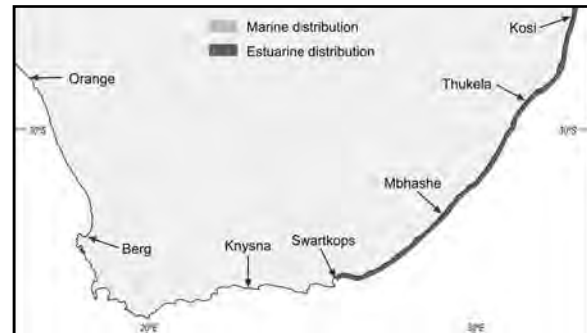
African waters:  $\pm 22$  cm SL

### Distribution

This goby occurs in coastal streams and rivers, from Tanzania southwards to the Eastern Cape Province where it is rare (Skelton 2001). It has also been recorded from estuaries, especially the headwaters, within this geographical range (Crass 1964).

### Biology and ecology

Very little is known about the life-history of *Awaous aeneofuscus* but there is a possibility that it is an amphidromous species in parts of its range. The freshwater goby is found in both still and flowing water, usually over sandy bottoms into



which it may bury itself with only the head and eyes exposed (Skelton 2001).

The recorded salinity range of the freshwater goby is 1-35, with greater abundance of this species in subtropical rather than warm-temperate waters. The diet is dominated by benthic invertebrates and the subterminal mouth is larger in males than females (Hoese 1986a) which may influence prey selection.

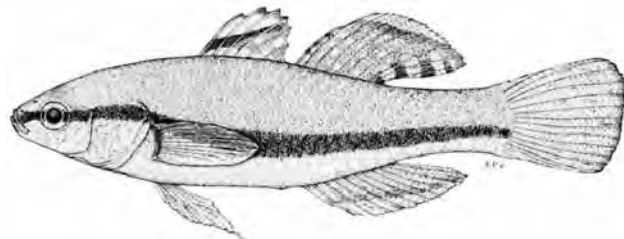
Family: ELEOTRIDAE

Species: *Hypseleotris cyprinoides*

(Valenciennes 1837)

Common name: Golden sleeper

Illustrated specimen length: 41 mm SL



### Selected anatomical features

Fin elements: Dorsal VI+I, 8;

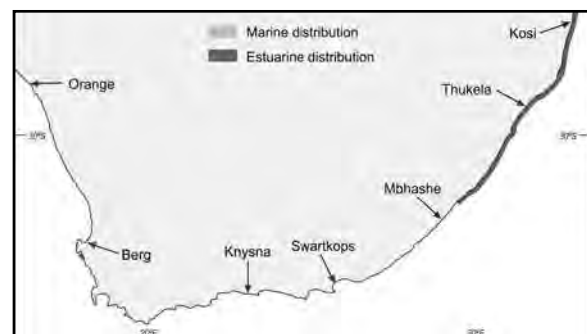
Anal I, 9; Pectoral 12-14

Lateral scales: 24-25

Maximum recorded length:  $\pm 60$  mm SL

### Distribution

*Hypseleotris cyprinoides* is a southern African endemic, ranging from the Mtamvuna system in southern KwaZulu-Natal to at least the Kosi system in the north (Bruton 1996). Although this species is mostly recorded in the mouth region of streams that enter estuarine lakes and lagoons, it also occurs in other estuarine types.



### Biology and ecology

This rare species is known only from a few coastal streams and estuaries in KwaZulu-Natal, some of which are being threatened by human activities. Indeed, there are indications that it may have disappeared from some localities where it was previously recorded, e.g. Lake St Lucia (Bruton 1996).

According to Skelton (2001) the golden sleeper favours shallow vegetated margins of freshwater streams entering estuaries but has also been recorded in Lake St Lucia where salinities were greater than 35. Within the upper reaches of the Kosi system it is reasonably widespread, occurring in the reed margins of the lakes and channels where low salinities prevail.

According to Bruton (1996) breeding takes place in the shallow margins of estuarine lakes and lagoons following river flooding. This statement

is supported by observations which indicate that *H. cyprinoides* is more abundant during wet periods when shallow vegetated marginal habitats are more extensive (Skelton 1987). In addition, Kyle (1989) reports that after heavy rain *H. cyprinoides* appears to migrate upstream into newly flooded areas to spawn. Support for the above hypothesis on spawning requirements also comes from the fact that although individuals have been kept in aquaria for up to 15 years, there have been no reports of breeding in captivity.

No specific biological or ecological studies have been conducted on *H. cyprinoides*. According to Crass (1968) the golden sleeper may remain resting on the bottom for long periods, but will dart to and fro if disturbed or when searching for food. Dietary information from the natural environment is lacking, but in captivity they feed readily on small insect larvae (Skelton 1987).



### 3.5 CATADROMOUS GUILD

Family: ANGUILLIDAE

Species: *Anguilla mossambica* (Peters 1852)

Common name: Longfin eel

Illustrated specimen length: 46 cm TL

#### Selected anatomical features

Fin elements: Distance between verticals at dorsal fin origin and anus = 9-17% TL

Vertebral count: 100-106

Maximum recorded length:  $\pm 115$  cm SL

#### Distribution

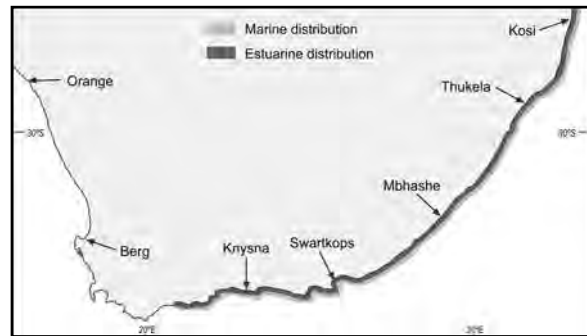
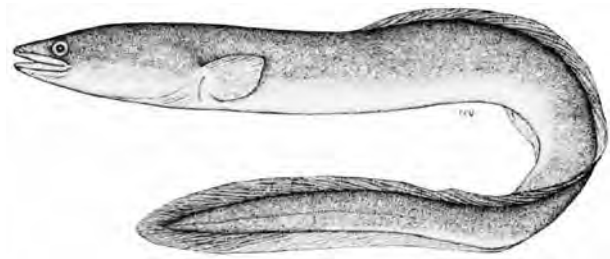
The longfin eel is well known from most of the larger freshwater systems of the warm-temperate region northwards into East Africa, including islands such as Madagascar and Mauritius (Castle 1986b). Three other less common anguillid species *Anguilla marmorata*, *Anguilla bicolor* and *Anguilla bengalensis* overlap part of their southern African distribution with that of *Anguilla mossambica*.

#### Biology and ecology

The longfin eel is the most common of the anguillid eel species in local systems (Jubb 1967) and, in contrast to *A. marmorata*, which tends to remain in the coastal portion of river catchments, *A. mossambica* penetrates into both the middle and upper reaches of most rivers.

Male *A. mossambica* are usually smaller than females and remain in fresh water for 8-10 years, females for 15-20 years (Jubb 1970). This species has the slower growth rate when compared to other southern African anguillids, reaching only 50 cm TL after 10 years and 65 cm TL after 15 years in fresh water (McEwan & Hecht 1984).

On maturity the eyes enlarge, the snout becomes more pointed and body fats increase in preparation for the seaward spawning migration. The gonads only ripen when the eels are in the marine environment. The return migration by adults down the river and through the estuary takes place during summer, usually in association with strong river flows after heavy rains (Skelton 2001). Larvae of *A. mossambica* are carried southwards from the Western Indian Ocean



spawning grounds by the warm Agulhas Current. Metamorphosis of the leptocephali larvae into glass eels occurs once they approach continental shelf waters where estuarine and other land based cues are often present.

Entry into estuaries occurs at a body length of 50-60 mm, mainly during spring and summer (Harris & Cyrus 1995), with most glass eels migrating up the adjoining rivers between November and January. Strong summer river flow into an estuary, especially during the spring tidal cycle, appears to attract large numbers of glass eels for the nocturnal upstream migration (Bruton et al. 1987).

In fresh water, the glass eels change into elvers and continue to migrate upstream, ascending natural and artificial barriers. Once an eel has attained 25-30 cm TL, it ceases to move upstream and remains in a particular pool or river stretch until fully mature (Skelton 2001).

Elvers <20 cm prey mainly aquatic larval insects (Diptera), but copepods and fish remains have also been recorded in the stomach contents (Wasserman et al. 2012). Between 20 and 50 cm TL, the proportion of these smaller food items declines, and crustacea and fish increase in importance. Above 50 cm TL the diet consists primarily of fish, crabs and frogs (Bruton et al. 1987). Most foraging takes place at night.



## Chapter 4

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### Estuarine ecosystems and their ichthyofauna

#### 4.1 INTRODUCTION

SOUTH OF LATITUDE 26°S Africa has approximately 3 400 km of coastline with a total estuarine area of about 600 km<sup>2</sup>, some 70% of which is located in the subtropical areas of KwaZulu-Natal, the Eastern Cape and Mozambique. However, more than 80% of KwaZulu-Natal's 400 km<sup>2</sup> estuarine area consists of the St Lucia and Kosi lake systems. The dominance of coastal lakes in terms of estuarine surface area is overwhelming but the geographic spread of this type of system is very limited.

This chapter assesses the relative importance of different types of systems to the estuary-associated fish groups, and highlights broader ecological processes operating within the region's estuaries. The reader's attention is also drawn to a valuable series of survey papers summarizing ichthyological information from estuaries around the South African coast, namely Harrison (1997a, 1997b, 1998, 1999a, 1999b) and James & Harrison (2008, 2009, 2010a, 2010b, 2011, 2016).

It has been postulated by several authors (e.g. Day 1981d, Blaber 1981a, Whitfield & Patrick 2015) that southern African estuaries are ecologically important because they provide the only significant sheltered areas for the juveniles of some marine fish species that are attracted to shallow, predominantly turbid waters, with a minimum of wave action. In contrast to the high energy coastline associated with south-eastern Africa, the south-western Australian inshore waters are used as an alternative nursery by many estuary-associated marine fish species, mainly because of the physical protection afforded by fringing reefs and rocky headlands (Potter et al. 1990).

Although the large estuarine systems such as Lake St Lucia dominate the subcontinent in terms of habitat availability, Cooper et al. (1995) have emphasized that, in the wave-dominated and

current-swept KwaZulu-Natal coastal region, even small, seasonally open estuaries are important for juvenile marine fishes. They also suggested that collectively, fish from these estuarine nursery areas make a considerable contribution to the adjacent Indian Ocean coastal ecosystem.

A variety of factors influence the use of estuaries by fishes and it is highly unlikely that these factors will be exactly the same for any two systems. Since no two estuaries are identical in terms of either biotic or abiotic characteristics (Figures 152 and 153), it could be postulated that the ichthyofauna of each system will also differ. However, if the resident and marine migrant fishes are responding to the environment in a consistent manner, then the communities occupying similar types of estuaries in a particular region would be expected to reflect this similarity. Indeed, a separation of fish assemblages according to broad estuarine types has been shown to occur but there will always be blurred boundaries, with some fish compositions being more similar and others less so according to the respective driving variables.

There is increasing evidence to suggest that climate change has accelerated over the past few decades and that progressive warming and drying of river catchments in many areas is causing the 'marinisation' of some permanently open systems (e.g. Kariega). Accompanying these trends is a change in species composition, with more tropical taxa moving southwards into the warm-temperate region and increasing numbers of stenohaline fish moving into the lower and sometimes middle reaches of those estuaries deprived of river inflow. Similarly, decreasing river flows are resulting in many TOCEs remaining closed for longer periods, inhibiting the extent to which fish recruitment from the sea can occur but also reducing access to the marine environment for those fish that are reproductively mature and need to breed.



**Figure 152.** View of the lower portion of the Cunge Micro-estuary in the Eastern Cape Province during the closed mouth phase (Photo: Alan Whitfield).



**Figure 153.** View of the middle and upper portion of the Mtendwe Micro-estuary in the Eastern Cape Province during a closed mouth phase (Photo: Tatenda Dalu).

In the following sections the fish assemblages of different estuary types in the different biogeographic regions are reviewed and compared. There is also a detailed analysis of the different types of fish nursery habitats within southern African estuaries and how macrophytic plants play a

crucial role in this regard. A detailed review of fish biomass and production in estuaries is also presented and how the number of estuaries in each South African biogeographic region is not an accurate reflection of total fish production per region.

## 4.2 MICRO-ESTUARIES

Southern African estuary types have generally been classified according to their geomorphology (Harrison 2000) or a combination of physiographic, hydrographic and salinity features (Whitfield 1992). However, micro-estuaries and micro-outlets do not feature in any formal system of classification, as a result of which more than 200 micro-systems on the subcontinent were, until recently, excluded from any form of detailed analysis. A recent study of selected micro-estuaries and micro-outlets in the warm-temperate region of the Eastern Cape coast (e.g. Figure 152 and 153) has provided valuable knowledge on the ecology of these previously poorly studied systems (Magoro 2018).

In terms of physico-chemical characteristics these small systems are usually oligohaline or mesohaline and lack any horizontal or vertical temperature stratification. Overall, salinity, turbidity, water depth and area appear to be the most distinct physico-chemical parameters that separate micro-estuaries from micro-outlets. The former type of system is generally larger and has more frequent connections to the sea, a higher salinity and turbidity, and is deeper than the latter. However, variables such as water temperature, pH and dissolved oxygen appear to be very similar across both system types (Magoro 2018).

Due to their shallow nature and high water transparency, both micro-estuaries and micro-outlets have a healthy phytoplankton and micro-phytobenthos community. This is especially the case during the closed mouth phase but everything changes when these systems are flushed out following catchment flooding (Figures 154 and 155). In general the results from the Eastern Cape micro-systems study showed that micro-algal communities are diverse in both micro-estuaries and micro-outlets (Dalu et al. 2018), and

function in a manner similar to that in TOCEs. However, when compared to POEs, these small systems have lower phytoplankton stocks per unit volume but benthic micro- and macro-algae have the ability to develop bloom conditions during summer due to nutrient enrichment from natural sources (Human et al. 2018).

Zooplankton assemblages in Eastern Cape micro-systems were generally influenced by factors such as phytoplankton biomass, salinity, dissolved oxygen and turbidity (Magoro 2018). Micro-estuaries exhibited a greater variety of zooplankton species, as well as higher abundances, than micro-outlets. Zooplankton assemblages in the latter systems were mainly characterized by freshwater species, while those in the micro-estuaries were characterized by a combination of both freshwater and estuary-associated taxa, with the latter being marginally dominant. There was also a marked decrease in zooplankton abundance and diversity across the study systems following winter flooding, with visible recovery of the stocks only occurring during spring and summer (Magoro 2018).

The macrozoobenthic assemblages in the micro-estuaries are usually different from those in the micro-outlets. Both water column (e.g. salinity) and benthic (e.g. sedimentary organic matter) parameters appeared responsible for structuring macro-invertebrate assemblages in the micro-systems. Overall, however, these systems generally have low macro-invertebrate densities and diversity when compared to TOCEs and POEs in the region. The micro-systems also have lower sedimentary organic matter and benthic microalgal concentrations when compared to TOCEs, all of which contributes to a more depauperate zoobenthos in these small systems (Magoro 2018).





**Figure 154.** A downstream view of the lower portion of the Mtendwe Micro-estuary showing the lack of suitable fish habitat during the open mouth phase (Photo: Alan Whitfield).



**Figure 155.** An upstream view of the lower portion of the Mtendwe Micro-estuary showing the lack of suitable fish habitat during the open mouth phase (Photo: Alan Whitfield).

Overall, fish assemblages in Eastern Cape micro-estuaries were dominated by *Pseudomyxus capensis*, *Oreochromis mossambicus* and *Glossogobius callidus* (Magoro 2018). In general, micro-estuary fish assemblages were more diverse and had much higher abundances than those in micro-outlets. If present, *P. capensis* and other Mugilidae were the only fish taxa present in micro-outlets, and then in very low numbers. Estuarine spawners were represented by *Gilchristella aestuaria*, *Glossogobius callidus*, *Atherina breviceps*, *Caffrogobius gilchristi* and *Psammogobius knysnaensis* in micro-estuaries but were absent from the micro-outlets (Magoro 2018). Furthermore, marine fish species in all micro-systems appeared to be represented by only 0+ individuals, with a distinct absence of 1+ and 2+ age classes. This indicates that micro-systems are unable to fulfill the nursery requirements of estuary-associated

marine fish species and are also of limited value to resident estuarine species.

The above findings suggest that micro-outlets do not act as potential estuarine environments for fishes, a conclusion that is supported by the almost complete absence of anuran tadpoles (*Xenopus laevis*) in micro-estuaries but an abundance of these frogs in certain micro-outlets where fish were absent (Magoro 2018). Predation by fish on the eggs and tadpole life stages, and the possible aversion by adult *X. laevis* to spawn in water bodies containing fish populations, is probably a major reason for this observed ecological pattern. In addition, based on the low overall fish densities in micro-estuaries when compared to nearby TOCEs, it can be concluded that micro-systems as a whole do not contribute significantly to the ecology of estuary-associated fishes on the subcontinent.

#### 4.3 TEMPORARILY OPEN / CLOSED ESTUARIES

Although limited ichthyological information is available on most subtropical TOCEs (Begg 1984a, 1984b), five systems (Tongati, Mdloti, Mhlanga, Damba and Zotsha) on the KwaZulu-Natal coast have been well studied (Blaber et al. 1984, Whitfield 1980b, Harrison & Whitfield 1995). Similarly, among small warm-temperate estuaries on the subcontinent, only the East and West Kleinemonde and Kleinmond systems have received detailed ichthyological surveys (Blaber 1973a, Bennett 1989, Cowley & Whitfield 2001a) but coastal sector reviews (Harrison 1999b, James & Harrison 2008, 2009, 2010a, 2010b, 2011, 2016) have synthesized much information on the fish in TOCEs from this region. In the cool-temperate region, the Diep was the first system to be studied from an ichthyological perspective (Millard & Scott 1954) but comprehensive surveys have also been undertaken by Harrison (1997a, 1997b, 1998, 1999a).

In temporarily closed KwaZulu-Natal estuaries the cichlid *Oreochromis mossambicus* is the dominant freshwater species. *Gilchristella aestuaria* is usually the most abundant estuarine species, with *Ambassis ambassis* and *Glossogobius callidus* also reaching high densities in certain

systems (Begg 1984a, Harrison & Whitfield 1995). The dominant estuary-associated marine fishes include *Rhabdosargus holubi*, *Moolgarda cunnesius*, and *Pseudomyxus capensis*. The dominance of mugilids in terms of fish numbers and biomass in small subtropical estuaries has also been noted (Whitfield 1980b, Blaber et al. 1984).

A similar community structure to that described above exists in warm-temperate systems along the southeast and southwest coasts (Bennett 1989, James et al. 2007a). *Oreochromis mossambicus* represents the only freshwater fish component in most temporarily closed estuaries and has been introduced to systems south of the Riet. The abundant estuarine species in this biogeographic region are *Gilchristella aestuaria*, and *Atherina breviceps*. Although mugilids, especially *Chelon richardsonii*, *Mugil cephalus* and *Chelon dumerili* still comprise a large component of the estuary-associated marine fishes, the sparids *Rhabdosargus holubi* and *Lithognathus lithognathus* are of increasing importance, with *R. holubi* usually dominant (Blaber 1973a).

In cool-temperate estuaries the diversity declines further, with no indigenous freshwater fishes present (James et al. 2007a). Although





**Figure 156.** The Mhlanga Estuary in KwaZulu-Natal during the temporarily closed (a) and open (b) mouth phases (Photos: Alan Whitfield).

the major estuarine residents are similar to those found in warm-temperate estuaries (e.g. *Gilchristella aestuaria*), some of the common warm-temperate marine fishes (e.g. *Rhabdosargus holubi*) are either rare or absent. The marine group in small west coast systems is usually dominated by the endemic *Chelon richardsonii* (Millard & Scott 1954).

Intermittent estuaries are those temporarily closed systems which lose their estuarine characteristics, usually by evaporation of all surface water, for considerable periods each year. A range of intermittent estuaries are found in the arid Northern Cape and these systems, when they contain water, may act as temporary refuges for small populations of mainly mugilids (Bickerton 1981, Harrison 1998).

Marine stragglers (predominantly stenohaline taxa) are not dependent on estuaries and these fishes do not contribute significantly to the ichthyofauna of small systems on the subcontinent. Probable reasons include the minimal tidal exchange with the sea, frequent mouth closure and relatively low salinities, thus reducing the potential for the above group of fishes to utilise this estuary type. Harrison & Whitfield (1995) found that marine stragglers comprised 0.2-0.3% of the fish fauna in the Mhlanga and Zotsha systems, and were absent from the Damba Estuary. A similar situation pertains to temporarily open/closed estuaries in the Eastern Cape where marine stragglers were absent from this type of system (Dundas 1994).

Temporarily open/closed estuaries in KwaZulu-Natal are dominated at different periods by different assemblages of fishes. This changing pattern is linked to the spawning and migration patterns of the various species as well as the hydrological regime of each estuary. During the winter, these systems are normally closed off from the sea (Figure 154a), with relatively high food resource and habitat availability (Whitfield 1980b). Freshwater and estuarine species mainly inhabit the upper reaches of these systems, while marine species occur predominantly in the middle and lower reaches (Whitfield 1980a).

When these estuaries open after the spring/summer rains, subadult estuary-associated marine species migrate back to the sea and 0+ marine

juveniles begin recruiting into the systems. Spring is also the peak breeding period of resident estuarine and freshwater species, resulting in an increase in the contribution of these fishes to the overall ichthyofauna. When temporarily closed estuaries open (Figure 156b), the water level declines considerably, concentrating fishes in the lower reaches of these perched systems.

The prolonged spawning and recruitment of 0+ juveniles of estuary-associated marine species increases the proportion of these fishes present in the estuaries during summer. In autumn the systems usually close for the dry winter period, water levels rise and the available food resources and habitat increase. This allows the redistribution of freshwater and estuarine species upstream, leaving the marine species to again dominate the lower and middle reaches (Harrison & Whitfield 1995).

Mouth condition appears to be a major determinant of species diversity in small estuaries. As expected, higher numbers and biomasses of marine fish taxa were captured in estuaries with more frequent mouth openings (Harrison & Whitfield 1995). On average, the Damba Estuary remained closed the longest and it had the lowest number of marine fish species when compared to the Mhlanga and Zotsha estuaries. The Zotsha Estuary remained open the longest and, of the three systems, had the highest marine fish richness.

Although estuarine and freshwater taxa were well represented in all three estuaries, only the Zotsha and Mhlanga estuaries had diverse marine fish assemblages. The species composition of these latter two systems also exhibited the greatest similarity when compared to pairings with the Damba Estuary. The similarity between two fish communities is not only a function of the number of common and unique taxa, but also of the amount of each species present. A quantitative similarity measure (Ellenberg's index), which can use either fish numbers or biomass, revealed that the ichthyofaunal assemblages of the Mhlanga and Zotsha systems had a similarity greater than 95% (Harrison & Whitfield 1995). Comparative pairings between the fish communities of the Mhlanga/Damba and Zotsha/Damba still gave values above 80% for both numerical and biomass

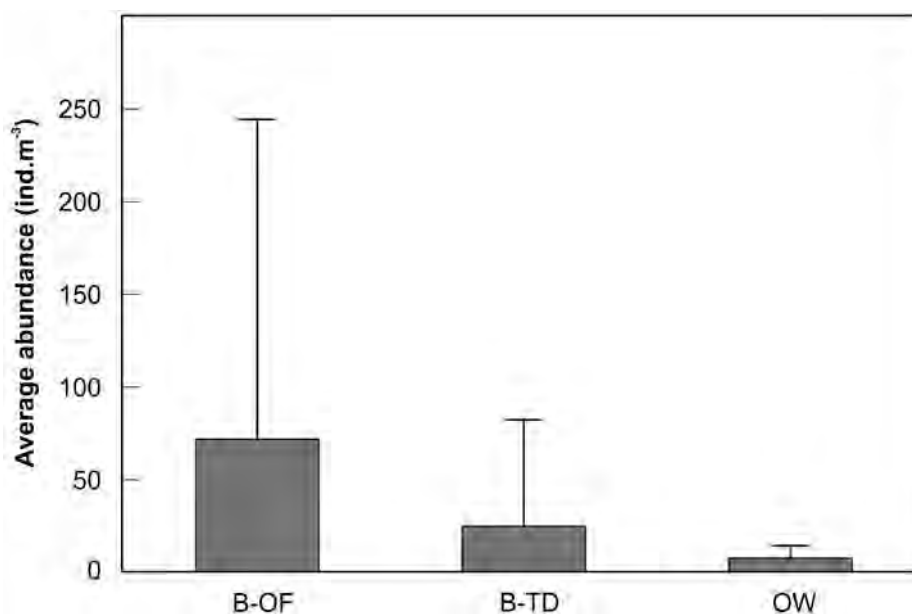
analyses. This indicates that temporarily open/closed estuaries on the KwaZulu-Natal coast, despite the changes in fish composition brought about by different magnitudes and periods of marine connection, have similarly structured fish assemblages.

In the warm-temperate region, results from gill and seine net catches in the Seekoei and Kabeljous estuaries revealed that the top 10 fish taxa were similar for both systems (Dundas 1994). The above analyses suggest that only a relatively short open mouth phase during the peak marine fish recruitment period is necessary to 'saturate' an estuary with a wide variety of postlarval marine fish. This view is supported by Tweddle & Froneman (2017) who found that maximal recruitment into the Mpekweni Estuary occurred during the outflow phase (i.e. immediately after mouth breaching) and declined during the subsequent tidal phase (Figure 157). As expected, the lowest relative recruitment was recorded during marine overwash events when postlarval fish risk everything by using wave transport that may (or may not) enter the estuary during very high tides or storm events (Bell et al. 2001, Cowley et al. 2001).

In contrast to permanently open estuaries where marine larvae and postlarvae are usually

well represented in ichthyoplankton catches (Melville-Smith & Baird 1980, Strydom 2015), temporarily closed systems have very low numbers of this guild. The ichthyoplankton of temporarily closed Eastern and Western Cape estuaries is overwhelmingly dominated by estuarine spawners (Strydom et al. 2003, Montoya-Maya 2009), especially the clupeid *Gilchristella aestuaria*. In the subtropical Mhlanga Estuary, *G. aestuaria* larvae also dominated the ichthyoplankton during the closed phase.

Although available information tends to support Begg (1984a) in his assessment of the importance of estuarine mouth state in structuring fish communities, his conclusions regarding the marine nursery value of temporarily open/closed estuaries do not appear to be accurate. Begg's data showed that permanently open estuaries were dominated by migrant marine species but that temporarily closed systems were dominated by resident estuarine and freshwater taxa. These findings led him to conclude that temporarily closed estuaries on the KwaZulu-Natal coast did not serve a major nursery function for estuary-associated marine fishes. However, sampling in his study was confined to a 1 m beam trawl which tended to under sample mugilids and other marine species. Harrison & Whitfield (1995), using



**Figure 157.** Average abundance (individuals per m<sup>3</sup>) of juvenile fish recruiting into the Mpekweni Estuary during three different estuarine phases; the outflow phase following berm breaching (B-OF), tidal phase (B-TD) and marine overwash phase when the mouth was closed (OW) (after Tweddle & Froneman 2017).

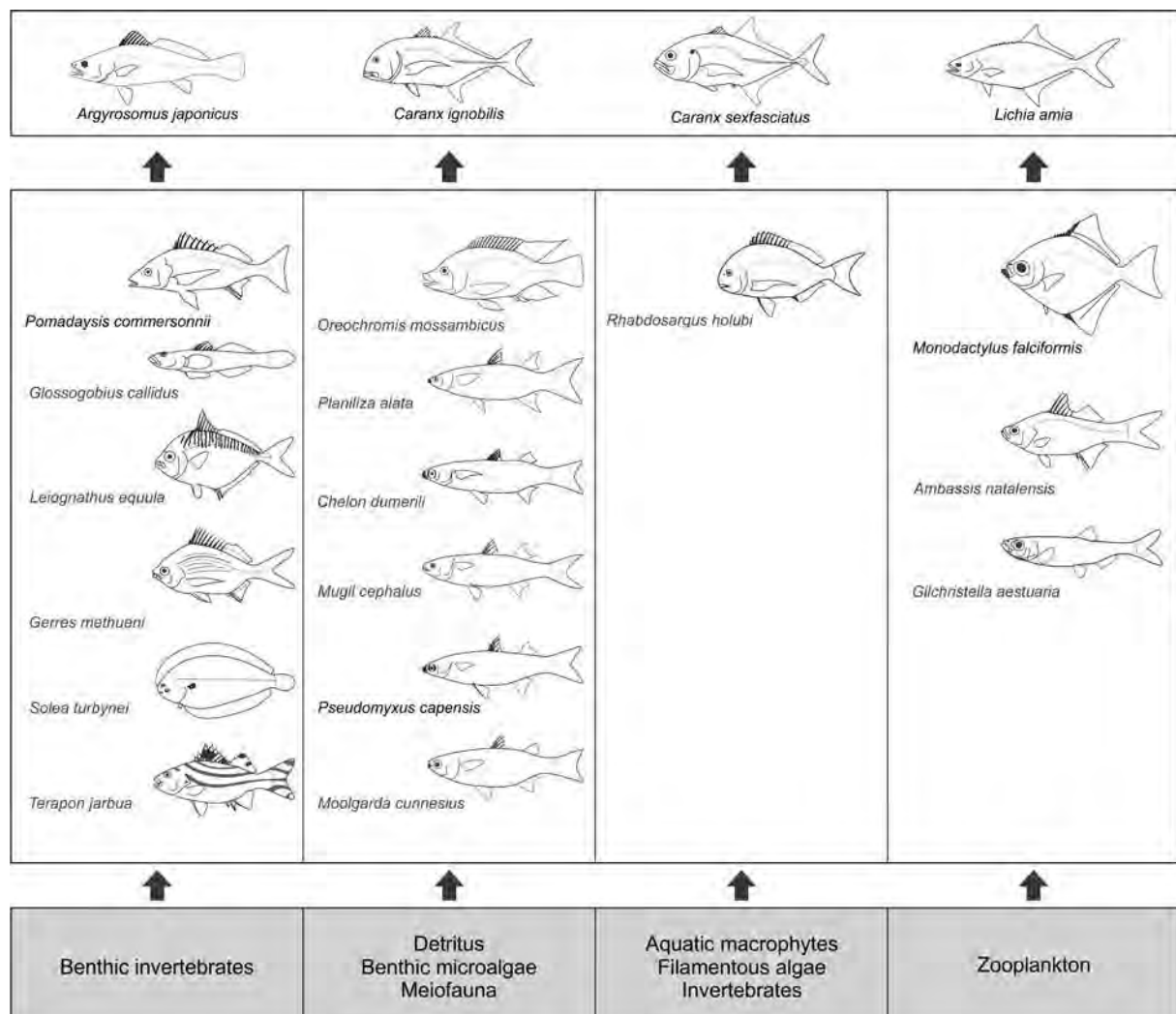


four types of sampling gear, have shown that a 1 m beam trawl gives the poorest representation of fish assemblages in TOCEs.

The distribution of the majority of fishes in the Mhlanga Estuary was closely associated with that of their dominant food, except for the mugilids where sediment particle sizes influenced fish composition in an area (Whitfield 1980a). Zoobenthos feeders such as *Pomadasyss commersonnii*, *Leiognathus equula* and *Gerres methueni* were most common in the lower reaches of the estuary where invertebrate stocks were highest. The detritivorous *Oreochromis mossambicus* was found to be most abundant in the upper reaches where benthic floc was most readily available. The mugilid *Planiliza alata* was concentrated in the lower reaches, *Moolgarda cunnesius* in the middle reaches

and *Pseudomyxus capensis* in the upper reaches. Zooplanktivorous species such as *Gilchristella aestuaria* showed no zonation pattern, thus reflecting the relatively even distribution of zooplankton throughout the estuary.

The trophic structure of the Mhlanga fish community was similar to that of the available food resources (Figure 158, Whitfield 1980b). These resources attained maximum biomass during the closed phase of the estuary (Figure 154a), possibly due to the relative stability of the physical environment together with increased water volume, surface area and habitat availability, e.g. zooplankton stocks were an order of magnitude higher during the winter closed phase when compared to the summer open phase. A similar peak in zooplankton and zoobenthos was recorded



**Figure 158.** Simplified trophic structure of the dominant fish species in the Mhlanga Estuary (information from Whitfield 1980b, Harrison & Whitfield 1995).

during winter in the Mdloti Estuary when the mouth was closed (Blaber et al. 1984) and peaks in zooplankton density and biomass have also been recorded in other South African TOCEs during the closed phase (Ortega-Cisneros et al. 2014). The inundation of supratidal estuarine habitats may play an important role in supporting a higher fish biomass, especially when such areas contain highly productive reed or sedge environments (Adams et al. 1999).

The relatively high numerical contribution of estuarine fish species in the Mhlunga system during the spring of 1990 and 1991 was attributed by Harrison & Whitfield (1995) to the successful reproduction of *Gilchristella aestuaria* during the winter closed phase. When temporarily closed estuaries are breached (Figure 154b), the available habitat and food resources are drastically reduced due to the loss of plankton, prolonged exposure of the benthos, and the effect of floodwater scouring on accumulated benthic floc (Whitfield 1980b, Blaber et al. 1984). Competition among fishes in the shallow estuary channel, both for suitable habitat and food, increases during this tidal phase (Harrison & Whitfield 1995) which is fortunately of limited duration.

The ichthyofauna of temporarily closed estuaries is less diverse than permanently open estuaries, but the importance of the former systems in supplementing estuarine-dependent marine fish stocks should not be underestimated, particularly due to the more frequent occurrence of

TOCEs along the eastern and southern coasts when compared to other estuarine types. Seine and gill net catch per unit effort data quoted by Dundas (1994) suggests that temporarily closed and permanently open estuaries possess similar standing stocks of fishes. This is probably because of the high densities of estuarine resident species such as *Gilchristella aestuaria* and *Glossogobius callidus* in TOCEs and the stable and productive environment provided for such taxa during the closed phase. Rapid growth rates and the ability of residents to breed within a single year will also boost fish production within such systems.

The frequency of occurrence of TOCEs around the South African coastline varies considerably. In the  $\pm 900$  km cool-temperate region there are only 14 TOCEs (mean = 1.5 per 100 km of coast). However, the frequency of occurrence of these systems increases considerably in the larger warm-temperate region where there are 88 TOCEs over the  $\pm 1\ 100$  km stretch of coast (mean = 8.0 per 100 km). The occurrence of such systems increases further in the subtropical zone where 100 TOCEs occur over a relatively shorter stretch of coastline ( $\pm 800$  km), giving an average estuary density of 12.5 per 100 km. By providing an almost continuous sequence of sheltered estuarine environments in the warm-temperate and subtropical regions, and a more intermittent sequence in the cool-temperate region, millions of marine and estuarine fishes are able to make use of these vital nursery areas.

#### 4.4 PERMANENTLY OPEN ESTUARIES AND RIVER MOUTHS

Limited ichthyofaunal information is available from permanently open systems in the KwaZulu-Natal portion of the subtropical coastline (Hill 1966, Begg 1984a, 1984b). In contrast, several detailed studies have been undertaken on these systems in both the subtropical and warm-temperate regions of the Eastern Cape (e.g. Beckley 1984a, Marais 1981, Plumstead et al. 1985, 1989a, 1989b, 1991), as well as from warm and cool-temperate regions of the Western Cape (e.g. Bennett 1994, Harrison 1997a). Reviews of the ichthyofauna from cool and warm-temperate regions are also available (Harrison 1997a, 1997b,

1998, 1999a, 1999b, James & Harrison 2008, 2009, 2010a, 2010b, 2011, 2016).

In permanently open subtropical estuaries, *Oreochromis mossambicus* is the only freshwater species which is regularly found in these systems. *Gilchristella aestuaria* is usually the most abundant estuarine species. The dominant marine fishes include species such as *Acanthopagrus vagus*, *Argyrosomus japonicus*, *Caranx sexfasciatus*, *Hilsa kelee*, *Leiognathus equula*, *Chelon dumerili*, *Monodactylus falciformis*, *Mugil cephalus*, *Planiliza macrolepis*, *Pomadasy commersonnii*, *Pseudomyxus capensis*, *Rhabdosargus holubi*,

*Rhabdosargus sarba*, *Solea turbynei*, *Terapon jarbua* and *Osteomugil robustus*.

A similar community structure exists in warm-temperate systems along both the southeast and southwest coasts, with *Oreochromis mossambicus* still representing the freshwater component. The most abundant estuarine species in this biogeographic region are *Atherina breviceps* and *Gilchristella aestuaria*. Although mugilids, especially *Chelon dumerili* and *Chelon richardsonii* tend to dominate the marine fish component, species such as *Argyrosomus japonicus*, *Chelon tricuspidens*, *Galeichthys feliceps*, *Heteromycteris capensis*, *Lichia amia*, *Lithognathus lithognathus*, *Monodactylus falciformis*, *Mugil cephalus*, *Pomadasyss commersonnii*, *Pseudomyxus capensis*, *Rhabdosargus holubi* and *Solea turbynei* are also sometimes common.

In cool-temperate west coast estuaries the biodiversity declines even further, with indigenous freshwater fish species seldom present. Although the majority of estuarine residents (e.g. *Atherina breviceps* and *Gilchristella aestuaria*) are similar to those found in warm-temperate estuaries, some of the common warm-temperate estuarine-dependent marine fishes (e.g. *Chelon dumerili*, *Pseudomyxus capensis* and *Rhabdosargus holubi*) are either rare or absent from west coast systems. The marine group in open west coast estuaries is overwhelmingly dominated by *Chelon richardsonii*, with *Lichia amia*, *Mugil cephalus*, *Lithognathus lithognathus*, *Pomatomus saltatrix*, *Solea turbynei* and *Rhabdosargus globiceps* occurring in smaller numbers.

Marine stragglers are often recorded in permanently open estuaries, particularly in the lower reaches of these systems. In subtropical estuaries these are usually warm water species, whereas in warm-temperate systems more cosmopolitan taxa are often represented. The lesser guitarfish *Acroteriobatus annulatus* is known to enter both warm-temperate and cool-temperate estuaries, especially when upwelling occurs along the coast.

Permanently open estuaries tend to be dominated at different periods by changing assemblages of fishes. This is linked to the spawning and migration patterns of the various species as well as the hydrological regime of each estuary. During

spring and summer, large numbers of 0+ marine juveniles enter these systems which, by virtue of the permanently open mouth, allows nursery access by the full range of potential species from a particular coastal region. However, the well-developed mouth also permits estuarine entry by a wide size range of piscivorous fishes, including large *Elops machnata*, *Argyrosomus japonicus* and *Lichia amia* that prey on the resident marine and estuarine fish species (Marais 1984).

The magnitude of juvenile fish recruitment into permanently open Eastern Cape estuaries is related to the longitudinal salinity gradient and therefore the amount of river water entering these systems (Whitfield 1994a). Those estuaries with a poorly developed longitudinal salinity gradient have a relatively low fish abundance when compared to systems with a well-developed gradient. However, it is probable that riverine and estuarine based olfactory cues entering the marine environment, and not salinity gradients or reduced salinities *per se*, stimulate immigration of these euryhaline fishes into estuaries (Strydom & Whitfield 2000). Although fish abundance is usually higher in those systems with a perennial water supply, permanently open systems with little or no freshwater input often have a higher species diversity because of the sheltered marine conditions prevailing in the lower reaches (Whitfield et al. 1994).

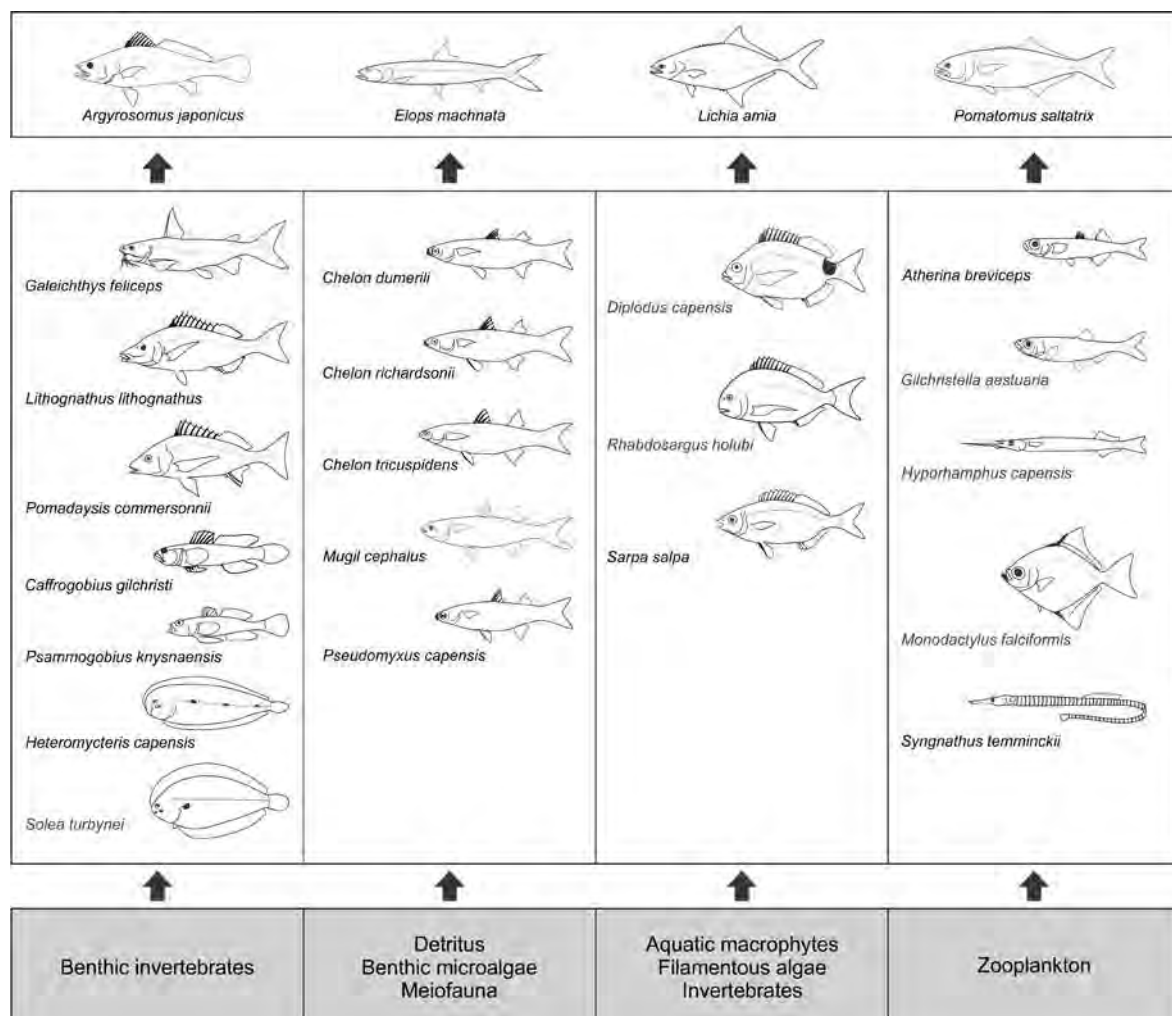
The food and feeding ecology of fishes in permanently open Eastern Cape estuaries has been studied by several authors (e.g. Masson & Marais 1975, Marais 1984). Systems that are deprived of an adequate river flow have a food web which is centred around autochthonous detrital sources, usually derived from intertidal saltmarshes and submerged aquatic macrophytes (Heymans & Baird 1995, Paterson & Whitfield 1997). In contrast, those estuaries that receive regular pulses of fresh water usually have a phytoplankton dominated trophic structure (Wooldridge & Bailey 1982, Allanson & Read 1995) that supports large zooplanktivorous fish populations. Intermediate estuaries such as the Swartkops have considerable energy flows along the macrophytic, benthic microalgal and phytoplanktonic pathways (Baird 1988), and the fish faunas of these systems reflect

this range of energy sources with a wide spectrum of well represented feeding guilds (Figure 159).

Although a moderate supply of fresh water appears to be essential for the maintenance of high primary and secondary productivity within permanently open estuaries (Figure 160), fish research in the Great Fish Estuary (Ter Morshuizen et al. 1996a) has indicated that large riverine inputs in the form of floods into these systems can temporarily depress fish abundance by forcing marine and estuarine species towards the sea. These influences can take the form of large-scale fish mortalities caused by excessive silt loads carried by flood waters (Whitfield & Paterson 1995). Marais (1982) also identified the key role of river flooding on the food resources of fishes in permanently open estuaries. These resources may be either temporarily enhanced

in the case of broad floodplain type estuaries (e.g. Swartkops) where deposition is widespread, or depleted in the case of channel like estuaries (e.g. Sundays) where scouring is the dominant process and recovery of fish stocks is likely to take many months.

A river mouth differs from a permanently open estuary (POE) in that processes within the former system are riverine dominated. Indeed river volumes are sometimes so great that fresh-water species may even be found outside the mouth of this type of system (Day 1981c). Since most rivers of southern Africa support relatively few species (Skelton 2001), and most marine taxa are incapable of surviving prolonged periods in fresh water, this invariably leads to river mouths which are depleted both in terms of fish biodiversity and abundance.



**Figure 159.** Simplified trophic structure of the dominant fish species in the Swartkops Estuary (information from Masson & Marais 1975, Marais & Baird 1980a, Beckley 1983, Marais 1984, Baird 1988, Baird et al. 1991).

In the cool-temperate Orange River mouth region, <10 fish species were recorded in earlier published surveys, with freshwater taxa predominating during high river flow and marine species during low flow conditions (Day 1981c, Harrison 1998). Along the warm-temperate Tsitsikamma coast, a number of river mouths have been sampled by Harrison et al. (1996), with most of these small systems also having <10 fish species (James & Harrison 2009).

Although the subtropical ichthyofauna of the Thukela River mouth type estuary is more diverse, there are considerably fewer species than in the nearby permanently open Mlalazi Estuary (Hill 1966). Similarly, despite the Mfolozi River mouth being the only estuarine system available adjacent to the closed St Lucia Estuary, it was dominated by only a few fish species (Vivier & Cyrus 2009, Vivier et al. 2010), possibly linked to low zoobenthic food resources (Ngqulana et al. 2010, Nhleko et al. 2012).

Indications are that estuarine phytoplankton

and invertebrate food resources in river mouths are severely limited by the widely fluctuating salinities and frequent freshwater flooding (Brown 1958). In addition, residence time of water within these systems is generally too short for phytoplankton stocks to develop, and benthic invertebrates have to cope with major sediment movements associated with river flow characteristics. The scarcity of large piscivorous fishes from southern African river mouths is perhaps indicative of an unpredictable food supply in the form of either migrant or resident fish species and also high water turbidity that make finding prey difficult.

From the above it is apparent that river mouth estuaries are extremely demanding biotic and abiotic environments that are not conducive to permanent colonization by large numbers of marine, estuarine or even freshwater fish species. River mouths are, however, used opportunistically by estuary-associated fishes when suitable salinity regimes and other conditions (e.g. aquatic food resources) prevail.



**Figure 160.** The key ingredients for an abundant and diverse fish fauna in permanently open estuaries include a perennial river, large tidal prism, wide variety of aquatic habitats, and a mouth that is stabilized on one side by a rocky shore (Photo: Alan Whitfield).



#### 4.5 ESTUARINE LAKES AND BAYS

There are very few estuarine lakes (3% of southern African systems) or estuarine bays (1% of systems) along the coast. Although neither type of estuary is currently present in the cool-temperate region, Verlorenvlei and Langebaan Lagoon come close to qualifying as an estuarine lake and bay respectively. Despite the fact these ecosystems are poorly represented on the subcontinent, in terms of surface area they are dominant, with Lake St Lucia alone comprising >50% of available estuarine habitat in the region.

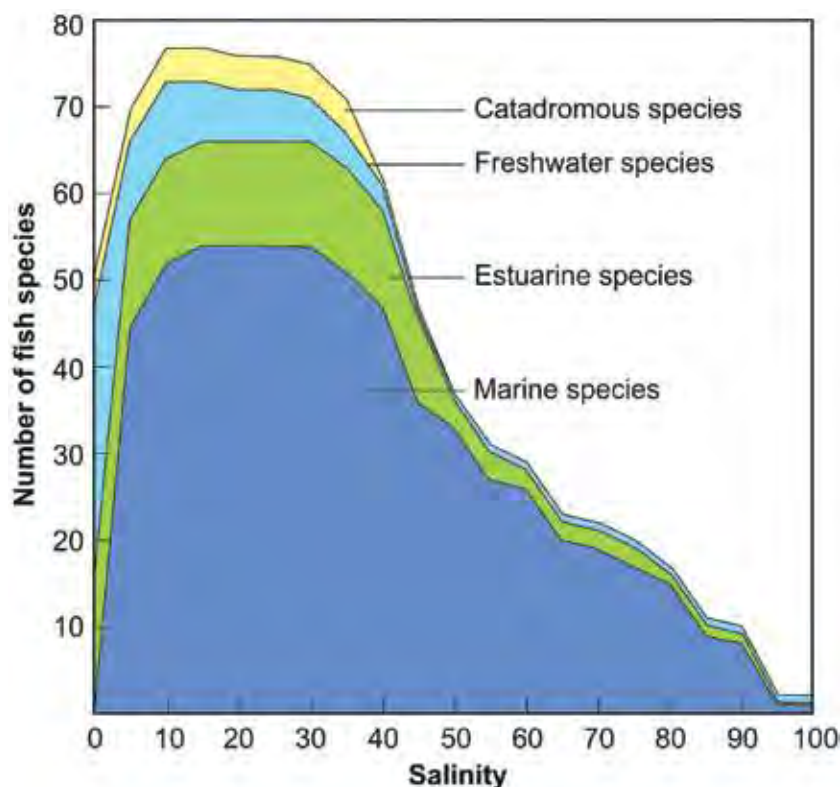
Two major estuarine lake systems occur in the subtropical zone, viz. St Lucia and Kosi, with the former being a very well-studied system in terms of the need to understand the influence of large-scale salinity fluctuations on the flora and fauna of the lake (Day et al. 1954, Whitfield et al. 2006).

Although more than 100 fish species have been recorded from both the St Lucia and Kosi systems (Whitfield 1980d), fewer than 30 of these species are abundant within the large lake

compartments of these estuaries. In Lake St Lucia the dominant taxa vary according to both salinity and season, with *Argyrosomus japonicus*, *Elops machnata*, *Gilchristella aestuaria*, *Glossogobius callidus*, *Hilsa kelee*, *Hyporhamphus capensis*, *Johnius dorsalis*, *Leiognathus equula*, *Chelon dumerili*, *Mugil cephalus*, *Oreochromis mossambicus*, *Planiliza macrolepis*, *Platycephalus indicus*, *Pomadasys commersonnii*, *Rhabdosargus holubi*, *Rhabdosargus sarba*, *Solea turbynei*, *Terapon jarbua* and *Thryssa vitrirostris* being numerically dominant.

More than 80% of the recorded taxa in both Lake St Lucia and the Kosi lakes are marine species (Blaber 1978, Mann 1993). The sensitivity of the various fish guilds to both low (oligohaline) and high (hyperhaline) salinity is well illustrated in Figure 161 and shows the dominance of marine taxa over a wide salinity range.

A number of relatively small estuarine lakes occur in the warm-temperate region, the most important of which are the Swartvlei, Wilderness,



**Figure 161.** Species diversity changes of freshwater, catadromous, estuarine and marine fish species in the St Lucia system according to recorded salinity ranges (Whitfield et al. 2012a).

Botrivivlei and Klein systems. All these lakes are dominated by marine fish taxa but estuarine spawners are also well represented (Scott et al. 1952, Bennett et al. 1985, Hall et al. 1987). Species diversity is lower than that recorded in the subtropical systems, with fewer than 40 species recorded in each of the warm-temperate lakes and less than 20 species resident in these systems at any one time. The dominant fish species are usually *Atherina breviceps*, *Caffrogobius gilchristi*, *Chelon dumerili*, *Galeichthys feliceps*, *Gilchristella aestuaria*, *Hyporhamphus capensis*, *Lichia amia*, *Lithognathus lithognathus*, *Chelon richardsonii*, *Mugil cephalus*, *Monodactylus falciformis*, *Oreochromis mossambicus*, *Psammogobius knysnaensis*, *Pseudomyxus capensis* and *Rhabdosargus holubi*.

Studies by Scott et al. (1952), Bennett et al. (1985), Kok & Whitfield (1986), Hall et al. (1987) and Whitfield & Kok (1992) have all emphasized the importance of an open mouth phase to the structuring of fish communities within estuarine lakes. More recent work by Russell (1996) indicates that opening of the estuary mouths for relatively short intervals during peak recruitment periods will ensure the maintenance of healthy fish assemblages within these water bodies.

Estuarine waters in the Kosi system, even during flood conditions, are relatively clear when compared to Lake St Lucia. Consequently, turbid water species such as *Hilsa kelee*, *Johnius dorsalis* and *Thryssa vitrirostris* are absent from the Kosi system and clear water taxa such as *Gerres longirostris*, *Monodactylus argenteus* and *Rhabdosargus sarba* are common. Piscivorous fish taxa that are predominantly visual hunters (e.g. carangids and sphyraenids) are considerably more diverse and abundant in the clear Kosi system (Figures 162 and 163) when compared to Lake St Lucia (Blaber 1982a, Blaber & Cyrus 1983). Conversely the piscivorous *Argyrosomus japonicus*, which is more dependent on its olfactory and other senses when foraging, is abundant in turbid Lake St Lucia but rarely captured in the Kosi system.

The estuarine waters of Swartvlei have low suspensoid levels but are stained by humic substances carried into the lake by inflowing rivers (Allanson & Howard-Williams 1984). Fish

species which are indifferent to water turbidity, as well as those associated with clear or turbid waters, are found within the Swartvlei system. Typical turbid water species such as *Argyrosomus japonicus* and *Galeichthys feliceps* avoid the clear littoral zone of the lake during daylight hours but are frequently captured in these areas at night (Whitfield 1993). In contrast, predominantly clear water taxa such as *Monodactylus falciformis* and *Chelon dumerili* are common in shelf waters during the day and night.

Both the subtropical Lake Mpungwini (Kosi system) and warm-temperate Swartvlei have been shown to be meromictic (Begg 1980, Allanson & Howard-Williams 1984). This condition results in the hypolimnion in both lakes being unavailable to fishes because of depleted oxygen levels and presence of hydrogen sulphide. In addition, zoobenthic and zooplanktonic prey organisms are confined to the littoral zone and epilimnion for as long as these conditions persist. Erosion of the hypolimnion in Swartvlei does occur under certain conditions (Allanson & Howard-Williams 1984) and colonization of the lake basin by both invertebrates and fishes is rapid during such interludes.

A feature that is shared by both the subtropical Kosi and the warm-temperate Wilderness lakes system is segmentation, a process that results in each compartment having very different physico-chemical characteristics, particularly in terms of salinity regime. Thus in the Kosi system, Lake Amanzimnyama is fresh, Lake Nhlanga oligohaline, Lake Mpungwini normally mesohaline and Lake Makhawulani usually polyhaline. These differential salinity regimes and associated food resources have a major influence on the fish species composition in the various lake compartments (Blaber 1978, Blaber & Cyrus 1981).

In addition to salinity changes, the degree of constriction between lake compartments influences the ability of juvenile marine fish to recruit into particular sections, thus determining the ichthyological composition. Hall et al. (1987) have shown that the depth of interconnecting channels in the Wilderness system had a major influence on fish community structure within the component lakes. A marked decline in marine fish



**Figure 162.** Aerial view of the mouth region of the Kosi lakes system. By virtue of the combination of a permanent connection with the sea, series of interconnected lakes with different salinity regimes, great diversity in habitats, and strategic locality in the northern part of the subtropical region, it has the highest fish richness (numbers of species) of any South African estuary.



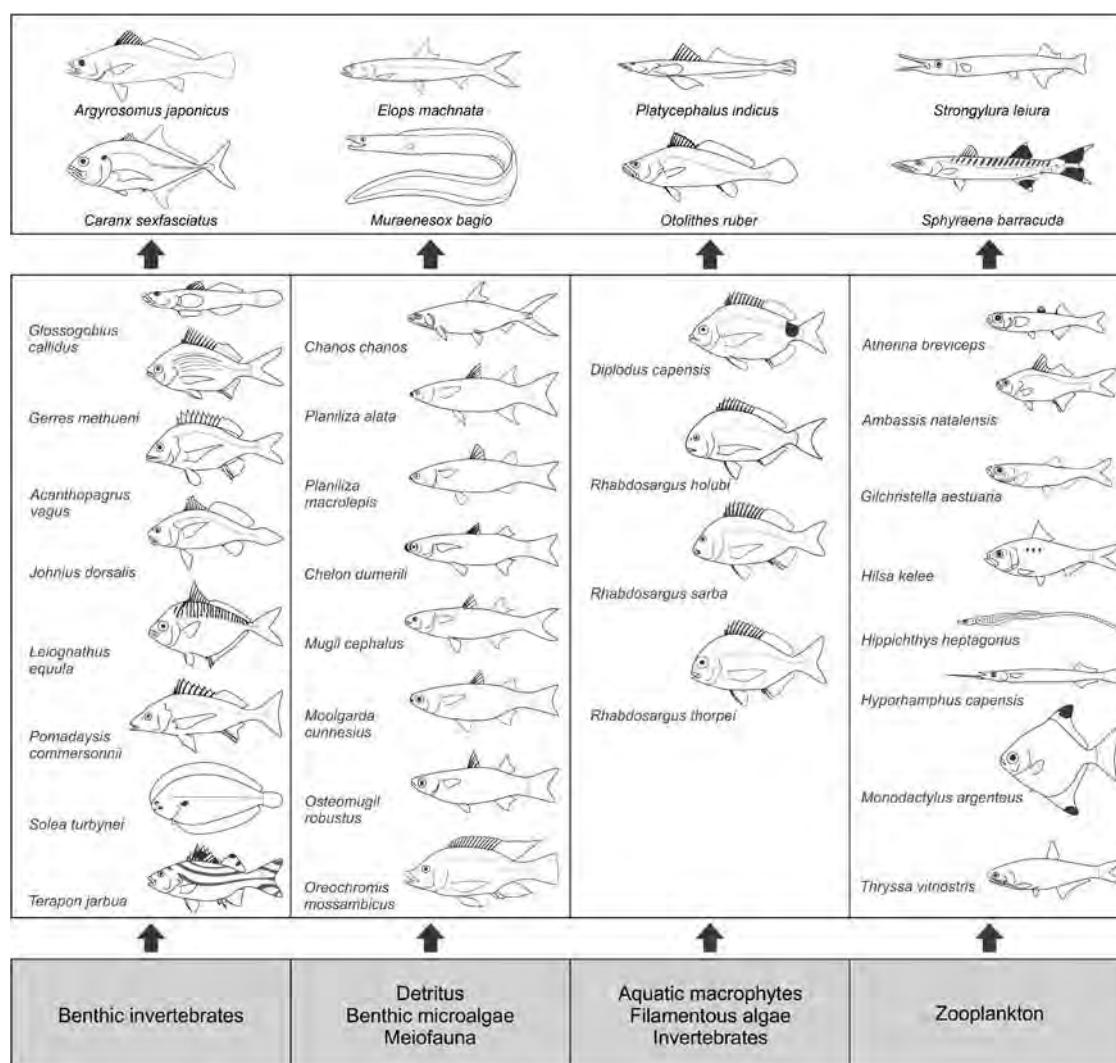
**Figure 163.** View of a sandy littoral and reed bed in the Kosi system. Note the clear water and numerous sandprawn holes in the subtidal area (Photo: Alan Whitfield).

species diversity between Eilandvlei and Langvlei occurred due to the tenuous connection between these two lakes. A similar situation probably pertains to Lagoa Poelala in southern Mozambique due its 75 km long connection to the sea via narrow lakes and interconnecting channels. The salinity of Lagoa Poelala in 1973 was 8 but only two marine fish species were recorded in the system (Hill et al. 1975). In contrast, Blaber (1978) has shown that marine species dominate the Kosi system by virtue of the well-developed permanent connections between the lake compartments.

The Mgobozeleni lake system is an example of an estuary in transition. The lake itself has an elevated chloride level and feeds a stream that enters a small estuary (Bruton & Appleton 1975). This lake appears to be in the final stages of losing

its marine link. The only marine fish species found in the lake are *Pseudomyxus capensis* and *Megalops cyprinoides*, both of which will disappear from the system once the tenuous estuarine connection is finally broken.

The feeding ecology of fishes in southern African estuarine lakes has been well studied, particularly in the large St Lucia system. Aquatic plants provide the primary sources of food but there is an absence of phytoplanktivorous fish species from the system. However, *Gilchristella aestuaria*, *Thryssa vitrirostris* and *Hilsa kelee* (Figure 164) are abundant and all feed extensively on zooplankton (Blaber 1979), with *G. aestuaria* and *T. vitrirostris* being preyed upon in large numbers by the dominant piscivorous fishes *Argyrosomus japonicus* and *Elops machnata*



**Figure 164.** Trophic grouping of some of the dominant fish species in Lake St Lucia during 1975 (modified from Whitfield 1980e, Blaber 1982b).





**Figure 165.** A foraging great egret *Ardea alba* wading in the shallows of Lake St Lucia (Photo: Alan Whitfield).



**Figure 166.** Part of a flock of white pelicans, *Pelecanus onocrotalus*, in the St Lucia Narrows where they used to congregate to prey on adult *Mugil cephalus* participating in the annual spawning migration (Photo: Alan Whitfield).



(Whitfield & Blaber 1978a). Indeed, it was found that the numbers of these pelagic piscivores in an area was related to the densities of the above zooplanktivorous fishes. Zooplankton is also a major food item of *Hyporhamphus capensis* in the lake and this species was, in turn, intensively preyed upon by *Strongylura leiura* (Whitfield & Blaber 1978a).

Despite sometimes extensive beds of *Zostera capensis*, *Ruppia spiralis* and *Stuckenia pectinata* in Lake St Lucia, aquatic macrophytes are not directly utilized by fishes. Although *Rhabdosargus holubi* consumes the above plants, it digests only the epiphytic growth from the leaf blades (Blaber 1974b). The omnivorous *Rhabdosargus sarba* also feeds extensively on aquatic plants in the lake, especially filamentous algae (Blaber 1984). The absence of an exclusively herbivorous fish species from Lake St Lucia may be due to the cyclical disappearance of aquatic macrophytes during hypersaline conditions. However, the organic debris from decomposing plants in the form of detritus is permanently available to the aquatic fauna. Indeed, the cyclical destruction of aquatic macrophytes in the lake during high salinity regimes may increase the amount of detritus available, and is therefore beneficial to detritivores in the system (Hutchison 1977).

Although the detritus pool may be temporarily increased by the mass decomposition of plant beds, the long-term effects are probably negative because growing macrophytes are absent during high salinity conditions. Detritivorous fishes (Figure 164) are abundant in Lake St Lucia, with the Mugilidae represented by eleven species. In addition, the detritivorous cichlid *Oreochromis mossambicus* maintains high standing stocks and dietary flexibility during both oligohaline and hypersaline conditions (Carrasco et al. 2012).

The diets of the above mugilid and cichlid species overlap in terms of detrital consumption, but competition for microflora is reduced through different habitat preferences and feeding mechanisms (Whitfield & Blaber 1978b). Differential sand particle size selection by mugilids (Blaber 1976), which also influences the distribution of individual species within the lake (Whitfield and Blaber 1978e), has been postulated as a possible

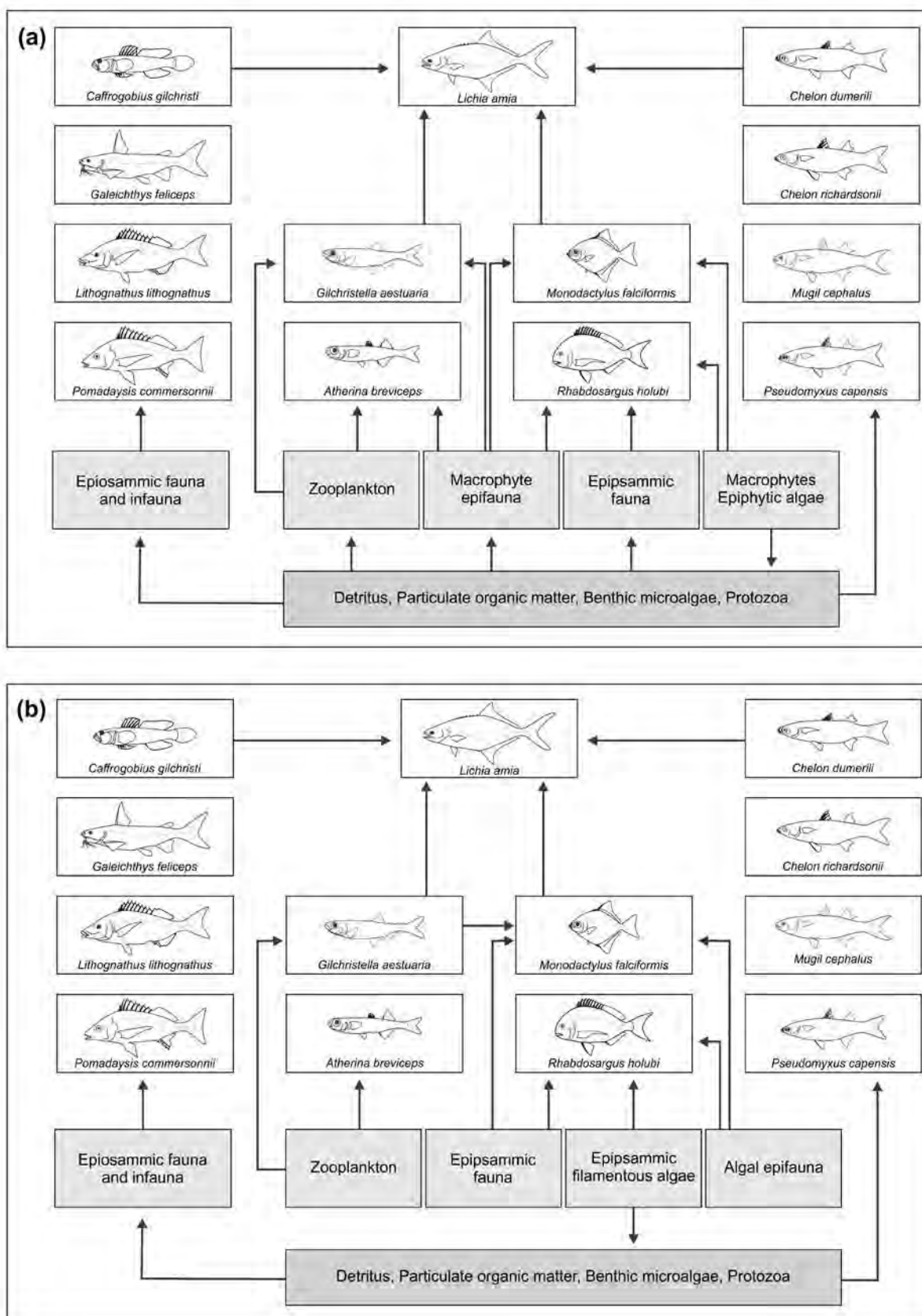
mechanism to assist in the partial segregation of abundant microalgal and meiofaunal food resources.

Resource segregation also occurs in terms of fish size, with juvenile mugilids 10-50 mm SL occurring in water <5 cm deep and those 50-100 mm SL frequenting areas <100 cm deep (Whitfield 1980a). However, by frequenting the lake margins these juvenile fishes become vulnerable to avifauna foraging in this zone (Figures 165 & 166, Whitfield & Blaber 1978d, 1979a, 1979b). The piscivorous birds appear to concentrate fishing activities in those parts of the lake where small fish are most abundant because the number of birds in an area was found to be positively correlated to the number of fish captured during seine net operations (Whitfield 1978).

The feeding habits of predatory fishes and birds at St Lucia vary both seasonally and according to location in different parts of the lake. *Argyrosomus japonicus* prey extensively on penaeid prawns in summer but not in winter (Whitfield & Blaber 1978a). Similarly, the white pelican *Pelecanus onocrotalus* changes its feeding pattern according to the availability of fish in different parts of the lake and time of the year. Between April and June the pelicans prey intensively on *Mugil cephalus* shoals migrating through the estuary towards the sea (Figure 163b); between June and October they feed on freshwater fishes from the evaporating Phongolo pans; and from October onwards they revert to preying on fishes in the lake (Whitfield & Blaber 1979b).

Sudden fish kills during oligohaline conditions (Blaber & Whitfield 1976) also result in temporary changes in the energy flow pattern at St Lucia. During June 1976 a wide variety of piscivorous birds were recorded feeding on dead or dying fish at the lake, some of which were not part of the individual bird species' normal diet. An extensive fish kill in June 1987, and subsequent shortage of food, was given as the reason for the failure of the Caspian tern breeding attempt that year (Cyrus & McLean 1994, 1996).

During high salinity conditions, the decline in fish stocks has a major impact on both the numbers and breeding success of piscivorous birds. Hypersaline conditions in 1968 resulted



**Figure 167.** Simplified food web in Swartvlei during (a) the macrophyte phase, and (b) the macrophyte senescent phase (modified from Whitfield 1982).

in low invertebrate and fish populations (van der Elst et al. 1976) and led to depleted bird populations and an absence of breeding activity by most piscivorous bird species (Forrest 1969). Of the approximately 1 000 white pelican chicks hatched in 1968, only four reached maturity. Similar breeding failures by other piscivorous bird species (e.g. herons) were also recorded.

A wide variety of zoobenthic feeding fishes also occur in Lake St Lucia (Figure 164). Although there is considerable overlap in the diets of benthic foraging fishes, there is also a degree of resource partitioning. During 1981 and 1982 approximately 80% of the diet of *Solea turbynei* comprised siphon tips of the bivalve *Solen cylindraceus*, with limited amounts of the amphipod *Grandidierella lignorum* and tanaid *Apseudes digitalis* also being consumed (Cyrus 1988b). In contrast the haemulid *Pomadasys commersonnii* preyed intensively on *A. digitalis* with few *G. lignorum* in its diet. The sparid *Rhabdosargus sarba* was almost the complete opposite of *P. commersonnii*, showing a definite selection for *G. lignorum* and with a minimal contribution by *A. digitalis* (Blaber 1984).

Another invertebrate species which features in the diet of many zoobenthic predators from Lake St Lucia is the crab *Hymenosoma orbiculare*. Approximately 50% of the diet of *Johnius dorsalis* and 19% of items consumed by *Terapon jarbua* comprised *H. orbiculare* (Whitfield & Blaber 1978a). However, the dominant food of *T. jarbua* was fish scales removed from living fishes (Whitfield & Blaber 1978c).

Epibenthic invertebrates such as penaeid prawns are an important component of the diet of several fish predators in Lake St Lucia. Certain piscivorous species such as *Argyrosomus japonicus* and *Elops machnata* feed extensively on these prawns during the summer months when this prey component is particularly abundant (Joubert & Davies 1966). However, the highly significant correlation ( $r=0.68$ ,  $p<0.001$ ) between the composition of prey fish species in the lake and prey fish species in the diet of the piscivores (Whitfield & Blaber 1978a) suggests that these predators are primarily fish consumers, with prawns acting as a supplementary food source.

Turbidity can affect food availability to individual fish species, with both factors sometimes interacting to influence fish distribution within Lake St Lucia. Although the juveniles of some marine fish species have been shown to have a distribution which corresponds with both turbidity preferences and food availability, others were distributed according to turbidity and not their preferred foods (Cyrus & Blaber 1987a).

Episodic flood events cause widespread scouring and deposition of new sediments (Forbes & Cyrus 1992). In the St Lucia system these disturbances have short-term negative consequences for small benthic fish taxa such as *Croilia mossambica* (Martin et al. 1992). These authors also suggested that the elevated turbidity gradients in the sea off the St Lucia Estuary mouth may have resulted in the increased recruitment densities recorded for most marine migrant species in the months following a cyclone flood event. In addition, this cyclone provided increased amounts of nutrients for phytoplankton development, which in turn had beneficial effects on the stocks of both zooplankton and filter feeding fishes such as *Gilchristella aestuaria* (Martin et al. 1992).

Studies on the ichthyofauna of Swartvlei indicate a similar trophic guild composition to that recorded at Lake St Lucia (Figures 164 and 167). Prior to 1979 Swartvlei was characterized by extensive *Stuckenia pectinata* and charophyte beds (Howard Williams & Liptrot 1980). These plants, together with associated epiphytic algae and periphyton, accounted for 74% of the total aquatic primary production (Howard-Williams & Allanson 1981). In the spring of 1979 this community underwent a senescence that was to last more than a decade, and resulted in a 60% decline in primary production (Taylor 1983), a 74% slump in littoral invertebrate biomass (Davies 1982) and a 54% decline in the abundance of macrophyte associated fish species (Whitfield 1984).

These changes did not lead to the disappearance of fish species from the lake littoral but did result in alterations to the energy flow pathways (Figure 167) and a restructuring of the Swartvlei fish community (Whitfield 1986a). In particular there was an increase in the abundance and

biomass of all the mugilid species and decline in the dominant vegetation associated taxa such as *Monodactylus falciformis* and *Rhabdosargus holubi*. Invertebrate consumption by the latter two fish species declined from  $33 \text{ mg m}^{-2} \text{ d}^{-1}$  during the *Stuckenia* canopy phase to  $8 \text{ mg m}^{-2} \text{ d}^{-1}$  during the senescent phase (Whitfield 1984). It is noteworthy that *M. falciformis* began preying on the clupeid *G. aestuaria* as a result of the collapse of its dominant food, the isopod *Exosphaeroma hylecoetes*.

The decline in fish abundance associated with the senescence of submerged macrophyte beds and their associated food resources also impacts on piscivorous bird biomass. A recent study by Russell & Randall (2017) recorded a 99% decline in macrophyte standing crop in Swartvlei from  $892 \text{ g m}^{-2}$  in 2007 to  $3 \text{ g m}^{-2}$  in 2011 due to the littoral salinity rising above the level tolerated by *Stuckenia pectinata*. This decline in submerged plants was mirrored by a 67% decline in piscivorous bird biomass from 304 kg to 99 kg over the same period.

A detailed study on food consumption by six resident estuarine species in Botrivierlei revealed that this group of fishes had an annual invertebrate intake of approximately  $6 \text{ g m}^{-2}$  or an average of  $16 \text{ mg m}^{-2} \text{ d}^{-1}$  (Bennett & Branch 1990). These species consumed 17% of invertebrate secondary production during the closed mouth phase, indicating that under these conditions food was not in short supply. However, when the estuary mouth opened and extensive areas of the littoral zone were exposed, a major decline in invertebrate biomass occurred (de Decker 1987) and these fish then consumed almost 90% of secondary production. If one considers that some of the immigrant marine fish species in the Bot Estuary also prey extensively on aquatic invertebrates, it is likely that competition for food will be intense during the open mouth phase.

Estuarine bays are also large systems but differ from estuarine lakes in that the connection with the marine environment is very well developed. Although Durban Bay is essentially a marine dominated tidal system, it actually supports a biota that is similar to other KwaZulu-Natal estuaries. Day & Morgans (1956) recorded 181 fish species

from this system but many of those taxa were only represented by a few marine stragglers. Other scientists have also noted that the stenohaline marine fish component in Durban Bay was well represented when compared to other estuaries in the region but the system as a whole was dominated by typical euryhaline marine and estuarine species (Wallace 1975a).

In a study by Beckley et al. (1995), 53 fish species were recorded from a graving dock in the upper reaches of Durban Bay. Although typical estuary-associated fish species dominated catches in the graving dock, marine stragglers were also recorded. A similar situation pertains to the warm-temperate Knysna system where estuary-associated marine species predominated but typical marine taxa were also recorded (Whitfield & Kok 1992). During the summer months, marine species such as *Diplodus cervinus*, *Lithognathus mor-myrus*, *Pomadasys olivaceus* and *Spondyllosoma emarginatum* were relatively common in the lower reaches of this estuary.

The presence of marine stragglers in bays ensures that a greater variety of fish species occupy estuarine bays than any other type of estuary in a particular region. This view is reinforced by Whitfield et al. (1989) who found that the fish species richness index (R) within estuarine bay eelgrass beds was always higher than index values from the same habitat in other estuaries.

The stable salinity conditions that prevail for much of the year in estuarine bays results in several marine fish species, which usually breed at sea, spawning within these environments. Although the eggs of these fish are probably carried into the marine environment by the strong ebb tidal currents, the larvae are likely to be retained in coastal waters in the vicinity of the bays and therefore recruit into these systems at the postlarval stage of development.

Both subtropical and warm-temperate estuarine bays are dominated by 0+ juvenile marine fishes which utilize these systems as nursery areas (Whitfield & Kok 1992). The sheltered waters and rich food resources within these embayments (Day et al. 1952) are not the only attraction. Richards Bay and Durban Bay also provide the only large estuarine intertidal mud and sand

flats along the KwaZulu-Natal coast (Cyrus & Forbes 1996) and Knysna has extensive intertidal areas in the lower reaches (Day et al. 1952). Whereas saltmarshes and eelgrass beds are important nursery areas for fishes in the Knysna littoral, mangroves provide the equivalent habitat in the Durban and Richards Bay systems. Indeed,

Cyrus & Forbes (1996) have suggested that the estuarine nursery function is directly coupled with the mangrove component of the latter bays. Unfortunately, extensive mangrove areas in both Durban and Richards Bay, and saltmarshes at Knysna, have already been destroyed or are under threat (Figure 168).



**Figure 168.** The only patch of once extensive mangals present in Durban Bay. Although it has been declared a natural heritage site, its long-term protection is by no means secure due to planned expansion of ship loading facilities (Photo: Alan Whitfield).

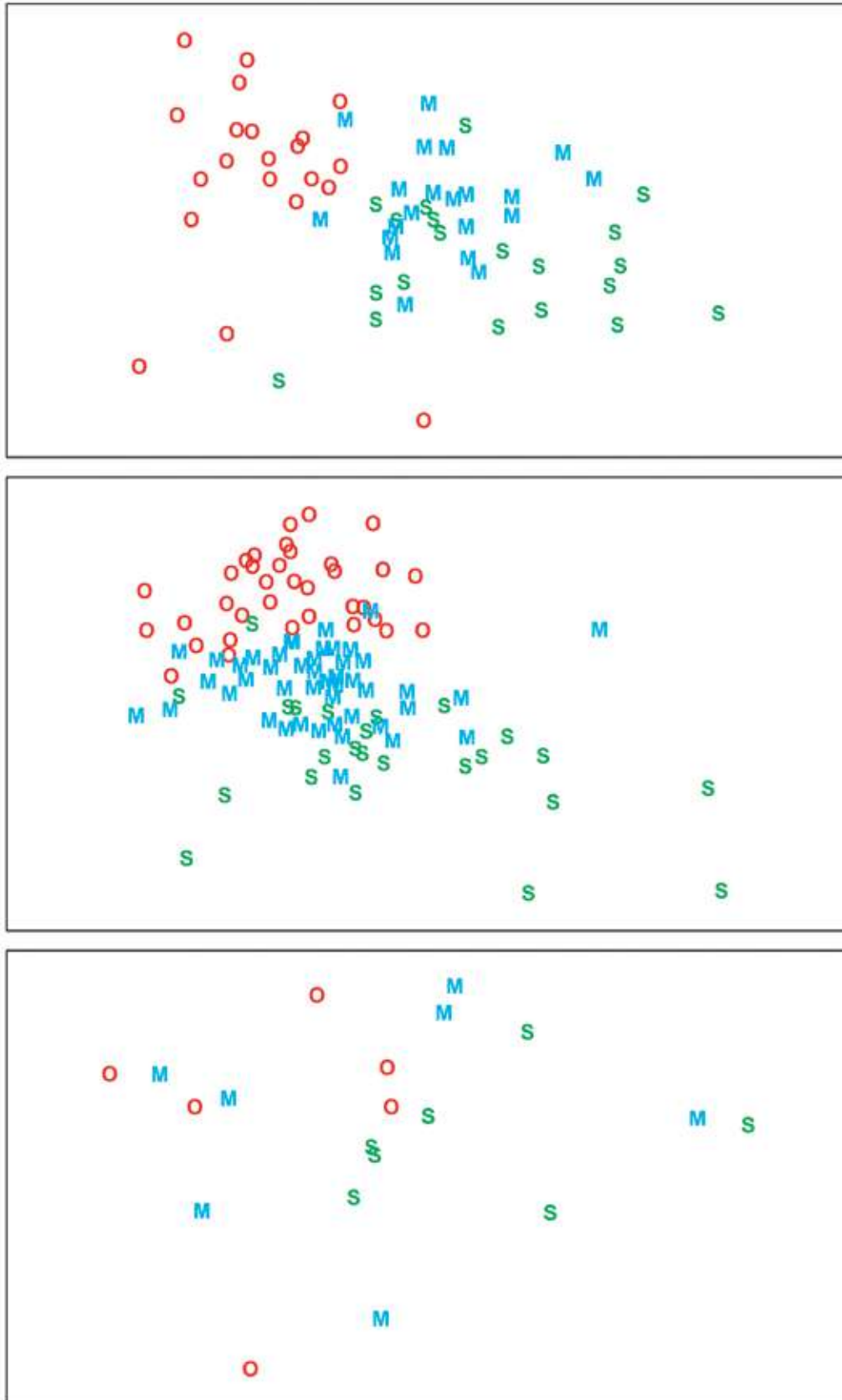
#### 4.6 ESTUARY TYPES AND ICHTHYOFAUNAL STRUCTURE

Southern African microtidal (mean tidal range  $<2$  m) estuaries differ considerably from the macrotidal (mean tidal range  $>4$  m) systems in other parts of the world. Although these microtidal estuaries are similar to those found in certain parts of Australia, the wave climate along the east and west coasts of the two continents is very different. Thus, the southern African coastline is subject to heavy wave action when compared to extensive areas in Western Australia or Queensland which are protected by offshore reefs. As a consequence, the only sheltered areas available to fishes along

the southern African neritic zone are estuaries, whereas relatively calm areas are often available in the marine environment in other parts of the world. It is therefore not surprising to find that the juveniles of most marine fish species found in temperate Western Australian estuaries are also abundant in the sea, whereas in temperate southern African waters there a number species whose juveniles are mainly confined to estuaries (Potter et al. 1990).

Based upon the information reviewed in this chapter it becomes apparent that biogeography





**Figure 169.** Ordination of fish assemblages in (a) subtropical, (b) warm-temperate and (c) cool-temperate estuaries based on estuary type (O = open, M = medium closed, S= small closed) and fish presence/absence data (after Harrison & Whitfield 2006c).

and estuary mouth condition are the two major factors influencing ichthyofaunal structure and functioning. Even in those tidal inlets that are permanently open, there are considerable differences in mouth depth, width, substratum, etc., all of which influence fish movements into and out of an estuary. At the other end of the spectrum are temporarily closed estuaries where fish migrations are severely constrained for extended periods, thus limiting the number and variety of fish taxa found in such systems.

A study by Schlacher & Wooldridge (1996b) has shown that calculated indices of southern African fish biodiversity are markedly higher in estuaries having a permanent connection to the sea than those which have a temporarily closed phase. This trend of declining biodiversity with increasing isolation from the marine environment is reflected in the low number of fish species present in coastal lakes that have lost their estuarine links with the sea (Whitfield et al. 2017b).

In both the subtropical and warm-temperate regions, the MDS ordinations suggested that the fish communities of predominantly open estuaries were distinct from both moderate to large closed estuaries and small closed estuaries (Figure 169). This pattern was also supported by an ANOSIM test where predominantly open estuaries were shown to be significantly different from closed systems (Harrison & Whitfield 2006c).

Cool-temperate estuaries, did not exhibit any clear pattern (Figure 169). The ANOSIM test also revealed that there was no significant difference between predominantly open and moderate to large closed estuaries; the fish communities of closed small estuaries, however, did appear to be significantly different to predominantly open estuaries (Harrison & Whitfield 2006c). Estuaries in the cool-temperate region have a relatively low species diversity and are typically dominated by a few abundant species, e.g. *Chelon richardsonii* and *Chelon tricuspidens*. Altogether 27 species have been recorded from cool-temperate estuaries, with a total of between three and 10 taxa documented per estuary (Harrison 2002). This low species diversity may partially account for the lack of distinctive faunas within each estuary type.

Overall, predominantly open estuaries within each zoogeographic region were characterized by a high species richness in relation to closed systems. Species with high importance values were also among the taxa identified by a SIMPER analysis as those contributing to the similarity within these systems. The SIMPER analysis also identified particular species that typically had high importance values in predominantly open estuaries and also accounted for some of the dissimilarity between these systems and closed estuaries. In the subtropical region these included species such as *Acanthopagrus vagus*, *Ambassis dussumieri*, *Argyrosomus japonicus*, *Caranx ignobilis*, *Caranx sexfasciatus*, *Chelon dumerili*, *Chelon tricuspidens*, *Elops machnata*, *Gerres methueni*, *Hilsa kelee*, *Leiognathus equula*, *Megalops cyprioides*, *Moolgarda cunnesius*, *Crenimugil burchanani*, *Oligolepis acutipennis*, *Oxyurichthys keiensis*, *Planiliza alata*, *Planiliza macrolepis*, *Pomadasys commersonnii*, *Rhabdosargus sarba*, *Solea turbynei*, *Terapon jarbua* and *Thryssa vitrirostris*. Species belonging to this group in the predominantly open warm-temperate estuaries were *Argyrosomus japonicus*, *Caffrogobius gilchristi*, *Chelon dumerili*, *Chelon tricuspidens*, *Clinus superciliosus*, *Diplodus capensis*, *Elops machnata*, *Galeichthys feliceps*, *Hyporhamphus capensis*, *Lichia amia*, *Lithognathus lithognathus*, *Pomadasys commersonnii*, *Pomatomus saltatrix*, *Psammogobius knysnaensis*, *Rhabdosargus globiceps*, *Sarpa salpa*, *Solea turbynei* and *Syngnathus temminckii*. In the cool-temperate region of the subcontinent these species included *Argyrosomus inodorus*, *Caffrogobius nudiceps*, *Galeichthys feliceps* and *Pomatomus saltatrix*.

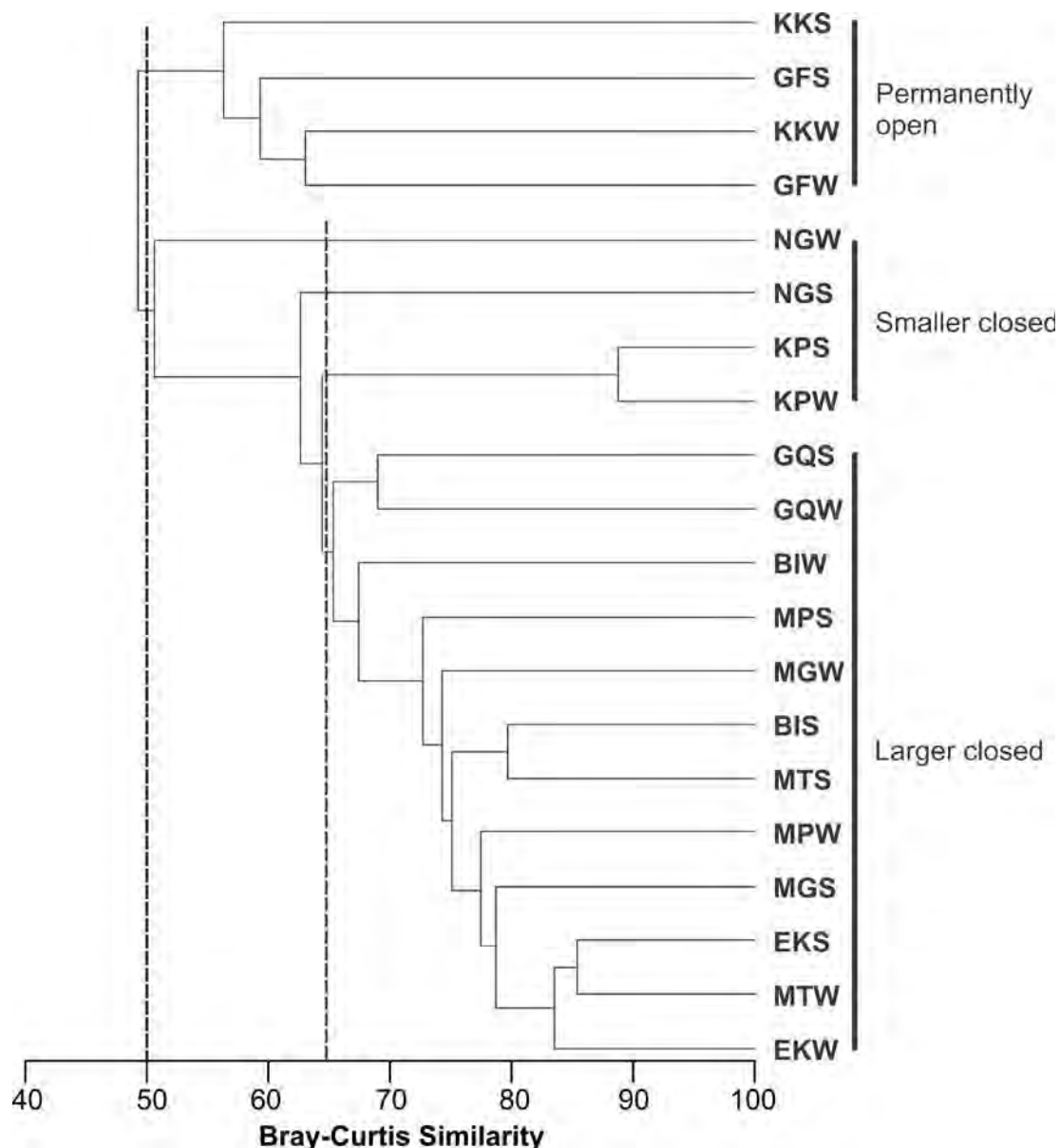
An earlier study of the seine net catches in a range of Eastern Cape Province estuaries (Vorwerk et al. 2003) demonstrated that the greatest difference in fish assemblages occurred between permanently open and temporarily closed systems, with a separation at the 50% similarity level (Figure 170). There was an additional separation of the smaller and larger temporarily closed systems at a 65% similarity level. The spatial arrangement of fish groupings within permanently open, smaller and larger temporarily closed estuaries are evident when plotted graphically as

an MDS ordination (Figure 171). The ordination shows fish assemblages that are similar occupying positions closer to one another, with the communities being distributed according to estuarine size and/or mouth status (Vorwerk et al. 2003).

The composition of Eastern Cape seine net fish assemblages in permanently open systems differed significantly ( $p < 0.001$ ) from those recorded in temporarily open/closed estuaries. In addition, small temporarily closed estuaries were found to have a lower fish species richness and density

than that recorded in larger temporarily closed and permanently open estuaries (Vorwerk et al. 2003).

Bennett (1989) also found that the intermittently open Bot Estuary had a lower species richness and abundance when compared to the permanently open Palmiet Estuary. Similarly, Whitfield & Kok (1992), reported a higher species count in the permanently open Knysna Estuary when compared to the intermittently open Swartvlei Estuary, but abundance of



**Figure 170.** Similarity dendrogram of the seasonal fish assemblage data for selected Eastern Cape estuaries (after Vorwerk et al. 2003). Each sample is represented by a three letter code; the first two letters are an estuary code (BI = Bira, EK = East Kleinemonde, GF = Great Fish, GQ = Gqutywa, KK = Keiskamma, KP = Klein Palmiet, MG = Mgwala, MP = Mpekweni, MT = Mtati, NG = Ngculura) and the third is a season code (S = Summer, W = Winter).

individuals within the two systems was similar.

### Littoral zone and fish composition

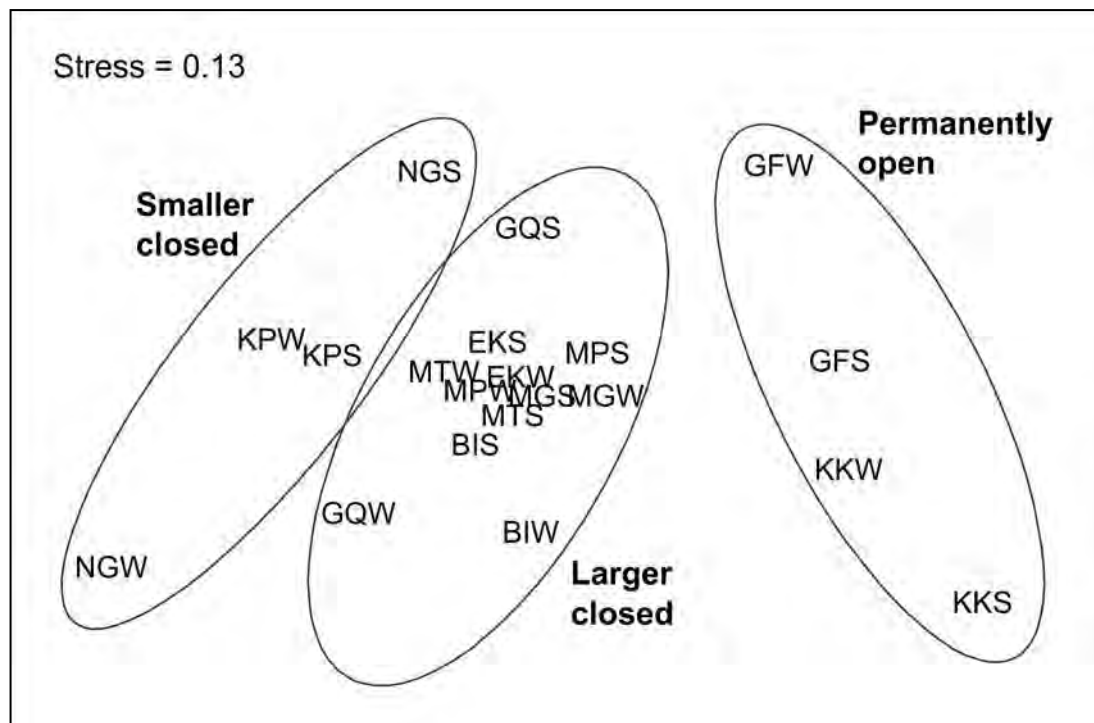
The importance of shallow littoral habitat for fishes is a long standing paradigm of estuarine ecology, particularly in facilitating the nursery role they play for many species. Diel cycles have been linked to the redistribution of fish between habitats and may also influence the movement of various sized fish within the littoral zone of different estuary types.

Fine scale temporal (hourly) movements of four size classes of fish (< 100 mm, 100-300 mm, 301-500 mm and >501 mm total length) onto a shallow (< 0.7 m) littoral zone within the East Kleinemonde Estuary was examined using a dual frequency identification sonar (DIDSON) continuously over 24 h periods (Becker et al. 2011a). Fish in the size classes of 100-300 mm and 301-500 mm were more abundant in the littoral zone during twilight and at night compared to the day, while the largest size class (>501 mm) showed no difference in abundance among these periods

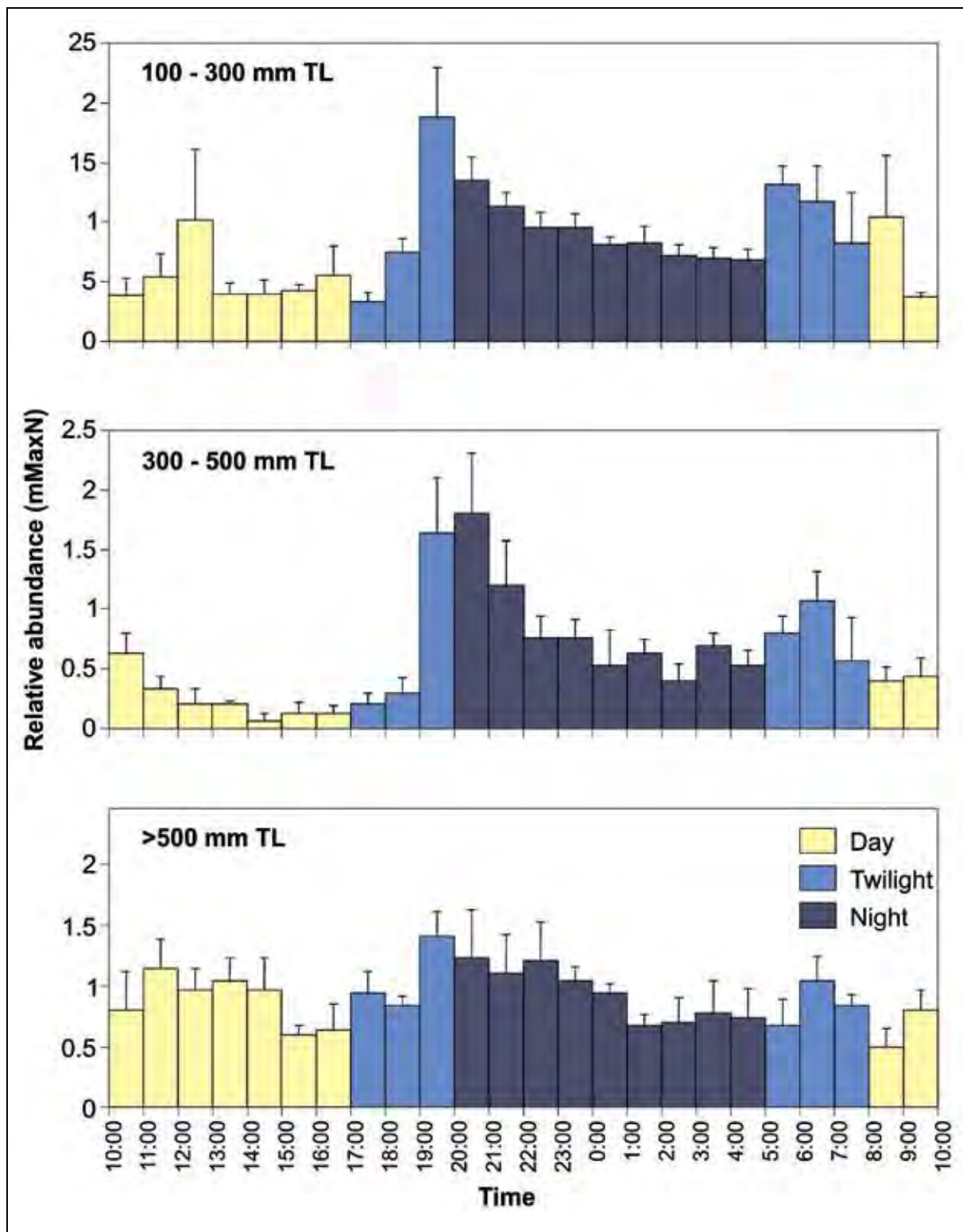
(Figure 172).

The strongest diel patterns were observed within the smallest fish cohort (<100 mm), which were abundant in the littoral zone during the day but never observed in this habitat after dark (Becker et al. 2011a). Daily commuting onto and off the shallow littoral zone by this smallest size class occurred within tight time periods (<45 minutes), and were synchronous with sunrise and sunset respectively. It is hypothesized that these movements are linked to feeding ecology and predator avoidance by small zooplanktivorous fish species. However, very large predatory fish up to 1 m TL were sometimes observed to enter the littoral zone during both the day and night (Becker et al. 2011a).

Overall, the above results support the theory that littoral zone habitats harbour high abundances of small shoaling fish such as *Atherina breviceps* and *Gilchristella aestuaria* during the day and thus provide refuge from large piscivorous predators that are more abundant in deeper channel waters during this period.



**Figure 171.** Multidimensional scaling plot of the estuarine fish assemblage data from selected Eastern Cape estuaries (after Vorwerk et al. 2003). The circled groups indicate estuaries with significantly different communities representing permanently open and small and large temporarily open/closed systems. Each sample is represented by a three letter code the same as that used in Figure 170.



**Figure 172.** Hourly mean abundance ( $mMaxN \pm SE$ ) for each of the three larger size classes within the littoral zone of the East Kleinemonde Estuary. Attention is drawn to the scale differences on the Y-axis for each of the analyzed size classes. Daytime, twilight and night time periods (after Becker et al. 2011a). Note that the mean abundance of the <100 mm TL fish cohort is not represented in this figure due to an inability to individually count members of large shoals of small fishes that moved onto and off the littoral on a diel basis (see text for a more detailed information).



#### 4.7 ESTUARINE VERSUS COASTAL NURSERY AREAS

Much has been written about estuaries being important nursery areas for a wide range of fish species, including those of commercial importance. This is mainly because estuaries appear to be dominated by the juveniles of a range of fish species. Apart from coastal mangrove, seagrass and coral reef habitats, less attention has been focused on the littoral marine environment acting in a similar manner to estuaries (Figures 173 and 174) for different or even overlapping sets of fish assemblages. Nevertheless, the coastal marine environment has been shown to also provide important nursery areas for certain commercially and ecologically important fish species.

A primary aim of this section is to assess the degree to which specific habitats appear to fulfil the nursery function for particular fish species or assemblages, and how these may differ between coastal marine and estuarine environments. Although the mix of species utilizing these very different coastal habitats as nursery areas can be easily described and quantified, the actual drivers that attract these fish taxa to particular nurseries is much more difficult to assess and requires detailed research in the future.

Due to the large amount of published juvenile fish information from a diverse range of littoral habitats, both marine and estuarine, within the Eastern Cape region of South Africa, the fish nursery function of this area is examined in more detail. Particular attention is therefore given to the degree of separation or overlap in habitat use by dominant marine fish species from this coastal zone, with all recognised major habitat types having at least one focused fish study completed and published (Whitfield & Patrick 2015).

##### **What constitutes a nursery area?**

For a habitat to serve as a nursery area for fish it must:

- (a) Be physiologically suitable in terms of chemical and physical features;
- (b) Have connectivity to enable colonisation by larvae and /or early juveniles;
- (c) Provide abundant and suitable food;
- (d) Afford a degree of protection from predators.

##### **Biotic influences and nursery value**

The success of a nursery area for fish species is influenced by at least four major biotic factors, namely a healthy supply of larvae /postlarvae to stock the habitat, abundant food resources that are appropriate for juvenile fishes, a moderate degree of shelter from predation, and limited competition from other species (Beck et al. 2001). If all these factors are positive, then the yield of new recruits on a per-unit-area to adult populations is likely to be high, although other non-biotic drivers will also influence recruitment success.

The supply of marine larvae or postlarvae to littoral nursery areas is likely to be linked to locality and cohort strength in a particular breeding season, as well as factors such as water currents which can vary in both strength and direction over different time scales. Recruitment of marine species into estuarine nursery areas can be challenging during ebb tides when there is a net flow of water from the estuary to the ocean, with current velocities often exceeding larval swimming speeds (Harrison & Cooper 1991). In addition, those marine species recruiting into estuaries are strongly influenced by river flooding which can act as both an attractant for postlarvae to locate estuaries (James et al. 2008a) and a temporary deterrent in terms of immediate occupation of estuarine nursery areas.

Most southern African estuaries close off to the sea for prolonged periods, during which time the only access to these nursery areas by estuary-associated species is via overwash events (Cowley et al. 2001). The fact that fish larvae and postlarvae of certain taxa are prepared to undertake such a risky recruitment strategy is testimony to the value of estuaries as nursery areas for these species.

Shallow nursery areas are assumed to have higher food abundance when compared to deeper adult habitats but this may not always be the case. It is probable that shelter from predation interacts closely with food abundance, with the optimum nursery areas being both rich in food resources and providing low predator mortalities.

A number of studies have shown that estuaries tend to have a lower diversity of species associated with their nursery areas when compared to



**Figure 173.** Typical littoral nursery habitats for fishes in a subtropical southern African estuary, namely mangroves, reeds and submerged aquatic plants (Photo: Alan Whitfield).



**Figure 174.** Littoral marine kelp beds in the cool-temperate region can provide nursery areas for a different set of fish species (Photo: Alan Whitfield).



adjacent marine areas (Unsworth et al. 2009). Other studies have shown that the juvenile fish assemblage found in coastal nursery areas is strongly dependent on individual species choice, with some taxa located in mainly estuarine waters and others preferring more marine salinities (Woodland et al. 2012). However, river flooding can cause a decline in juvenile densities of certain marine fish species using estuarine nursery areas (Ter Morshuizen et al. 1996a).

#### **Abiotic challenges for juvenile fish**

Different coastal nursery areas pose different physiological and hydrodynamic challenges to juvenile fishes. For example, the salinity in most marine surf zones closely approximates that of seawater whereas the salinity in estuarine nurseries has the potential to fluctuate widely, depending on river flow and state of the tide. Therefore estuaries tend to provide shallow sheltered habitats for juvenile fishes in a fluctuating physiological environment whereas marine surf zones usually provide high energy but stable physiological habitats for small

fishes that can withstand turbulent waters (Figure 175).

Another feature of most coastal and estuarine fish nurseries is that they are located in littoral waters which limit the access by large piscivorous fishes at low and sometimes mid-tidal levels (Figure 176, Paterson & Whitfield 2000a). Piscivorous fishes can, however, invade littoral nursery areas at high tide, and especially during nocturnal hours, without increasing their vulnerability to land-based predation by birds or mammals.

A strong abiotic driver having a major impact on estuarine nursery areas is climate. Oceanic and climatic variability have been shown to be very important drivers influencing variation in fish assemblage composition and abundance in estuaries, as well as the growth of juvenile marine fish within these systems. Global warming is also likely to affect the occupation of estuarine nursery areas by both temperate and tropical fish species in southern African estuaries (James et al. 2013) and will also affect their growth within these systems.



**Figure 175.** An illustration of the high energy nature of the southern African coast on a relatively calm day (Photo: Alan Whitfield).

Turbidity can vary widely on both spatial and temporal scales in potential fish nursery areas (Cyrus 1988a). Although the juveniles of many coastal marine species are attracted to shallow waters, of those that make extensive use of estuaries, turbidity has been singled out as an extremely important factor in attracting and providing protection for small fishes in these environments (Blaber & Blaber 1980). This conclusion has been corroborated by the field and laboratory work of Cyrus and Blaber (1987a, 1987b) who determined that very few marine species that used subtropical estuaries in south-eastern Africa as nursery areas, preferred clear water.

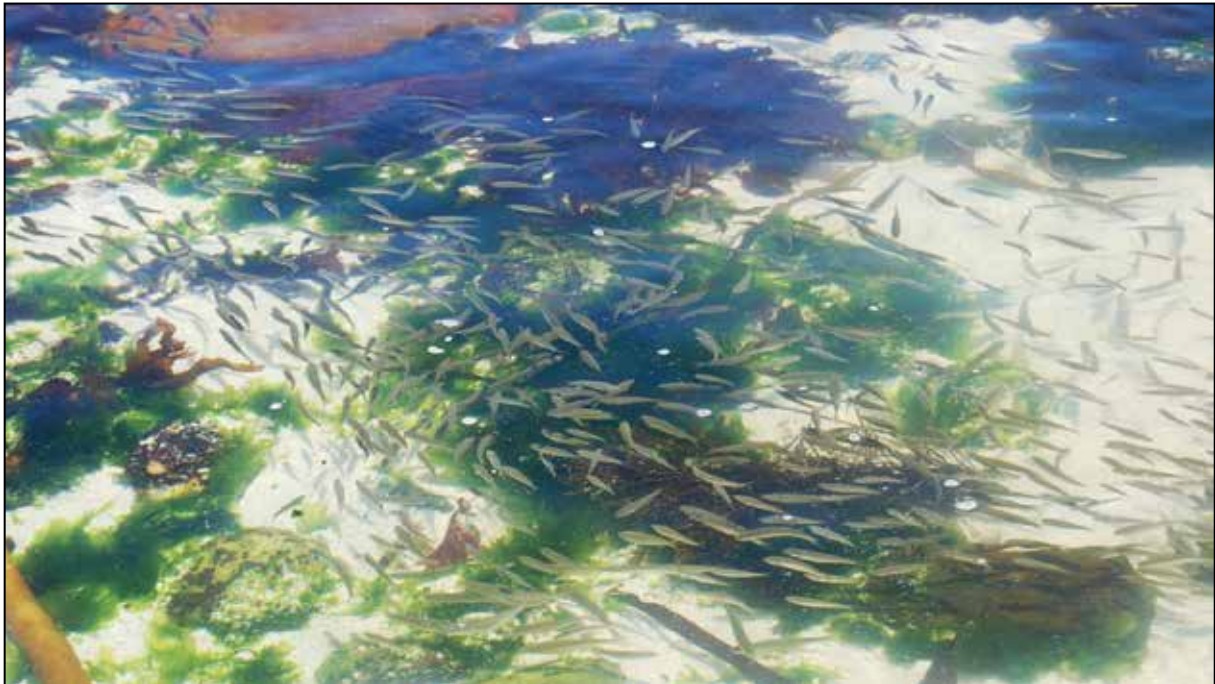
Large coastal marine fishes seldom spawn in the nursery areas that are subsequently occupied by the juveniles of those very same species. Locating and entering these habitats by the post-flexion larvae or early juveniles is an arduous and difficult task that may well be aided by on-shore winds, currents and distinctive olfactory cues emanating from such habitats (James et al. 2008a). The initial coastal habitats that are settled by early juveniles are often a transit area

to the main nursery area for a particular species, e.g. Whitfield (1989c) suggested that most of the postlarvae sampled in the sandy Swartvlei Bay surf zone were using that particular area as an 'interim' nursery prior to entering the nearby Swartvlei Estuary where the final nursery was located.

#### **Specific coastal habitats as nursery areas**

Early papers on estuaries tended to consider the whole estuary as a nursery area, with marine fish moving into estuaries as larvae and early juveniles, growing rapidly and accumulating biomass within these systems, before moving back to the sea. However, later research focused on specific habitats within both estuaries and the coastal zone as potential nursery areas (e.g. Nagelkerken et al. 2000). Seagrass meadows, saltmarshes, mangrove forests, intertidal pools and subtidal rocky reefs have all been identified as performing specific nursery functions for nearshore marine and estuarine fish populations, with some species moving from one habitat type to another with increase in size (Beck et al. 2001, Whitfield 2017).

Coastal habitats serving as fish nursery areas



**Figure 176.** Sheltered marine intertidal rocky and sandy pools can provide important shelter (at low tide) for small fish along parts of the coast (Photo: Alan Whitfield).

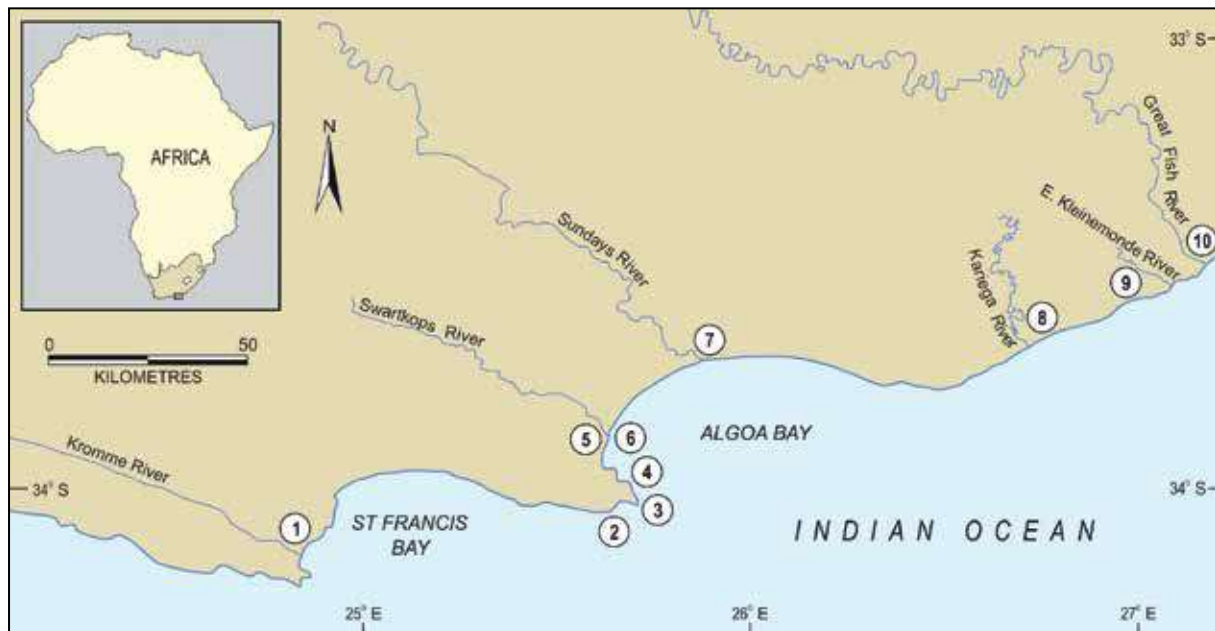
in southern Africa have not received equal research attention. Most studies have focused on juveniles occupying eelgrass beds (e.g. Hanekom & Baird 1984) and, in many instances, these studies compared fish species compositions in vegetated versus non-vegetated habitats (e.g. Beckley 1983, Pollard et al. 2017) in order to confer nursery roles. The attractiveness of eelgrass and other aquatic macrophytes to particular fish species is well established and is based primarily on their provision of both shelter from predators and abundant food resources (Whitfield 2017).

Although mangrove fringes were a particularly important nursery habitat for juvenile fish in the Mhlathuze Estuary, other habitats (eelgrass beds, mudflats and sandbanks) within this system also provided nursery areas for particular fish assemblages (Weerts & Cyrus 2002a). Similarly, the juvenile fishes associated with an intertidal saltmarsh creek in the Kariega Estuary were very different to the juvenile fish assemblage associated with an adjacent eelgrass bed (Paterson & Whitfield 2000b), thus emphasizing the specific nature of nursery areas for different ichthyofaunal components but not negating the dual use of these habitats by certain species.

### Eastern Cape coastal zone case study

Generally, high densities of marine species as juveniles in a particular habitat indicate that such an area is functioning as a nursery (Strydom et al. 2014). It is on this basis that a range of Eastern Cape coastal habitats in both estuaries and the sea (Figure 177) were analysed (e.g. Figures 178 and 179), with particular attention being given to the dominant juvenile marine fish taxa found in each area. Table 21 documents the two primary coastal zone environments that are utilized by juvenile fishes and therefore serve as nursery areas for important /abundant marine fish species.

Despite the fact that marine ecosystems may support a greater diversity of fishes, and cover a much larger area than estuaries, the data highlight the dependence of numerous coastal fishes on estuarine habitats as a primary nursery area. In addition, Table 21 does not include some of the estuarine resident and freshwater fish species that also use estuaries as a nursery area. This combined evidence clearly indicates that, despite the smaller estuarine littoral habitat when compared to the extensive adjacent marine littoral habitats (Figure 180), these former systems are vital nursery areas for many fish species.



**Figure 177.** Localities of Eastern Cape sampling sites shown in Table 20 (after Whitfield & Patrick 2015).

1. Kromme Estuary littoral, 2. Schoenmakerskop subtidal rocky gullies, 3. Cape Recife intertidal rock pools, 4. King's Beach surf zone, 5. Swartkops Estuary littoral, 6. Swartkops mouth marine zone, 7. Sundays Estuary littoral, 8. Kariega Estuary saltmarsh creeks, 9. East Kleinemonde Estuary littoral, 10. Great Fish Estuary littoral.





**Figure 178.** A typical sandy beach surf zone at low tide showing the type of littoral marine habitat available for small fishes (Photo: Alan Whitfield).



**Figure 179.** A typical rocky shore intertidal pool at low tide, indicating potential nursery habitat for juvenile fishes (Photo: Alan Whitfield).



**Figure 180.** The contrast between the high wave energy fish nursery areas off the coast and the more sheltered nursery areas provided by estuaries is clearly illustrated in this picture (Photo: Alan Whitfield).

Table 20 shows the ranking of the five most common marine fish species in different Eastern Cape coastal environments. The sparid *Diplodus capensis* is perhaps the most ubiquitous species and is highly ranked within tidal pools, as well as being common in subtidal gullies (Smale & Buxton 1989), the surf zone (Lasiak 1981) and even estuaries (Beckley 1983). The mugilid *Liza richardsonii* can be equally abundant in both estuaries and the surf zone (Beckley 1983, Lasiak 1984b), thus indicating that this species is also not dependent on particular coastal environments but is capable of utilizing a wide variety of littoral nursery habitats (Figure 180), depending upon availability.

In contrast, juvenile *Rhabdosargus holubi* use southern African estuaries as their primary nursery area (Blaber 1974c) and are usually one of the most abundant marine fish species in these systems, to the extent that this sparid is widely considered to be estuary dependent (Whitfield et al. 2018). Although the juveniles of *R. holubi* are generally rare in the marine environment (Wallace et al. 1984b), they have been recorded in intertidal pools and adjacent marine littoral waters. In contrast, the adults seldom occur in

estuaries and are normally confined to subtidal coastal reefs (Buxton & Kok 1983).

Numerous studies have been undertaken to document the nursery function of coastal habitats for marine fish species around the world. However, most of these studies have focused on particular habitats and have generally been confined to a limited range of fish species associated with specific nursery areas (e.g. Olds et al. 2018).

The review by Whitfield & Patrick (2015) highlights the diversity of fish nurseries across both littoral estuarine and marine environments in the Eastern Cape. Although the above review does not assess the relative growth, food availability or predation in nursery and non-nursery areas within the coastal zone, it does document which habitats are important to the juveniles of dominant marine species within each area. These habitats do appear to perform a key role in the biological success of species assemblages, with the juveniles of particular marine fishes tending to favour specific nursery areas. According to a multivariate analysis of nursery habitat use within this region, marine fish species using estuaries tend to differ significantly from those using habitats in nearshore coastal waters.

Table 20. The five most abundant marine fish species, recorded mainly as juveniles, in 10 Eastern Cape coastal areas (see Figure 174 for localities). This data was extracted from published ichthyological studies in the respective habitats (after Whitfield & Patrick 2015).

EASTERN CAPE NURSERY AREAS FOR MARINE FISH SPECIES	
<b>Sundays Estuary (littoral zone along the lower, middle and upper reaches)</b> 1. <i>Rhabdosargus holubi</i> 2. <i>Chelon dumerili</i> 3. <i>Monodactylus falciformis</i> 4. <i>Mugil cephalus</i> 5. <i>Solea turbynei</i>	<b>Swartkops Estuary (eelgrass and non-vegetated littoral areas in the lower reaches)</b> 1. <i>Rhabdosargus holubi</i> 2. <i>Diplodus capensis</i> 3. <i>Chelon dumerili</i> 4. <i>Mugil cephalus</i> 5. <i>Chelon richardsonii</i>
<b>East Kleinemonde Estuary (littoral zone along the lower, middle and upper reaches)</b> 1. <i>Rhabdosargus holubi</i> 2. <i>Chelon dumerili</i> 3. <i>Chelon richardsonii</i> 4. <i>Pseudomyxus capensis</i> 5. <i>Lithognathus lithognathus</i>	<b>Kromme Estuary (eelgrass and non-vegetated littoral areas in the lower and middle reaches)</b> 1. <i>Chelon dumerili</i> 2. <i>Rhabdosargus holubi</i> 3. <i>Mugil cephalus</i> 4. <i>Monodactylus falciformis</i> 5. <i>Heteromycteris capensis</i>
<b>Kariega Estuary (saltmarsh creeks in the lower reaches)</b> 1. <i>Chelon dumerili</i> 2. <i>Mugil cephalus</i> 3. <i>Rhabdosargus holubi</i> 4. <i>Chelon tricuspidens</i> 5. <i>Pseudomyxus capensis</i>	<b>Great Fish Estuary (littoral zone in the lower, middle and upper reaches)</b> 1. <i>Rhabdosargus holubi</i> 2. <i>Chelon dumerili</i> 3. <i>Chelon richardsonii</i> 4. <i>Pomadasys commersonii</i> 5. <i>Lithognathus lithognathus</i>
<b>Swartkops (nearshore marine zone just beyond the estuary mouth)</b> 1. <i>Pomadasys olivaceum</i> 2. <i>Engraulis capensis</i> 3. <i>Caffrogobius agulhensis</i> 4. <i>Argyrosomus inodorus</i> 5. <i>Galeichthys feliceps</i>	<b>Algoa Bay (sandy subtidal beach within the surf zone)</b> 1. <i>Diplodus capensis</i> 2. <i>Lithognathus mormyrus</i> 3. <i>Chelon richardsonii</i> 4. <i>Pomadasys olivaceus</i> 5. <i>Rhabdosargus globiceps</i>
<b>Schoenmakerkop (subtidal rocky gullies)</b> 1. <i>Chirodactylus brachydactylus</i> 2. <i>Sarpa salpa</i> 3. <i>Cheilodactylus fasciatus</i> 4. <i>Galeichthys ater</i> 5. <i>Diplodus capensis</i>	<b>Cape Recife (intertidal rock pools)</b> 1. <i>Clinus superciliosus</i> 2. <i>Chirodactylus brachydactylus</i> 3. <i>Diplodus capensis</i> 4. <i>Caffrogobius caffer</i> 5. <i>Sparodon durbanensis</i>

Table 21. Utilization of estuarine and/or marine littoral habitats by the juveniles of common coastal fish species in the Eastern Cape Province, South Africa. A plus sign (+) indicates partial or complete dependence by the juvenile fishes on estuarine and/or marine littoral habitats as nursery areas (after Whitfield & Pattrick 2015).

Family	Species	Estuarine littoral habitats	Marine littoral habitats
Ambassidae	<i>Ambassis dussumieri</i>	+	+
	<i>Ambassis natalensis</i>	+	
Arridae	<i>Galeichthys ater</i>		+
	<i>Galeichthys feliceps</i>	+	
Atherinidae	<i>Atherina breviceps</i>	+	+
Blenniidae	<i>Omobranchus woodi</i>	+	+
Carangidae	<i>Caranx sexfasciatus</i>	+	
	<i>Lichia amia</i>	+	
Cheilodactylidae	<i>Cheilodactylus fasciatus</i>		+
	<i>Cheilodactylus brachydactylus</i>		+
Clinidae	<i>Blennioclinus brachycephalus</i>		+
	<i>Cirrhibarbis capensis</i>		+
	<i>Clinus cottoides</i>		+
	<i>Clinus superciliosus</i>	+	+
	<i>Pavoclinus grammus</i>		+
Clupeidae	<i>Gilchristella aestuaria</i>	+	
Eleotridae	<i>Eleotris fusca</i>	+	
Elopidae	<i>Elops machnata</i>	+	
Engraulidae	<i>Engraulis encrasicolus</i>		+
	<i>Stolephorus holodon</i>		+
Gerreidae	<i>Gerres longirostris</i>	+	+
Gobiesocidae	<i>Chorisochismus dentex</i>		+
Gobiidae	<i>Caffrogobius gilchristi</i>	+	
	<i>Caffrogobius agulhensis</i>		+
	<i>Caffrogobius saldanha</i>		+
	<i>Caffrogobius nudiceps</i>	+	+
	<i>Glossogobius callidus</i>	+	
	<i>Glossogobius giuris</i>	+	
	<i>Oxurichthys keiensis</i>	+	
Gobiidae	<i>Psammogobius knysaensis</i>	+	+
Haemulidae	<i>Pomadasys commersonnii</i>	+	
	<i>Pomadasys olivaceum</i>		+
Hemirhamphidae	<i>Hyporhamphus capensis</i>	+	
Leiognathidae	<i>Leiognathus equula</i>	+	
Monodactylidae	<i>Monodactylus falciformis</i>	+	
Mugilidae	<i>Crenimugil crenilabis</i>	+	+



Table 21 (cont.). Utilization of estuarine and/or marine littoral habitats by the juveniles of common coastal fish species in the Eastern Cape Province, South Africa. A plus sign (+) indicates partial or complete dependence by the juvenile fishes on estuarine and/or marine littoral habitats as nursery areas (after Whitfield & Patrick 2015).

Family	Species	Estuarine littoral habitats	Marine littoral habitats
Mugilidae (cont.)	<i>Chelon dumerili</i>	+	
	<i>Chelon richardsonii</i>	+	+
	<i>Chelon tricuspidens</i>	+	+
	<i>Crenimugil buehneri</i>	+	+
	<i>Moolgarda cunnesius</i>	+	
	<i>Mugil cephalus</i>	+	
	<i>Pseudomyxus capensis</i>	+	
Ophichthidae	<i>Ophisurus serpens</i>	+	+
Platycephalidae	<i>Platycephalus indicus</i>	+	+
Pomatomidae	<i>Pomatomus saltatrix</i>	+	+
Sciaenidae	<i>Argyrosomus japonicus</i>	+	
Serranidae	<i>Acanthistius sebastoides</i>		+
	<i>Epinephelus marginatus</i>		+
Sillaginidae	<i>Sillago sihama</i>	+	+
Soleidae	<i>Heteromycteris capensis</i>	+	
	<i>Solea turbynei</i>	+	
Sparidae	<i>Acanthopagrus vagus</i>	+	
	<i>Diplodus capensis</i>	+	+
	<i>Diplodus hottentotus</i>		+
	<i>Lithognathus lithognathus</i>	+	
	<i>Lithognathus mormyrus</i>		+
	<i>Rhabdosargus globiceps</i>	+	+
	<i>Rhabdosargus holubi</i>	+	
	<i>Sarpa salpa</i>	+	+
	<i>Spondyllosoma emarginatum</i>		+
Syngnathidae	<i>Syngnathus temminckii</i>	+	+
Teraponidae	<i>Terapon jarbua</i>	+	
Tetraodontidae	<i>Geneion honckenii</i>		+



#### 4.8 PLANT HABITATS AS FISH NURSERY AREAS

Although there is wide acceptance that one of the primary roles of southern African estuaries is the provision of nursery areas for certain juvenile marine and other estuary-associated fish species (e.g. Wasserman & Strydom 2011), there is less knowledge concerning the relative value of different estuarine habitats regarding this nursery function (Edworthy & Strydom 2016). Whilst emergent and submerged macrophytes (reeds, mangroves, saltmarsh plants and seagrasses) have been well studied with regard to the associated ichthyofauna (Whitfield 2017, Nel et al. 2018), there is still a lack of general acceptance that these habitats are essential to the juveniles of fish species associated with estuaries. This is to be expected, as marine species in particular have a variety of potential nursery areas in the coastal zone, including rocky shores and their associated habitats. In this regard the review by Whitfield & Patrick (2015) clearly shows that different habitats in coastal waters provide nursery areas for different suites of fish species.

In contrast to some of the above reservations concerning the universal nursery role of littoral macrophytes for coastal fish species, much has been written about the high value that is attached to large estuarine plants, and how their loss from such systems invariably results in a decrease in the diversity, abundance, biomass and productivity of estuary-associated fish and their invertebrate food sources (e.g. Whitfield 1984).

In this section, which is based on components of a global review by Whitfield (2017), the relative contributions of the above plant groups to the shelter and nutrition of juvenile fishes are assessed, thereby giving a more holistic perspective to the nursery value of these major habitats to estuary-associated fish species. Particular attention is given to the different physical structures provided by the different macrophyte species, as well as the availability of these habitats to juvenile fishes over tidal cycles. There is also a strong emphasis on potential food sources for fishes within the different macrophyte habitats and to what extent these plants are responsible for the carbon that is assimilated by the associated ichthyofauna.

##### **Mangrove forests**

Mangrove creeks are favoured nursery areas for juvenile fishes, particularly those estuary-associated marine species that enter these systems in large numbers. It would appear that such species continue to use mangroves in estuaries as nursery areas, even when an estuary ceases to have a river flow and the system becomes hypersaline (Vidy 2000). However, a freshwater aquifer at one of the estuarine sites in the above study resulted in typical estuarine salinities and juvenile fish abundance in the mangroves at this site was much higher than mangrove sites where estuarine conditions were lacking.

Whilst mangrove habitats often support a richer juvenile fish assemblage than nearby open areas, this is not always the case, e.g. fish composition associated with mangroves and nearby sandbanks in the Mhlathuze Estuary was similar (Weerts & Cyrus 2002a), perhaps reflecting that fish assemblages are forced to leave mangrove habitats at low tide and occupy adjacent non-mangrove areas.

##### **Submerged plant meadows**

Submerged aquatic macrophytes in southern African estuaries appear to be important foraging and refuge habitats for a wide variety of fish species (Sheppard et al. 2011, Pollard et al. 2017). There are three main types of submerged plants that occur in these estuaries depending on salinity and estuarine type. The eelgrass *Zostera capensis* (Figure 181) is most abundant in permanently open estuaries where tidal currents occur and euhaline salinities are prevalent. *Ruppia cirrhosa* (Figure 182) occurs in both permanently open and temporarily open/closed estuaries where salinities may range from mesohaline to euhaline. *Stuckenia pectinata* also favours the calm waters of temporarily open/closed estuaries where oligohaline salinities prevail.

Submerged plant beds are not only important habitats and nursery areas for fishes, they also harbour a large number and biomass of invertebrates (Barnes 2010). A number of studies have shown that densities of benthic invertebrates and



**Figure 181.** The eelgrass *Zostera capensis* usually occurs in intertidal and subtidal areas of the lower and middle reaches of some permanently open estuaries (Photo: Alan Whitfield).



**Figure 182.** The aquatic grass *Ruppia cirrhosa* usually occurs in shallow waters of most temporarily open/closed estuaries (Photo: Alan Whitfield).

epifauna are highest in seagrass meadows than unstructured sand or mud-flats (Siebert & Branch 2007). It is these prey in particular that attract carnivorous fish species, particularly demersal foragers, to this type of habit (Whitfield 1988a).

Penaeid prawns and *Palaemon peringueyi* are strongly associated with submerged plants, e.g. caridean shrimps use eelgrass beds as nursery areas in many southern African estuaries (Emmerson 1986) and are an important food source for demersal carnivorous fish species within these systems (Coetzee & Pool 1985).

At the fish family level there appears to be some consistency in seagrass colonization on sometimes very broad spatial scales, e.g. Pollard (1984) found 10 fish families associated with seagrasses in Australia and nine of these families are also associated with *Zostera capensis* beds in South Africa (Whitfield et al. 1989). Perhaps the above similarity can be partially attributed to the Indo-Pacific linkages between the ichthyofaunas of Australia and South Africa, but the morphological similarity of the leaves of seagrass genera may also play a role. It also appears that fish species not utilizing eelgrass beds as a food source (e.g. Mugilidae) may also attain high numbers in such habitats (Pollard et al. 2017), possibly due to the refuge they provide from predators.

When seagrass habitat is compared to salt-marsh habitat, it would appear that some studies have shown similar overall fish species richness but considerable differences in fish assemblage composition. For example, Paterson & Whitfield (2000b) recorded almost the identical number of species from a seagrass bed and adjacent saltmarsh creek, but found a significant difference in species composition and juvenile fish use between the two habitats. Similarly, Weerts & Cyrus (2002a) found distinct fish assemblages associated with eelgrass beds in the Mhlathuze Estuary when compared to nearby mangrove habitats.

Most seagrasses exhibit cyclical growth rates, with maximum plant density and biomass usually being recorded during summer, and minimum values in winter. This pattern is reflected in fish assemblages associated with the seagrass beds, reaching peak fish densities in summer and minimum densities in winter (Hanekom & Baird

1984). The fact that the main arrival period for a number of 0+ juvenile marine fishes in southern African *Zostera* beds (Beckley 1983) coincides with the main growth period of this seagrass and the associated invertebrates is therefore appropriate.

It should also be noted that the benefits of seagrass primary production can extend well beyond the macrophyte beds and immediate surroundings, e.g. Whitfield (1988b) has shown that tidal transport of eelgrass wrack plays an important role in providing energy subsidies to upstream and downstream estuarine areas where no submerged macrophytes are present but benthic detritivorous invertebrates are dominant (Whitfield 1988a). On a broader scale, estuarine seagrass meadows and saltmarshes are very important at providing energy and nutrient subsidies to the marine environment (Baird et al. 1987), especially following river flood events.

### Salt marshes

A comparison of the abiotic drivers of fish composition in three saltmarsh fish assemblages in the Kariega Estuary showed little or no influence of salinity, temperature or turbidity on the ichthyofaunal groupings, but creek water depth and mouth area (entrance to the main estuary channel) appeared to be highly influential in this regard (Paterson & Whitfield 2003).

Most saltmarsh research indicates that these habitats are not homogeneous environments and that they vary in terms of elevation, topography and location within a wider estuarine system. These attributes, together with tides and climatological events, determine the marsh hydroperiod, a critical element that controls fish access to marsh microhabitats, as well as influencing invertebrate prey abundance and vegetation stem density (Rozas 1995).

In small saltmarsh habitats, where high marsh pools or permanently inundated creeks are absent, juvenile marine species tend to dominate the marsh during spring high tides, retreating into the main estuary channel at low tide (Paterson & Whitfield 1996). The Kariega Estuary saltmarsh creek was dominated by mugilids which comprised 70% of the total number and 86% of total



fish biomass entering the marsh on the flood tide. A parallel situation was recorded in Mont Saint-Michel Bay (France) saltmarshes where mugilids comprised 92% of the fish biomass entering this habitat during inundation (Laffaille et al. 1998). In the above studies juvenile marine fish dominated the fish assemblages, emphasizing once again the role of saltmarshes as secure nursery areas with a low abundance of large piscivorous fishes (Paterson & Whitfield 2000a).

In the Kariega Estuary saltmarshes, a high variability in the numbers and biomass of fish was recorded from one high tide to another, but broad seasonal trends for many species were evident (Paterson & Whitfield 1996).

### Reed beds

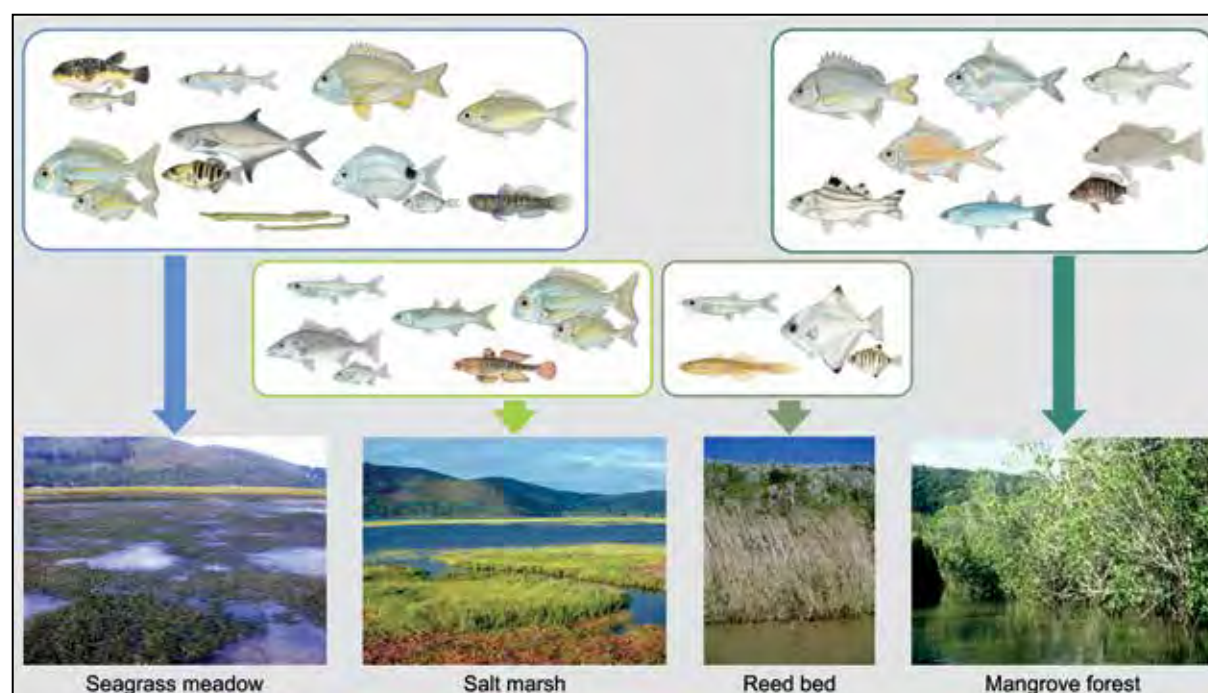
The common reed *Phragmites australis* (Figure 183) occurs on virtually all continents and in a wide variety of estuaries where conditions are suitable. Other more herbaceous reed species such as *Juncus* spp. and *Scirpus* spp. also occur in low salinities, often in association with *P. australis*. Where an estuary main channel becomes shallow due to excessive sedimentation, *P. australis* is known to colonise these previously open water areas (Schleyer & Roberts 1987), thus reducing

habitat diversity for fishes in such estuaries.

*Phragmites australis* litter input in some estuaries ( $1.61 \text{ kg m}^{-2} \text{ a}^{-1}$ ) can exceed the estimated mineralisation rate, thus leading to anaerobic conditions in which aquatic invertebrate consumers are unable to access the large detrital pool (Schleyer & Roberts 1987). In addition, if the accumulated leaf litter is not removed from dense reed beds during estuary flushing events, the dissolved oxygen uptake from the water column can be further accentuated.

The juveniles of a number of fish species are not attracted to littoral reed beds (e.g. Nel et al. 2018). For example, in the East Kleinemonde Estuary species belonging to the family Mugilidae were more attracted to bare sand than reed habitats, whereas juvenile *Rhabdosargus holubi* (Sparidae) were evenly distributed across reef, bare sand and reed bed habitats (Becker et al. 2010).

There is strong evidence in the above study to suggest that some fish species are attracted to the physical shelter that reed beds provide. For example, small shoaling zooplanktivorous fish (*Atherina breviceps* and *Gilchristella aestuaria*) had highest daytime abundances within these *Phragmites* beds than other littoral habitats



**Figure 183.** Diagrammatic representation of a few dominant fish species associated with four different types of aquatic macrophyte habitats in southern African estuaries (after Whitfield 2017).

(Becker et al. 2010). In the nearby Grant's Valley Micro-estuary, some fish species exhibited restricted movement patterns due to their preference for refuge and foraging areas provided by littoral *P. australis* beds (Lukey et al. 2006).

Periphyton and invertebrate epifauna associated with reed stems often develop in those systems where semi-permanent inundation of the *Phragmites* occurs. In the temporarily closed Mhlanga Estuary, epiphyton, tube-dwelling polychaetes and amphipods colonized the submerged *P. australis* stems in the littoral, thus providing a rich food source for small fishes associated with this habitat (Whitfield 1980b).

## Biotic and abiotic drivers

### Food availability and predation pressures

Submerged and emergent estuarine macrophyte habitats have often been quoted as offering good protection from predation for small fishes. However, the level of protection will depend on the type of macrophyte habitat and the structural complexity provided by the habitat concerned. A detailed study of Cape stumpnose *Rhabdosargus holubi* habitat utilization in the Bushmans Estuary showed that habitat complexity indices were notably higher in seagrass (*Zostera capensis*) than saltmarsh (*Spartina maritima*), and that the abundance of *R. holubi* was significantly higher in the former habitat (Leslie et al. 2017). However, dietary analyses of Cape stumpnose from the different habitats revealed that *R. holubi* is a generalist, opportunistic feeder that does not rely on specific habitats for food, thus emphasizing the shelter aspect of *Zostera* for juveniles of this species.

Juveniles of fish species that are not strongly associated with submerged or emergent macrophyte habitats are unlikely to respond strongly to the presence or absence of such habitats and are presumably well adapted to avoiding predators in more open waters. For example, larval, juvenile and adult *Gilchristella aestuaria* are abundant in channel waters of most southern African estuaries and show no strong association with aquatic macrophyte beds.

There is some evidence to suggest that salt-

marshes may be more attractive as a shelter for juvenile fish than as a source of invertebrate prey. For example, most fish located on saltmarshes in the Kariega Estuary were juveniles that were not feeding in these habitats when captured (Paterson 1998). However, in the Knysna Estuary saltmarshes, fishes were recorded foraging in these areas (Le Quesne 2000).

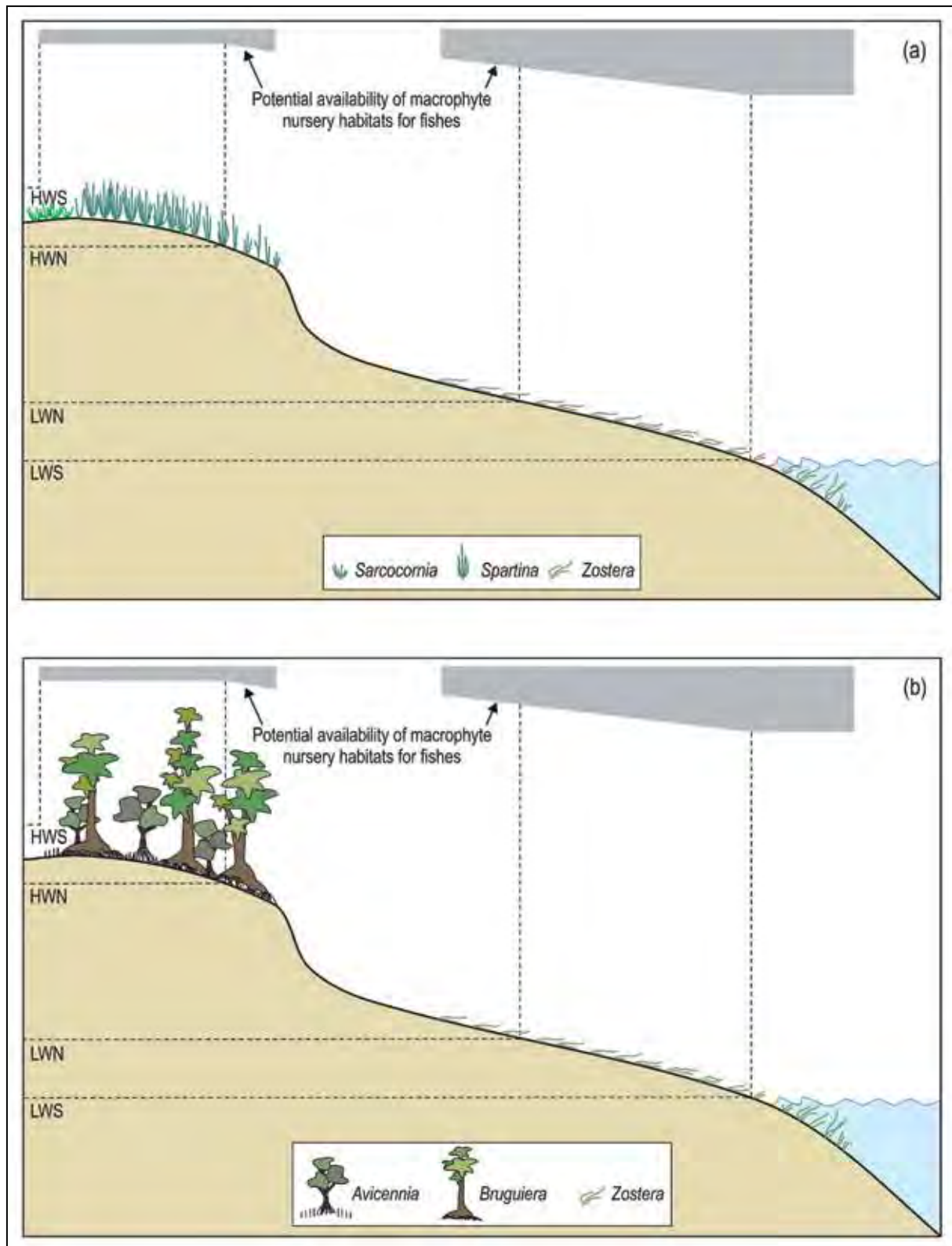
A number of studies have revealed that creeks associated with mangroves or marshes have a higher diversity and abundance of fishes than nearby sandy beaches or mudflats without any fringing aquatic macrophytes (Whitfield 2017). At low tide these plant structures are often unavailable to the fishes within these creeks, and juveniles may be forced into main channel habitats where piscivorous fishes are more abundant (Paterson and Whitfield 2000a). However, at high tide there is obviously much greater access by large predatory fish to the structural complexity and protection that intertidal aquatic macrophyte habitats provide for juvenile fishes.

Herbivorous and omnivorous fish species appear to be proportionally more abundant in seagrass beds than they are in other aquatic macrophyte habitats (Whitfield 2017, Le Quesne 2000). Those species that do ingest plant material often target epiphytic algae and diatoms growing in association with seagrass leaves, rather than the macrophyte material itself (Blaber 1974; Sheppard et al. 2012). Apart from the epiphytes, the invertebrates associated with the leaf fronds are also important in the diet of fishes associated with estuarine eelgrass beds in southern Africa. In contrast, infaunal invertebrates such as buried bivalves that only have siphon tips protruding to the surface, and anomuran prawns that are located in deep burrows in these plant habitats, are seldom preyed upon by the ichthyofauna associated with plant beds (Whitfield 1988a, Leslie et al. 2017).

### Spatial and temporal aspects

Climate change is likely to cause major changes in the distribution and extent of particular macrophyte habitats within estuaries (Tabot & Adams 2013) and this will lead to significant changes in fish assemblages within these nursery areas,





**Figure 184.** Diagrammatic representation of potential occupation of South African estuarine macrophyte habitats by fishes in (a) warm-temperate saltmarshes and seagrass beds and (b) subtropical mangrove forests and seagrass beds. The thickness of the 'fish occupation' bar provides an indication of the relative duration that the habitat or portion of the habitat is available as a nursery area (HWS = High Water Spring, LWS = Low Water Spring, HWN = High Water Neap, LWN = Low Water Neap). The water level shown in both diagrams is standardised at a low water spring tide (after Whitfield 2017).

particularly in biogeographic transition zones (Whitfield et al. 2016).

Evidence to support this view is provided by changes in fish species composition recorded in the mangrove dominated Mngazana Estuary between 1975-1977 and 2001-2002. This estuary, which is situated in the biogeographic transition zone between subtropical and warm-temperate coastal waters, has shown a more consistent occupation of the system by tropical fish species during summer and winter in 2001-2002 (Mbande et al. 2005) than during the summer and winter of 1975-1977 (Branch & Grindley 1979).

### Water depth and tidal action

Water depth also appears to be an important factor for fishes entering and leaving intertidal mangrove, saltmarsh and seagrass habitats. Paterson & Whitfield (2003) found that saltmarsh creek water depth was a major driver influencing fish abundance and composition in three small Eastern Cape saltmarshes, with these habitats already showing signs of substratum subsidence and therefore greater marine influence due to relative sea-level rise (Bornman et al. 2016).

The elevation (relative to mean sea level) of aquatic and emergent macrophyte habitats is particularly important, as this single factor determines whether occupation of a particular habitat can occur only at spring high tide, neap high tide or a combination of high and low tides (Figure 184). The value of a nursery area that is available for juvenile fish occupation at all tides is clearly an advantage over one that is only available at certain stages in the tidal cycle. Thus mangrove and saltmarsh habitats are generally situated higher in the intertidal profile and are fully inundated less frequently and for shorter durations than seagrass beds, which are usually situated lower down in the intertidal profile (Figure 184).

In general, the diversity and abundance of food resources for fishes will also vary according to habitat type, e.g. those littoral seagrass beds that are permanently inundated are likely to have a higher biomass of potential micro-algal resources and suitable aquatic invertebrate prey than a mangrove forest or saltmarsh that is completely exposed on each low tide (Figure 184).

Additionally, the detritus from the leaves of these estuarine macrophytes have differential decomposition rates and also vary in terms of food quality for invertebrate prey and detritivorous fishes during the decomposition process, with seagrass leaves having the most rapid and saltmarsh leaves the slowest decomposition rate. This is primarily due to differences in C:N ratios and crude fibre content of deposited leaf material from the different macrophytes.

Most southern African saltmarshes (Figure 185) are only completely inundated during spring high tides (Figure 184a), so fish species only have access to these environments for very short periods. In a Kariega Estuary high elevation saltmarsh studied by Paterson (1998), the fish used this habitat only during spring high tides and did not feed on the marsh, whereas in a low elevation Knysna Estuary saltmarsh, fish used the habitat as both a shelter and foraging area during neap and spring high tides (Le Quesne 2000).

### Plant habitat connectivity and quality

Within southern African estuaries there is also some evidence for juvenile fishes making use of plant habitat mosaics, e.g. juvenile *Sphyrna barracuda* recruit into the Kosi system (South Africa) at 20 mm SL and live in shallow seagrass beds until 80 mm, after which they move to fringing reed bed habitats until a length of 300 mm, at which stage they occupy open waters (Blaber 1982a).

Unfortunately there are strong indications that estuarine macrophytes are under threat globally from a diverse range of anthropogenic pressures. Widespread declines in both mangrove and seagrass habitats around the world from a variety of causes is of great concern. Within 20 years (1984-2003) non-degraded mangrove forests on islands in the Komati Estuary (Mozambique) declined by 25-40% and reed beds were adversely affected by seawater intrusion up the estuary as a result of increased freshwater abstraction within the river catchment (Le Marie et al. 2006). In other systems (e.g. Gazi Bay, Kenya) replanted mangroves in previously degraded areas have been shown to restore the nursery habitat for marine fishes (Crona & Rönnbäck 2007).



**Figure 185.** An aerial view of the extensive saltmarshes in the Swartkops Estuary (Photo: Alan Whitfield).



**Figure 186.** An aerial view showing extensive intertidal and subtidal eelgrass *Zostera capensis* beds in the Kariega Estuary (Photo: Alan Whitfield).

### Food chains and isotope signatures

It has been postulated that consumption of mangrove detritus by nektonic fish and invertebrates is limited, with C, N and S isotope studies failing to indicate extensive assimilation of mangrove production by higher consumers such as fishes (Sheridan & Hays 2003). This view is supported by stable isotope studies in the Mngazana Estuary where isotope signals suggested a more enriched source of carbon for fishes than that provided by mangroves in this system (Mbande et al. 2004).

In contrast to the poor food web linkages between fishes and mangroves outlined above, there is much descriptive and experimental evidence to suggest that mangrove roots and the deposited litter do provide shelter from predators for juvenile fishes, thus enhancing their survival. Nektonic invertebrates and small fish make extensive use of submerged mangrove detritus as a refuge. Indeed, macrophyte detritus in channels adjacent to mangrove, reed, saltmarsh or seagrass habitats may be very important from a camouflage perspective for small fishes that are forced into these areas at low tide.

Penaeid prawns in mangroves obtain limited organic carbon directly from these trees and appear to be more dependent on seagrasses and their associated epiphytes or even benthic algae as primary food sources. The hypothesis has therefore arisen that these macrophytes provided shelter from predation but not necessarily food for the

associated fishes and invertebrates. Confirmation that saltmarsh carbon does not appear to find its way into the littoral estuarine fish assemblage associated with these plant habitats in the Kariega Estuary is provided by Paterson & Whitfield (1997).

In contrast to the relative lack of major carbon inputs to fish species associated with mangrove and saltmarsh plants, there is increasing evidence that both seagrasses and their associated epiphytes are very important food sources for many fishes within these habitats. Paterson & Whitfield (1997) identified *Zostera capensis* and associated epiphytic algae as an important source of carbon for littoral fishes in the Kariega Estuary (Figure 186), some of which is assimilated by the fish through their invertebrate prey.

Nutrient enrichment of estuarine waters can alter or even compromise food webs, thereby changing the ability of submerged and emergent plant communities to support associated fish populations. Deegan et al. (2002) have described how nutrient enrichment of seagrass ecosystems in Waquoit Bay (USA) quickly resulted in the loss of physical structure, an alteration in the food web, and an invasion of the system by macroalgae. Expansion of the macroalga *Ulva* in the lower Knysna Estuary, and associated loss of eelgrass beds, has also been shown to have an adverse impact on the *Zostera*-associated estuarine fish assemblages in this system (Pollard et al. 2018).

## 4.9 FISH BIOMASS AND PRODUCTIVITY IN ESTUARIES

Estuaries are well known for their high levels of both primary and secondary production which, in turn, support a large biomass of fishes (Houde & Rutherford 1993). The literature is replete with evidence to show that these systems are characterised by fluctuating environmental conditions that can lead to differential utilisation of various habitats depending upon estuarine type, tidal regime, salinity, water temperature, turbidity, etc. (Whitfield 1996a). All of the above factors and drivers make the accurate determination of fish biomass in estuaries over medium to long-term time scales very difficult. What we do know from

intensive fish mark-recapture studies in temporarily closed southern African estuaries (Blaber 1973a, Cowley & Whitfield 2002) is that fish biomass values can fluctuate considerably over seasons and from one year to the next, and are strongly influenced by factors such as fish recruitment, mouth state, river flow and natural mortality due to fish and bird predation (James et al. 2007a, 2007b, Cowley et al. 2017).

Different fish species in estuaries can be allocated to different functional guilds (Potter et al. 2015), each of which will contribute to overall estuarine fish productivity at different rates

Table 22. Fish community standing stock (wet mass) estimates from estuarine and coastal marine environments around the world (modified from Whitfield 2016b).

Sampling region	Physical environment	Sampling method	Mean wet biomass (g m <sup>-2</sup> )	Reference
Todds Cove, North America	Estuarine bay	Seine net	4.8-104.0	Lubbers et al. (1990)
Queensland, Australia	Estuary	Gill, seine, beam trawl, block nets	1.2-70.6	Blaber et al. (1989)
Eastern Cape, South Africa	Closed estuary	Mark/recapture and seine net	28.4	Cowley & Whitfield (2002)
Queensland, Australia	Estuarine bay	Block nets	2.9-25.3	Morton (1990)
Mexico, North America	Estuarine lagoon	Seine and cast nets	8.0-12.5	Warburton (1979)
Western Cape, South Africa	Estuarine lake	Lift and gill nets	12.4	Whitfield (1993)
Solomon Islands	Mangrove estuary	Seine nets and rotenone	11.6	Blaber & Milton (1990)
Mexico, North America	Estuarine bay	Trawl net	1.0-11.3	Yanez-Arancibia et al. (1980)
Parsons Island, North America	Estuarine bay	Seine net	0.1-11.2	Lubbers et al. (1990)
Queensland, Australia	Estuary	Trap nets	10.9	Robertson & Duke (1990)
Mexico, North America	Estuarine lagoon	Trawl net	10.0	Flores-Verdugo et al. (1990)
Florida, North America	Marine lagoon	Visual census	10.0	Holm (1977)
Gulf of Aqaba, Red Sea	Coral reef	Visual census	96.2	Ben-Tuvia et al. (1983)
Sichang Islands, Gulf of Thailand	Coral reef	Rotenone	83.2	Menasveta et al. (1986)
Bermuda Islands, Western Atlantic	Coral reef	Visual census	49.0	Bardach (1959)
Eniwetok Atoll, Pacific Ocean	Coral reef	Visual census	36.7	Odum & Odum (1955)
KwaZulu-Natal, South Africa	Surf zone reef	Visual census	52.1	Berry et al. (1982)
Goat Island, New Zealand	Rocky reef	Visual census	1.0-103.0	Russell (1977)
Western Cape, South Africa	Rocky intertidal pools	Rotenone	49.6	Bennett & Griffiths (1984)
California, North America	Kelp bed/reef	Visual census and rotenone	35.0	Quast (1968)
Texas, North America	Coastal bay	Drop nets	22.3	Jones (1965)
Texas, North America	Coastal bay	Drop nets	11.5	Hellier (1962)
Florida, North America	Marine bay	Block nets	0.8-15.0	Thayer et al. (1987)



(Bennett & Branch 1990, Cowley & Whitfield 2002). Thus the two dominant fish guilds in southern African estuaries, marine migrants and estuarine residents, are likely to have different growth rates because they are represented in estuaries by different sizes, life stages and are associated with different food chains (Harrison & Whitfield 2012). Marine migrants are dominated by juvenile fish occupying these estuaries as nursery areas, whereas all life stages are usually represented in the estuarine resident guild. In addition, whilst a number of the larger marine species are important to the recreational and subsistence fishers in southern African estuaries (Lamberth & Turpie 2003), none of the small resident species, which are a highly productive component in these estuaries, are utilised by these fisheries.

In this section, based on a review by Whitfield (2016b), the available information on coastal fish biomasses and productivity is assessed to place southern African studies on these topics into a more global perspective. Using fish standing stocks ( $\text{g m}^{-2}$  wet mass) and productivity ( $\text{g m}^{-2}$  wet mass per year), together with estuarine water area and fish productivity in the different biogeographic regions on the subcontinent, the approximate total annual fish production in South African estuaries is estimated (Figure 187).

The above information is essential if we are to provide a broad understanding of the fisheries value of estuaries to people and also to contribute information that can support the sustainable management of these systems as vital nursery and foraging areas for a wide range of fish and piscivorous bird species.

### **Fish biomass in aquatic ecosystems**

Haedrich & Hall (1976) suggested that “few areas of the Earth support such large stocks of fish as do estuaries” but does the evidence support this view? Published information (Table 22) indicates that fish biomass tends to be highest in association with marine reefs, with estuaries and coastal embayments generally having slightly lower values. However, all the reef studies quoted in Table 22 were conducted during the day when many fish species are concentrated in these areas, whereas

at night adjacent habitats may be used as refuges or feeding grounds by some of these ‘reef’ taxa (Hobson 1972). Additional support for this view is provided by Berry et al. (1982) who noted the disappearance of certain fish species commonly found diurnally on a KwaZulu-Natal littoral reef during nocturnal hours. Thus, whilst all fish in an estuary are supported by that environment at all times, certain reef fish are often transitory.

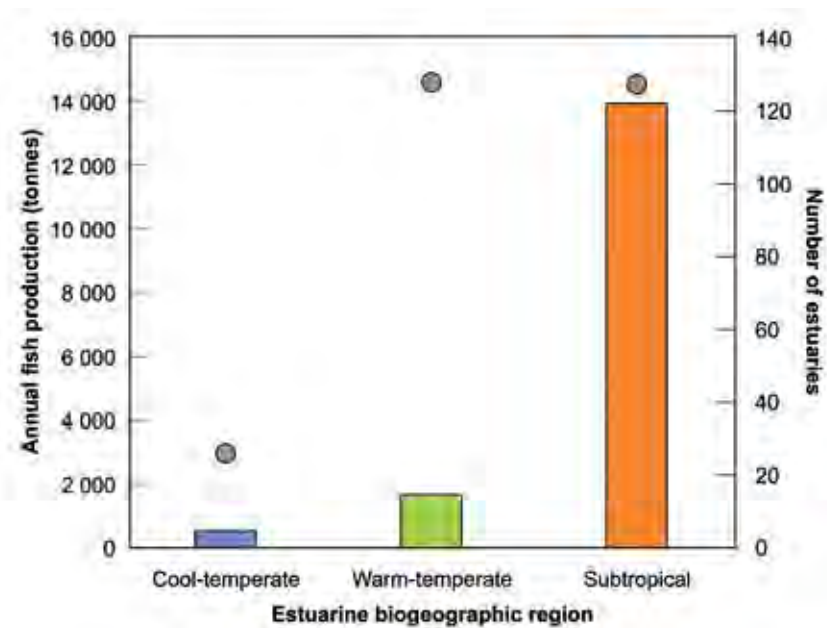
Table 22 also confirms that fish biomass values are highly variable, both between and within particular aquatic environments. Some of this variability can be attributed to different sampling techniques employed by ichthyologists working in the various systems, as well as the diel and seasonal movements of individual fish species at the study sites.

Based on the results outlined in Table 22, and the above discussion, it would appear that highly productive freshwater or marine habitats can have similar fish standing stocks to those recorded in estuaries. However, the effects of fishing also need to be taken into account, since unfished waters often have a higher biomass of predatory fish species, as well as total fish biomass, when compared to nearby fished waters (Jennings et al. 2013).

The above preliminary observations suggest that further research is required, especially using standardized fish sampling techniques in representative water bodies from different biogeographic regions, before we can contextualize fish biomasses and productivity within and between different types of aquatic ecosystems.

### **Fish productivity in coastal ecosystems**

There are a large number of scientific papers and chapters in books dealing with what is sometimes referred to as “fishery production” (e.g. Yáñez-Arancibia et al. 1985). However, a closer examination of these publications reveals that a more appropriate term for many of these studies would be “fishery yield” since fishing gear is highly selective and does not measure either the fish standing stock or the productivity of individual fish species. Indeed, fishery yields can initially be very high for certain teleosts in unexploited areas, whereas actual fish productivity in the same area may be very low due to the slow somatic



**Figure 187.** Number of functional South African estuaries in each biogeographic region (solid dots), together with fish production values for each region (coloured bars). More than 75% of the estuarine area in the region is located within the subtropical zone (after Whitfield 2016b).



**Figure 188.** Lake Nhlangwe, the largest estuarine compartment in the Kosi segmented lakes system (Photo: Alan Whitfield).

growth of the targeted species. This is particularly the case for many of the resident reef fish species along the southern African coast, some of which grow to a very large size but take many decades to achieve those dimensions (Smale & Punt 1991). Fortunately the growth rate of most estuary-associated fish species is fairly rapid (e.g. Farthing et al. 2016) and therefore the stocks are not as vulnerable to over-exploitation as marine reef fish species.

A review by Day et al. (1989) indicated that detailed studies of individual fish species in estuaries showed that these taxa were more productive than marine or freshwater counterparts. This was, in part, explained by the fact that estuaries tend to be dominated by the juveniles of mostly marine species at an age when somatic productivity on a per unit area basis is usually maximal. It might also be explained by the fact that estuaries are also one of the most productive aquatic environments on our planet, mainly due to the high primary and secondary productivity linked to high nutrient and organic matter availability (Wilson 2002). These views are supported by a comparison of fish community productivity in the North Sea ( $2.5 \text{ g wet mass m}^{-2} \text{ y}^{-1}$ ) which was much lower than that in one of the adjacent North Sea estuaries, namely the Forth system in Scotland ( $4.3 \text{ g wet mass m}^{-2} \text{ y}^{-1}$ ) (Costa et al. 2002).

### Productivity in southern African estuaries

The most accurate fish productivity estimates are likely to be derived from standing stocks and growth data from a closed fish population, i.e. where recruitment or emigration from the study fish population is effectively nullified for the duration of an investigation. Only one of the listed studies in Table 22 complies with the above criterion and it is also the only study that depended primarily on a mark-recapture investigation to determine the changing fish population sizes (Cowley & Whitfield 2001a). This particular study provided the foundation for the calculation of fish biomass and production in the small temporarily closed East Kleinemonde Estuary (Cowley & Whitfield 2002).

The wide range in fish productivity in the East Kleinemonde Estuary ( $5.4\text{--}55.9 \text{ g m}^{-2} \text{ y}^{-1}$ ) is

a function of the variability in annual recruitment to this system (James et al. 2007b), as well as differential annual avian predation on fish stocks within the estuary (Cowley & Whitfield 2002, Cowley et al. 2017). A mark-recapture study in the West Kleinemonde Estuary by Blaber (1973) revealed that stocks of *Rhabdosargus holubi* declined from approximately 55 000 just after mouth closure to about 11 000 six months later, and attributed this decline mainly to bird predation. Despite the above decline, Day et al. (1981) calculated that the biomass of *R. holubi* in this estuary actually increased from  $1.7$  to  $2.7 \text{ g m}^{-2}$  over that period due to fish somatic growth, thereby registering a fish productivity gain.

Fish biomass estimates for two southern African estuaries have been directly measured using quantitative methods over more than one season. The Swartvlei littoral fish biomass was primarily calculated using lift nets, and an annual mean value of  $12.4 \text{ g m}^{-2}$  was determined (Whitfield 1993). The fish biomass from the temporarily closed East Kleinemonde Estuary was measured mainly using mark-recapture studies and the standing stock in a good juvenile marine fish recruitment year was estimated at  $28.4 \text{ g m}^{-2}$  (Cowley & Whitfield 2002). Both these systems are situated in the warm-temperate biogeographic region and, based on trends mentioned above, are likely to have fish biomasses higher than those in the cool-temperate region and lower than those in the subtropical region.

The approximate fish production in southern African cool-temperate estuaries was based on an average rate of  $10 \text{ g m}^{-2} \text{ y}^{-1}$ , that of warm-temperate estuaries at  $20 \text{ g m}^{-2} \text{ y}^{-1}$  and subtropical estuaries at  $30 \text{ g m}^{-2} \text{ y}^{-1}$  (Figure 187). Using an estuarine water surface area of 5 846 ha in the cool-temperate region, 8 530 ha in the warm-temperate region and 46 347 ha in the subtropical region (van Niekerk & Turpie 2012), annual fish production in each region was estimated at 585, 1 706 and 13 904 tonnes respectively. The comparatively high value for the subtropical region is not only because of the elevated fish productivity per unit area, it is also due to the major estuarine systems of Lake St Lucia and the Kosi lakes (Figure 188) being

located within this particular biogeographic zone (van Niekerk & Turpie 2012).

The above southern African fish production figures are likely to be conservative since they do not include the surface areas of estuarine littoral plant habitats such as reeds and sedges, some of which are inundated at high estuarine water levels. Total annual fish production in southern African estuaries is therefore conservatively estimated at 16 195 tonnes, but this amount may fluctuate widely, depending on annual environmental conditions pertaining to these systems.

The large St Lucia system was mostly isolated from the sea during a prolonged drought from 2002 until 2012 and, during this time, massive losses of estuarine habitat and fish stocks occurred (Cyrus et al. 2010a). Lake St Lucia accounts for almost 50% of the total estuarine surface area in South Africa; thus any functional impairment of this system as a fish nursery area and feeding ground for coastal fish species will have severe consequences for estuary-associated fish stocks on the subcontinent. During the 2002-2012 prolonged drought, the total surface area of Lake St Lucia was reduced to 9200 ha (25% of normal area) in December 2003, and by 2006 the northern sections of the system had completely evaporated, leaving <10% of the lake available to the remaining trapped fish stocks (Whitfield & Taylor 2009).

The majority of estuaries in South Africa are closed to the sea for varying periods each year. Fish productivity in temporarily open /closed estuaries is likely to be similar to that of nearby permanently open estuaries on a unit area basis but will differ in overall production due to the much larger size of the latter systems (Vorwerk et al. 2003). However, the much larger number of TOCEs compared to POEs will tend to even out these areas and in certain regions (e.g. KwaZulu-Natal) the former systems may have greater overall productivity than the latter. There will also be differences because the fish guilds in the two major system types have been shown to differ, with estuarine resident species being proportionally more abundant in TOCEs when compared to POEs (Vorwerk et al. 2003, Harrison & Whitfield 2006c).

An important question that requires further research is what percentage of annual fish production is exported to the marine environment? This amount is likely to vary considerably, depending on river flow and the mouth state of the large number of temporarily open /closed estuaries along the southern African coastline (James et al. 2007a). An indication of the importance of estuarine connectivity on the coastal populations of certain estuary-associated fish species is provided by the study of Mann & Pradervand (2007) who recorded a dramatic decline in the coastal marine fish stocks of the sparid *Rhabdosargus sarba* following the prolonged closure of the St Lucia system from the sea.

One of the few studies to estimate the biomass export of a fish species from an estuary to the sea is that of Carassou et al. (2016) for the Kowie system. These authors estimated that 7 tonnes of sub-adult *Rhabdosargus holubi* moved from the 142 ha estuary to the sea each year, a figure that will be considerably boosted by other estuary-associated marine fish species such as *Chelon dumerili*, *Mugil cephalus*, *Lithognathus lithognathus* and *Argyrosomus japonicus* making similar annual contributions (Figure 189).

Approximately 2 000 tonnes of fish, comprising 80 species, are estimated to be harvested by fishing activities in South African estuaries each year (van Niekerk & Turpie 2012), which represents approximately 12% of estimated annual fish production in these systems. Although this amount may appear sustainable, the reality is that there are a few heavily targeted estuary-associated marine species at the top of the food chain that are being over-exploited by both anglers and subsistence fishermen (Whitfield & Cowley 2010). Indeed, predatory species such as the estuary-dependent sciaenid *Argyrosomus japonicas* and sparid *Lithognathus lithognathus* are estimated to have declined to <5% of the original spawner stock biomass, primarily due to angling pressures (Cowley et al. 2013). Similarly, an expansion of the traditional Kosi fish traps into a semi-commercial operation now threatens the biomass and productivity of the sparid *Acanthopagrus vagus* and other fish species in this system (James et al. 2008b).

Natural mortalities due to fish and bird predation have been estimated at approximately 3% of total fish biomass per month in the East Kleinemonde Estuary (Blaber 1973a, Cowley & Whitfield 2002) but this percentage can vary considerably depending on bird abundance and foraging patterns by mobile piscivorous bird species along the coast (Terörde & Turpie 2012). In contrast to catches made by anglers and subsistence fishermen (Cowley et al. 2013), piscivorous fish and birds target mainly 0+ juvenile marine fish and small estuarine resident species that are very abundant and low down in the food web (Marais 1984, Froneman et al. 2011).

In conclusion, the review by Whitfield (2016) has provided an estimate of total estuarine fish production for an entire country (across three biogeographic regions) based on broad fish biomass, water area and productivity data. Although a number of assumptions underpin the above estimates, they are based on best available information from different disciplines. It would certainly be most useful if similar calculations were undertaken to estimate fish productivity for estuary-associated fishes over a range of latitudes in different countries and on different continents. This type of information is vital for the establishment of sustainable estuarine fisheries.



**Figure 189.** A shoal of subadult and adult flathead mullet *Mugil cephalus* attempting to leave the West Kleinemonde Estuary for the sea as it opened and getting stranded in the process. This fish species, together with a number of other estuary-associated marine fish taxa, contribute towards a major energy transfer from estuaries to the sea (Photo: Paul Cowley).





## Chapter 5

### Environmental change and fish responses

#### 5.1 INTRODUCTION

THE ESTUARINE ENVIRONMENT is attractive not only to fishes but also to people. Although the functioning of the natural biota and the recreational activities of humans are usually compatible, (e.g. canoeing and bird watching) there are often other anthropogenic impacts (e.g. power boating and overfishing by anglers) that have deleterious consequences for the fish community. Since estuaries are already highly stressed ecosystems due to fluctuating physico-chemical conditions, the additional pressures resulting from poor catchment and estuarine management all contribute to a degraded environment which is unable to fulfil its natural functions.

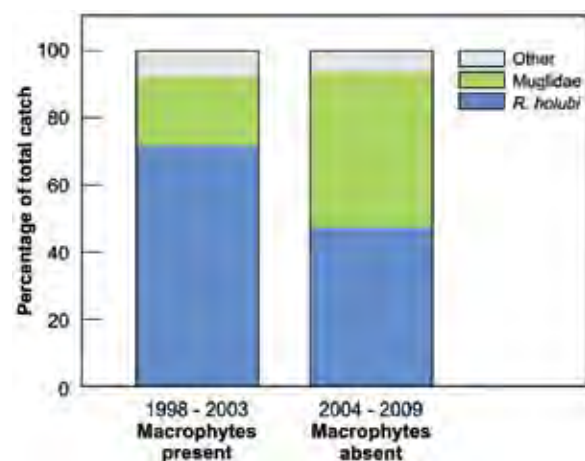
Estuaries, which are mainly driven by the balance between freshwater inflow and seawater influx, are highly impacted by altered river flow regimes (Grange et al. 2000). Since rivers bring vital nutrient and organic supplies to estuaries, the loss of freshwater inputs on the productivity of estuaries can be significant. However, it is not only water quantities that are vital to estuaries – water quality is just as important. Rivers with high sediment loads due to excessive catchment erosion will cause the smothering of submerged plants and a loss of nursery areas for fishes and invertebrates. Similarly, riverine or estuarine pollution is invariably taken up by the animals living within these ecosystems, the consequences of which are severe for both affected fishes and people utilizing estuarine resources.

Estuaries are particularly vulnerable to climate induced changes that affect the marine environment, e.g. a sea-level rise of only 5 cm caused by global warming will lead to major changes in the shape and size of most estuaries. In addition altered wave climates around the coast can lead to either increased shoreline erosion or deposition, both of which will influence estuarine connectivity with the sea.

#### Some southern African case studies

In a southern African context, global change is already impacting on estuarine fish populations in a variety of ways. In particular, habitat destruction, climate change and the excessive abstraction of fresh water from river systems have all been identified as major threats to the natural functioning of a number of estuaries on the subcontinent and this, in turn, has had a negative influence on the abundance of certain estuary-associated fish species, e.g. the estuarine pipefish *Syngnathus watermeyer* in the Eastern Cape.

Perhaps one of the most obvious ways to demonstrate how environmental change affects fishes is to compare the proportion of the total catch in a single estuary, with and without aquatic macrophytes. The graph below (Figure 190) shows the declining proportion of the omnivorous sparid *Rhabdosargus holubi* in the East Kleinemonde Estuary with and without macrophytes (Sheppard et al. 2012). This decline, which was also matched by a decline in CPUE between the two periods,



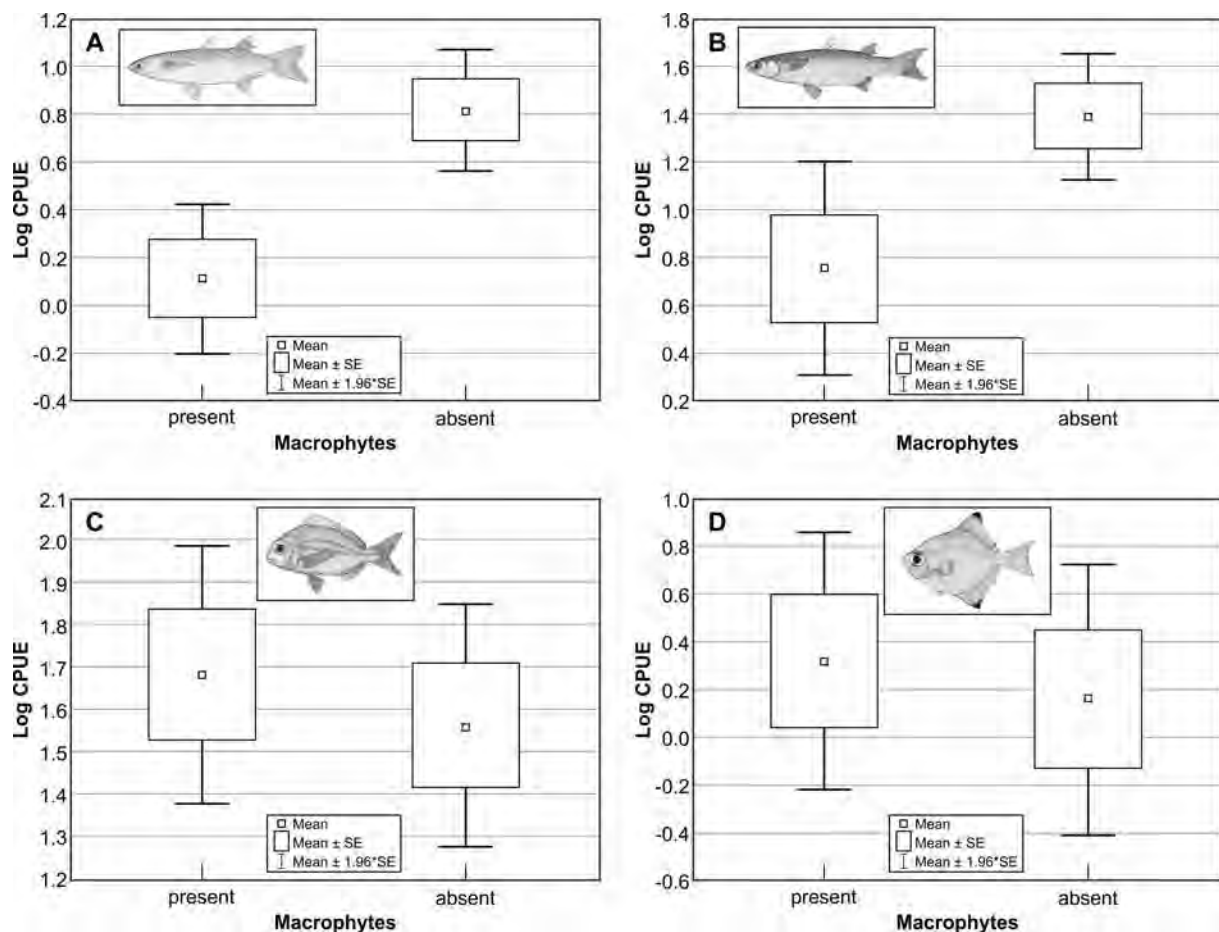
**Figure 190.** Percentage contribution of *Rhabdosargus holubi*, mugilids and other species to the total fish catch in the East Kleinemonde Estuary over two different five year periods, one with aquatic macrophytes present and one with them absent (after Sheppard et al. 2012).

was significant in that there was an increase in the proportion and CPUE of detritivorous mugilids (Figure 191) that benefitted from the exposed sediments and readily available detritus resources, as well as the higher microphytobenthos stocks.

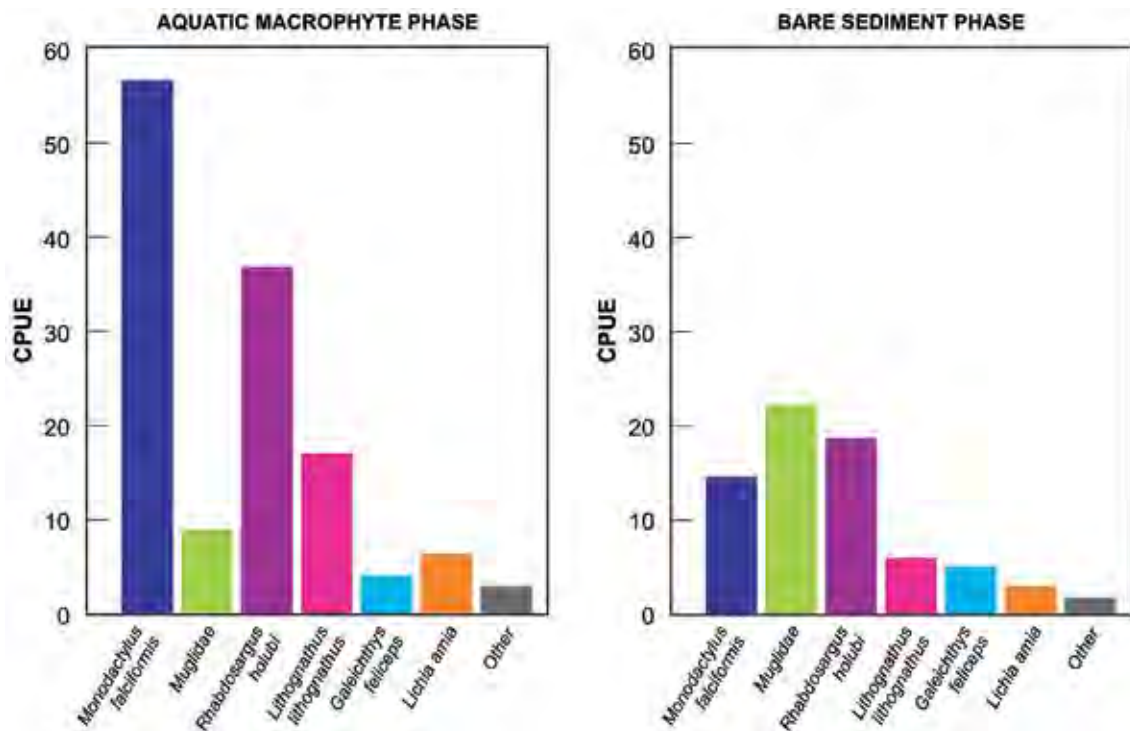
A similar pattern of change was documented in the Swartvlei littoral where the extensive beds of aquatic macrophytes underwent total senescence (Taylor 1983) which resulted in a total change in the food web of this system (Davies 1982). The littoral fish fauna, which was overwhelmingly dominated by two macrophyte-associated fish species, *Rhabdosargus holubi* and *Monodactylus falciformis*, also showed significant changes between the two phases (Whitfield 1984, 1986a), with *Rhabdosargus holubi* CPUE declining from 37 to 18 and *M. falciformis* declining from 57 to 14 (Figure 192). Similar to the East

Kleinemonde study above, there was an opposite response by mugilids in the Swartvlei littoral, with their CPUE and proportion of the overall fish catch increasing from 9 during the *Stuckenia pectinata* canopy phase to 22 during the bare sediment phase (Figure 192).

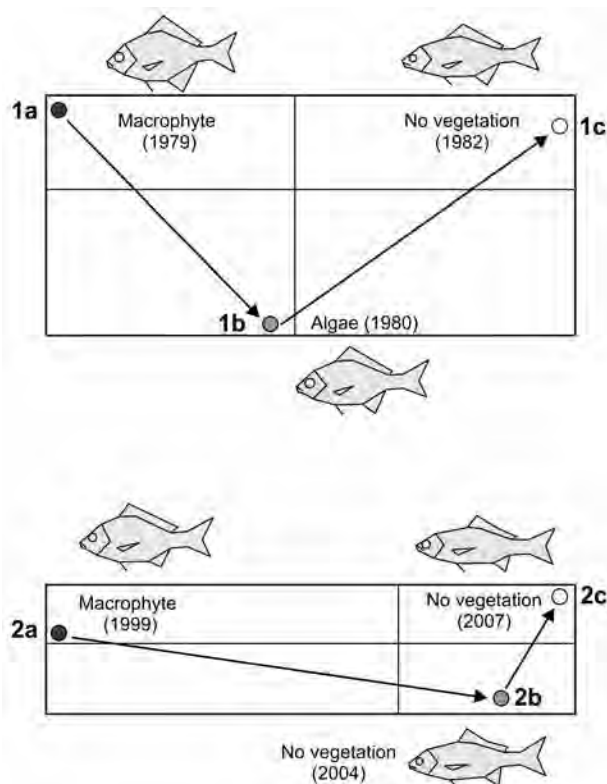
An innovative approach to the ecological interpretation of both the Swartvlei and East Kleinemonde natural estuarine macrophyte perturbations, and resultant changes in fish communities, is the use of an ecomorphological diversity index. This approach (Figure 193) showed that the fish 'consensus configurations' in the Swartvlei and East Kleinemonde estuaries changed in a similar manner (the fish consensus figure became thinner) after submerged macrophyte plant loss in both systems (Lombarte et al. 2012).



**Figure 191.** The mean large mesh seine net CPUE for (A) *Chelon dumerili*, (B) *Pseudomyxus capensis*, (C) *Rhabdosargus holubi* and (D) *Monodactylus falciformis* during periods of macrophyte abundance (present) and senescence (absent) in the East Kleinemonde Estuary (after Sheppard et al. 2011).



**Figure 192.** Gill net fish catch composition (CPUE) In the Swartvlei lake littoral during the *Stuckenia pectinata* canopy phase and the bare sediment phase at the same locality (see Whitfield 1986a for details).



1a = Aquatic macrophyte phase (Swartvlei)  
 1b = Filamentous algal phase (Swartvlei)  
 1c = Sandy bottom phase (Swartvlei)  
 See Lombarte et al. (2012) for details.

2a = Aquatic macrophyte phase (Kleinemonde)  
 2b = Sandy/muddy substratum phase after 1 year  
 2c = Sandy/muddy substratum phase after 3 years  
 See Lombarte et al. (2012) for details.

**Figure 193.** Fish consensus configurations during various habitat phases in the Swartvlei and East Kleinemonde estuaries (after Lombarte et al. 2012).

## 5.2 FISHES AND CLIMATE CHANGE

Changes in environmental conditions within an estuary may be fairly predictable, or they may be caused by short and /or long-term unpredictable climatic fluctuations, all of which have large effects on the abundance and distribution of estuarine fish species. In most parts of the world estuaries are shallow and strongly influenced by tidal action, freshwater inflow, wind, wave action, water and air temperature and rainfall. Consequently, climate change is expected to modify the physical structure and biological functioning of estuaries and will have a range of implications for estuary-associated fishes (Table 23). Such changes may also impact various life-history stages outside estuaries, depending on the timing and location of spawning and on when fish enter or leave estuaries.

In this section, which is based primarily on a review of the topic by James et al. (2013), we will focus primarily on present and future climate change impacts on the fishes associated with southern African estuaries. Despite the limited monitoring times, changes in fish assemblages are already discernible.

### Temperature

Increasing air temperatures will affect estuaries and may have a greater impact on temporarily open /closed than permanently open estuaries, as the former systems are cut off from the effect of sea temperatures for long periods and therefore respond to a greater degree to prevailing land, air and river water temperatures (James et al. 2008a). In this regard, Kruger & Shongwe (2004) investigated a time series of South African surface air temperatures for temporal and spatial trends for the period 1960 to 2003. They identified warming trends in the annual average and annual average maximum and minimum air temperatures over the period.

Water temperature and salinity were found to be the primary determinants influencing the biogeography of fishes, particularly tropical species, in southern African estuaries (Harrison & Whitfield 2006b). Climate change, which affects both these variables, has the potential to affect major aspects of fish physiology, such as their

salinity and temperature tolerances which, in turn, influences their ability to occupy estuarine habitats and ultimately the distribution of species.

Changes in the distributional patterns of estuarine and coastal species, associated with warming temperatures, have been recorded both locally and globally. The fish assemblages in the East Kleinemonde Estuary, a warm-temperate temporarily open /closed system on the south-east coast of South Africa, have been studied since December 1995. A total of 38 species of fish were recorded in the East Kleinemonde Estuary between December 1995 and July 2006 (James et al. 2008c). Indicative of warming waters, six new tropical species: *Moolgarda cunnesius*, *Osteomugil robustus*, *Planiliza alata* and *Planiliza macrolepis* (family Mugilidae), *Glossogobius giuris* (family Gobiidae) and *Terapon jarbua* (family Terapontidae) were only recorded in the surveys from 1999 onwards. As a result of the increased occurrence of tropical species, the number of species recorded in the estuary between 1996 and 2006 increased steadily (Figure 194, James et al. 2008a).

The effects of climate change on fish distributions have also been recorded further north in the permanently open Mngazana Estuary, which is situated in the transition zone between the subtropical and warm-temperate regions. In a study of the fish community undertaken in 1975 (Branch & Grindley 1979) the proportion of tropical species recorded was found to be lower during winter (43%) than summer (88%), while temperate species increased during winter (57%) and declined in summer. This was attributed to tropical species extending their ranges southwards during summer and temperate species extending their ranges northwards during winter (Branch & Grindley 1979).

In a similar study conducted in the Mngazana Estuary 25 years later, the proportion of tropical species recorded was identical in summer (71%) and winter (71%) (Mbande et al. 2005). The increase in the proportion of tropical species recorded in the estuary during winter indicates that warming may have increased minimum



Table 23. Major climate change drivers and likely impact on estuaries and estuary-associated fish assemblages in the three biogeographic provinces (after James et al. 2013).

Driver	Physical response	Fish response	Region
Wind regime shift	Increased frequency and intensity of upwelling	Fish kills Species range contractions	Cool- and warm-temperate
Increasing air temperatures	Increasing estuarine water temperatures	Physiological effects Species range changes Alterations in community composition	Cool- and warm-temperate, subtropical
Increasing SST	Increasing coastal and estuarine temperatures	Physiological effects Species range changes Alterations in community composition	Subtropical
Increasing rainfall and floods	Increasing runoff Changes in mouth state Increasing sediment delivery Increasing turbidity	Alterations in community composition	Subtropical
Decreasing rainfall	Decreasing runoff Changes in mouth state Increasing salinity Decreasing nutrients Increasing sediment deposition and decreasing estuarine surface area	Decreasing species diversity Decreasing fish stocks	Cool-temperate
Acidification	Decrease in coastal and estuarine pH Changes in solubility of nutrients and metals Decrease in prey abundance (calcifying organisms)	Physiological effects Alterations in community composition	Cool- and warm-temperate, subtropical
Sea level rise	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical
Increasing wave energy	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical
Increasing frequency and intensity of coastal storms	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical

winter water temperatures above the lower thermal limits of some of the tropical species. Higher winter water temperatures would favour tropical species, while limiting the northwards penetration of certain temperate species (Mbande et al. 2005). Rouault et al. (2010) documented warming of coastal SSTs for all months of the year in this region. Similarly, Kruger & Shongwe (2004) found that annual average maximum and minimum air temperatures recorded along the south-eastern coastal region have increased significantly for the period 1960 to 2003.

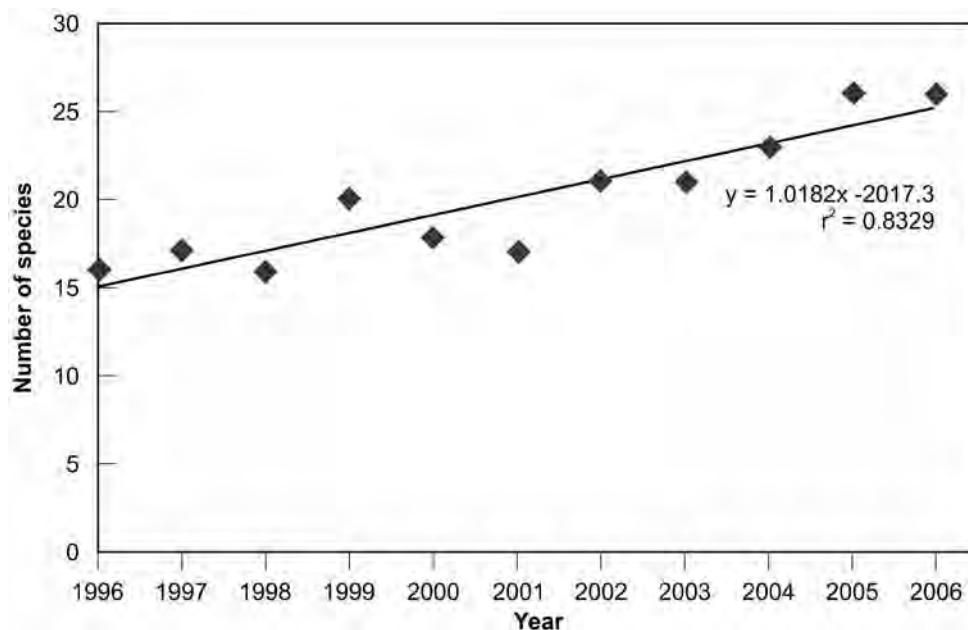
Although changes in the distribution of tropical fish species have been recorded, the abundance and distribution of temperate species has not changed significantly as yet, resulting in an increase in species richness in many warm-temperate estuaries due to the presence of both temperate and tropical species in these systems. Over time, however, there is the possibility of a decline in the number and abundance of temperate species in these systems as global warming proceeds and these taxa are forced to the south-west.

As climate change accelerates, it can be expected that there will be marked changes in the composition of estuarine fish communities, resulting in new mixes of predators, prey and competitive interactions. However, it is very difficult to

predict how communities will change in response to climate change, as each species responds differently to warming, and the assemblages are unlikely to shift their distribution as a unit (Mead et al. 2013). Nevertheless, if the current warming trend continues to gain momentum, it is likely that the contribution of temperate fish species to the overall south-western African estuarine ichthyofaunal community will decline (Lloyd et al. 2012). This is because any reduction in habitat on the warm-temperate south-east coast cannot be compensated for by an increased equivalent habitat on the west coast, where estuaries are scarce and upwelling within these coastal waters may actually increase.

In southern Africa, predicting temperature driven change is further complicated by the number of biogeographic zones found along a relatively short coastline and the contrasting changes expected in each zone. Seasonal cooling of nearshore SSTs, associated with intensified upwelling, further complicates predictions in temperate regions and may have severe consequences for coastal and estuarine species.

Sudden shifts in temperature can be lethal to fish, with mass mortalities of coastal fish having been recorded along the south coast of South Africa when upwelling causes a sudden drop in



**Figure 194.** The total number of fish species recorded in the East Kleinemonde Estuary between 1996 and 2006 (after James et al. 2008d).

water temperature (Hanekom et al. 1989). These decreases in temperature will affect both temperate and tropical species and may prevent or slow down the range extensions of tropical species into warm-temperate estuaries.

Grey mullet usually occur in large numbers and biomass in the estuaries of all three southern African biogeographic regions (Harrison 2005), thus making it an ideal family to use in terms of acting as an environmental indicator of global warming. A recent analysis (James et al. 2016) showed that the relative estuarine abundance of the dominant three groups of mugilids, namely tropical, warm-water and cool-water endemics (Figure 195), were related to sea surface coastal temperatures. The above study suggests a strong link between temperature and the distribution and abundance of the three mullet groups within estuaries, and indicates the potential of this family to act as an indicator for future climate change within these systems and adjacent coastal waters.

Although not tested as yet, it is possible that certain sparids could act as similar climate change indicators to the mugilids. For example, *Rhabdosargus sarba* is dominant in tropical estuaries, *Rhabdosargus holubi* in the subtropical and warm-temperate regions, and *Rhabdosargus globiceps* in cool-temperate systems. The distribution and abundance of these three species in estuaries is also expected to change as global warming proceeds, especially in response to the impact of climate change on coastal and estuarine water temperatures.

### Rainfall and run-off

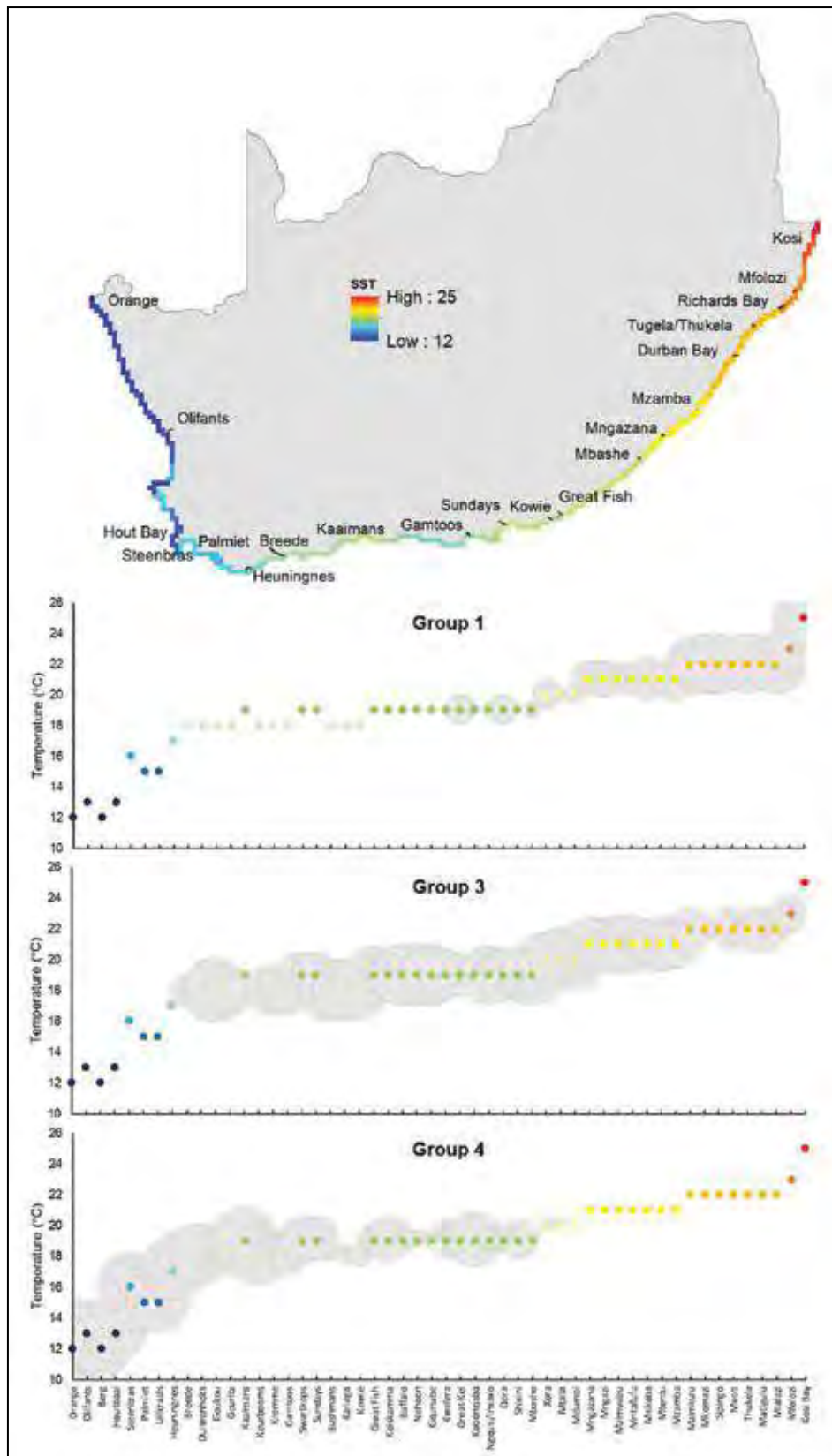
Climate change is predicted to alter precipitation patterns which will affect the quality, rate, magnitude and timing of freshwater delivery to estuaries and will potentially exacerbate human modifications of these flows. Estuarine functioning is strongly influenced by the magnitude and timing of freshwater runoff reaching them (Turpie et al. 2002). Downscaled regional climate models derived from global climate models indicate the likelihood of increased summer rainfall over the eastern part of southern Africa and a slight decrease in cool season frontal rainfall in the

Western Cape Province (Engelbrecht et al. 2009).

Schulze et al. (2005) assessed the impacts of climate change (including rainfall) on South Africa's water resources and predicted that the future climate may be characterized by "hot-spots" of hydrological change, one being the present winter rainfall region of the Western Cape. Reductions in the amount of fresh water entering the Western Cape estuaries would lead to an increase in the frequency and duration of estuary mouth closures and changes in the extent of seawater intrusion, nutrient levels, suspended particulate matter load, temperature, conductivity, dissolved oxygen and turbidity (Clark 2006). These changes are likely to have a major impact on the recruitment opportunities for juvenile marine fishes, as well as estuarine ecosystem productivity, and therefore the value of estuaries as nursery areas to both resident and migrant fishes. Because of the low number of estuaries in the cool-temperate coastal region, these changes are of particular concern.

In TOCEs, mouth opening and closing is directly linked to freshwater input, with estuaries becoming isolated from the sea by the formation of a sand berm across the mouth during periods of low or no freshwater inflow. These systems stay closed until increased freshwater inflow causes their basins to fill up and their berms to breach (Whitfield et al. 2008). Reduced freshwater inflow leads to prolonged mouth closure and shorter open phases, which inhibits the immigration and emigration of fish between estuaries and the sea (Whitfield & Wooldridge 1994), thus resulting in a reduction in the abundance of marine fish species in estuaries. In this connection, changes in the fish community structure in the East Kleinemonde Estuary were found to be primarily driven by mouth state, with optimal temporal openings to the sea (especially during spring) resulting in excellent juvenile marine fish recruitment (James et al. 2008b).

The findings of the above studies were supported by a detailed comparison between fish assemblages in the East and West Kleinemonde estuaries (Reddy et al. 2011). Fish sampling was conducted biannually over two years and during this period the East Kleinemonde Estuary opened



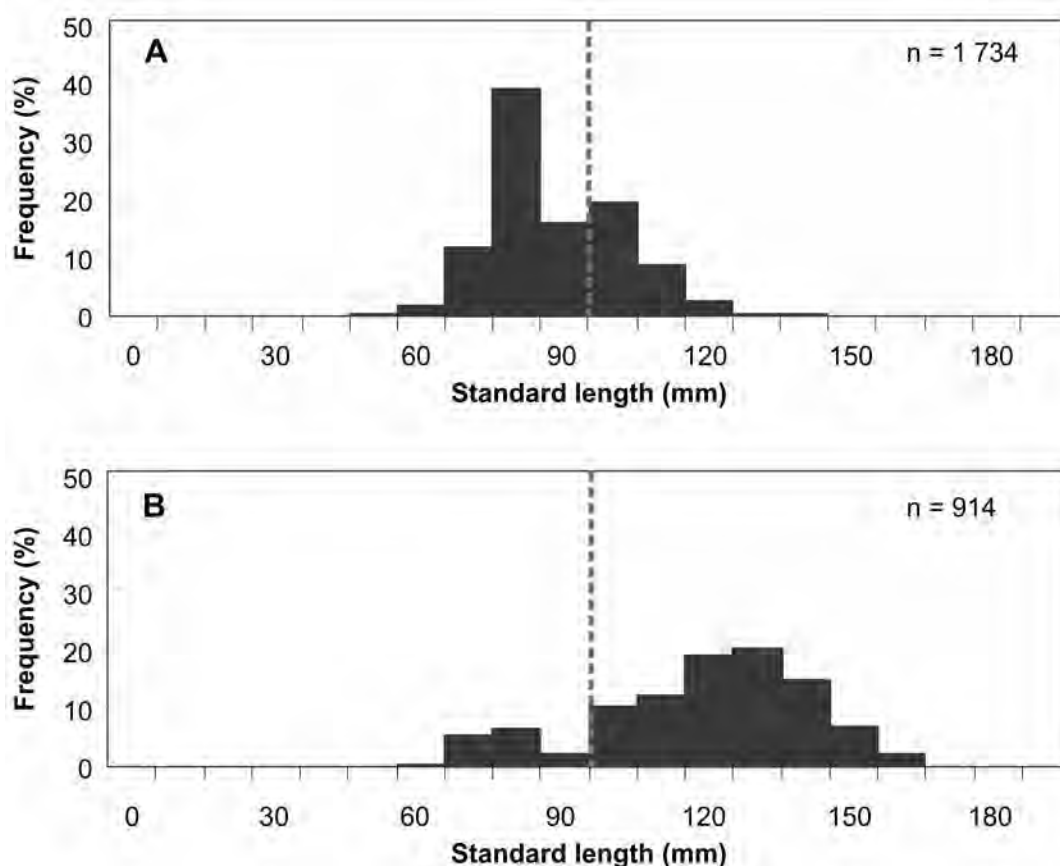
**Figure 195.** Mean annual *in situ* coastal temperatures, as well as mugilid relative abundance (bubbles) of Group 1 (tropical species), Group 3 (warm-temperate species) and Group 4 (cool-temperate species) in permanently open South African estuaries (after James et al. 2016).

more frequently than the West Kleinemonde Estuary. The former system also experienced a greater number of bar overwash events (when marine postlarval recruitment has been shown to occur). The timing of mouth opening and the frequency of marine overwash events did not influence species richness of marine-spawning species but had a pronounced effect on abundances (CPUE) of these taxa in each estuary. The species composition of both estuaries was similar, but the catch-per-unit-effort in the East Kleinemonde Estuary was more than three times greater than that of the West Kleinemonde Estuary due to the greater marine connectivity (Reddy et al. 2011).

The East Kleinemonde also supported a greater proportion of immature individuals of *Rhabdosargus holubi* (Figure 196) and *Monodactylus falciformis*, and the length frequency distributions of both these species differed significantly between the two estuaries. The larger fish sizes in

the West Kleinemonde Estuary were attributed to the prolonged mouth closure that resulted in the trapping of larger juveniles and mature fish within the estuary, as well as reduced 0+ juvenile recruitment.

In large permanently open systems a reduced river flow may initially result in a reduction in the extent of the River-Estuary Interface (REI) zone, i.e. that section of an estuary with an integrated vertical salinity of approximately 10. Major reductions in river flow can result in the complete elimination of this mixed zone so that, effectively, the system functionally becomes an 'arm of the sea' (Scharler & Baird 2000). If there is no river inflow for extended periods, a reverse salinity gradient may develop, where the salinity at the head of the estuary may exceed that of seawater due to higher rates of evaporation and lack of tidal exchange in the ebb and flow region, e.g. Kariega Estuary (Whitfield & Paterson 2003). In most affected



**Figure 196.** Length frequency distribution of individuals of *Rhabdosargus holubi* (10 mm size classes) recorded in the East Kleinemonde (A) and the West Kleinemonde (B) estuaries combined for 2008 and 2009 (after Reddy et al. 2011). The dotted line represents the length at age 1 year for *R. holubi*.



Table 24. Summary of selected biotic and abiotic characteristics in two similar sized Eastern Cape estuaries with high and low river flow (modified from Grange et al. 2000).

Characteristics	Kariega Estuary	Great Fish Estuary
<i>Abiotic:</i>		
Mean annual river flow	Low	High
Allochthonous input	Low	High
Turbidity	Low	High
Sediment load	Low	High
Nutrient load	Low	High
<i>Biotic:</i>		
Seston load	Low	High
Phytoplankton stocks	Low	High
Zooplankton abundance	Low	High
Ichthyofaunal abundance	Low	High

systems reversed salinity conditions are a function of excessive freshwater abstraction from the river.

River flow has been found to have a major impact on the structure and functioning of fish communities within the permanently open Kariega and Great Fish Estuaries (Table 24), particularly in the upper reaches or REI zone (Bate et al. 2002; Whitfield 2005b). Optimal conductivity in the REI zone of the Great Fish Estuary, a freshwater 'enriched' system, in which natural runoff is augmented by an inter-basin transfer of water from the Orange River (Grange et al. 2000), resulted in an abundance of marine and estuarine species in both the REI zone and the river above the ebb and flow (Ter Morshuizen et al. 1996). In contrast, the REI zone of the freshwater deprived Kariega Estuary was much smaller, resulting in fewer individuals and species being caught in this part of the system (Whitfield & Paterson 2003). Similarly, Whitfield et al. (1994) recorded a higher biomass of fish in the Great Fish Estuary compared with the Kowie Estuary (Table 25) and this was attributed to greater nutrient and organic matter contributions to the former estuary.

In contrast to fish abundance and biomass trends discussed above, the species richness is

often higher in those estuaries deprived of river inflow. This because a number of stenohaline marine species that do not normally occur in estuaries (e.g. ragged-tooth shark *Charcharius taurus*) enter these systems due to the seawater conditions prevailing in the lower and middle reaches. Some apparent stenohaline cephalopods (e.g. cuttlefish *Sepia vermiculata*) also enter estuaries that have become an 'arm of the sea' and are therefore additional fish predators that are usually absent from estuaries with a 'normal' salinity gradient. Water turbidity is also much lower in freshwater deprived systems, thus attracting a different set of species to more turbid estuaries.

Flood events play an important role in the morphology of estuaries as they scour out sediment that had been deposited during periods of low flow (Badenhorst et al. 1989). This accumulated sediment is both catchment derived and that brought into the lower reaches from the sea by flood tides and can persist for many years. Although sedimentation is a natural process in estuaries, elevated rates of sediment delivery to estuaries from the terrestrial environment can significantly alter the structure and functioning of these systems. The infilling of estuaries with

Table 25. Relative abundance of fishes in two Eastern Cape estuaries with differing riverine inputs (data from Whitfield et al. 1994).

Characteristics	Kowie Estuary	Great Fish Estuary
<i>Physical:</i>		
Annual river flow	20 × 10 <sup>6</sup> m <sup>3</sup>	224 × 10 <sup>6</sup> m <sup>3</sup>
Estuary length	21 km	12 km
Estuary width	30 -150 m	30 -100 m
Estuary channel depth	2 - 8 m	1 - 4 m
<i>Ichthyofauna:</i>		
Fish larval densities	26 larvae per 100 m <sup>3</sup>	77 larvae per 100 m <sup>3</sup>
Seine net fish CPUE	569 fish per 10 seine hauls	1 534 fish per 10 seine hauls
Gill net CPUE	130 fish per 100 gill net hours	352 fish per 100 gill net hours

excessive sediment due to poor catchment management has been a growing problem over the past century, especially with regard to the maintenance of estuarine habitat diversity and productivity.

Although shallow areas of estuaries are important for small fish, so too are the deeper areas as a habitat for larger juveniles and adults of many species (Becker et al. 2011a, 2017). Utilization of estuaries by marine fish species appears to be strongly linked to river flow (Nodo et al. 2018), with large volumes of water entering the sea acting as an attractant to immigrating postlarvae of these taxa in anticipation of increased estuarine productivity.

In addition, the increased primary and secondary estuarine production associated with the freshwater pulses will also support a higher density and biomass of fishes within these systems. Support for this view is provided by the work of Vorwerk et al. (2009) which showed that the relative densities of the juveniles and subadults of *Argyrosomus japonicus* and *Pomadasys commersonnii* were considerably higher during a wet spring compared to a dry spring period in the Kariëga Estuary (Figure 197), thus reinforcing the importance of the link between river flow and marine fish recruitment and maintenance.

Indirect support of the above hypothesis is provided by Lamberth et al. (2008) who predicted that with a 64% reduction in mean annual run-off in the permanently open Breede Estuary in the Western Cape Province, the abundance of two

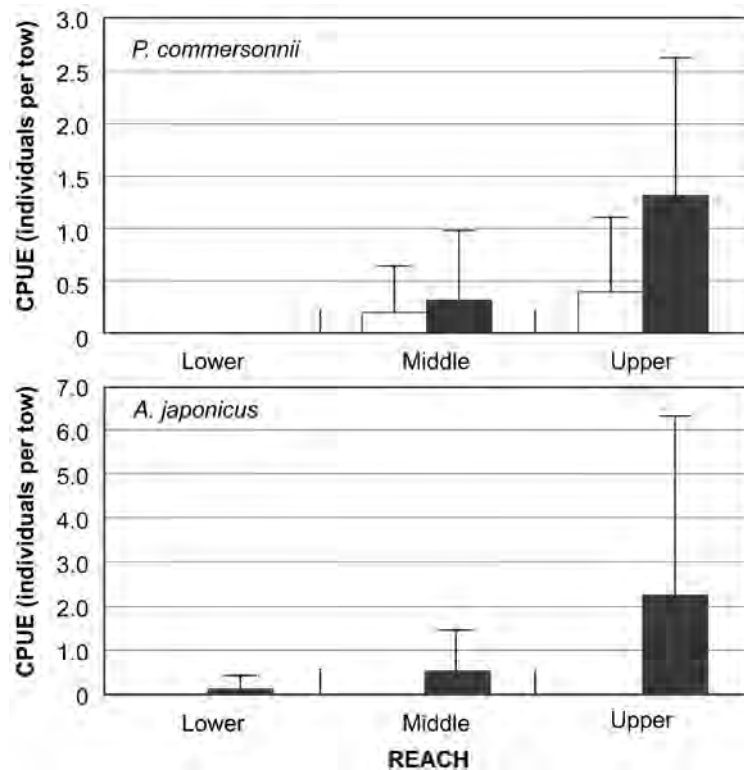
important fishery species, *Argyrosomus japonicus* and *Pomadasys commersonnii* would decrease by ±50%. Similar decreases in abundance as a result of declining river flow are likely to occur for a number of other estuary-dependent marine fish taxa.

#### Sea level rise and storm disturbance

Two significant predicted consequences of climate change are accelerated sea level rise and an increase in the frequency of high-intensity coastal storms and high water events. Several climate models project an accelerated rate of sea level rise over the coming decades but the extent of the rise varies from one model to the next. An assessment of sea level rise in South Africa, using available tide gauge data for the last 50 years, shows an annual 1.87 mm rise on the west coast, 1.48 mm rise on the south coast and a 2.74 mm rise on the east coast (Mather et al. 2009).

It is anticipated that the effects of sea level rise will be exacerbated by predicted increases in the frequency of severe storms and high tides impacting the coastal platform at a higher mean sea level (Figure 198). The South African coastline is intermittently impacted by extreme swells associated with tropical cyclones and cut-off low pressure systems (Mather & Stretch 2012) and these extreme weather events are predicted to increase in frequency and intensity during the 21<sup>st</sup> century (Engelbrecht et al. 2009).

An increase in the frequency of extreme weather events, together with sea level rise, will



**Figure 197.** The otter trawl catch per unit effort (+SD) for *Pomadasys commersonnii* and *Argyrosomus japonicus* in the lower, middle and upper reaches of the Kariaga Estuary during November 1996 (dry spring season = open bars) and November 2006 (wet spring season = solid bars). Zero *A. japonicus* were captured in any of the reaches during the dry spring (after Vorwerk et al. 2009).

alter the hydro-geomorphology of estuaries and may result in a loss of essential estuarine habitat (such as mangroves and saltmarshes), which will ultimately affect estuarine fish communities (Clark 2006).

A more difficult change to predict is the role of altered coastal wave conditions and sea level rise on estuarine functioning. High seas in recent years have seen major overwash events entering temporarily closed estuaries in the Eastern Cape (Figure 199). These events bring large amounts of marine water and sand into these small systems, thus altering the salinity and sediment regime of the estuary. In addition, large overwash events tend to flatten the sand bar at the mouth which can lead to an earlier opening of the estuary when river flow increases the lagoonal level (Begg 1978, Cooper 1990). Major overwash events may, however, represent important recruitment and emigration opportunities for the marine fish species associated with these systems, especially along those parts of the coast where river flow is reduced due to global change (Figure 200).

Of all climate induced changes, sea level rise is seen as the greatest threat to mangrove and salt-marsh ecosystems in estuaries (Adam 2002). If the rate of sedimentation within an estuary is able to keep up with the rate of sea level rise, the system will experience very little change (Reddering & Rust 1990). However, depending on the degree of protection at the mouth, raised water levels may allow more wave energy into the estuaries, which will negatively affect littoral plants that do not survive when exposed to strong wave action (Mather & Stretch 2012). Wave energy may also increase with climate change. This can promote the formation of sandbars across tidal inlets (Reddering & Rust 1990). All of the above could result in a new equilibrium in erosion-deposition cycles and ultimately cause a reduction in estuarine water volume. This will be aggravated in areas that are predicted to receive less rainfall in future.

A substantial rise in sea level (especially in sediment starved catchments) would have major implications for estuarine saltmarshes and mangroves, as the rate of sedimentation would not



**Figure 198.** Ingress of a marine water into the Kariaga Estuary during a major spring tidal surge event. Such events are likely to increase in frequency as the momentum of global warming increases in the future (Photo: Angus Paterson).



**Figure 199.** Major ingress of seawater into the temporarily closed East and West Kleinemonde estuaries (Photo: Paul Cowley).





**Figure 200.** A storm sea surge (March 2007) associated with an offshore cyclone breached the large sand berm at the mouth of the St Lucia Estuary and resulted in the prolonged ingress of marine water into the system (Photo: Ricky Taylor).

be able to keep up with the rate of sea level rise. Hughes et al. (1993) modeled the impacts of a one meter rise in sea level on the Diep Estuary in Cape Town. This estuary comprises a temporarily open /closed estuary (Milnerton Lagoon) and a wetland system (Rietvlei). The model predicts that the wetland area will effectively become a large shallow body of seawater connected to the sea via a long narrow channel (Hughes et al. 1993). However, given the lack of connectivity of the current Diep Estuary with the marine environment, an increase in sea level is likely to be beneficial to the estuarine functioning of this system.

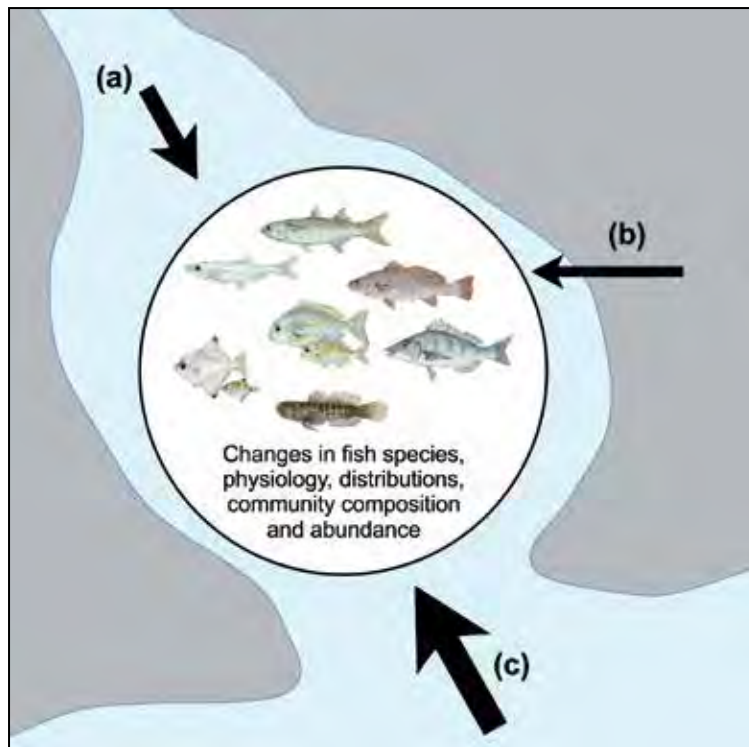
Fortunately Holocene sea-level changes have left most Khoi coastal middens in the Cape region unaffected. Professor JLB Smith was able to identify the large supra-occipital bones of *Pomadasy commersonnii* from middens in the False Bay area where this species is currently absent. According to Smith (1965) “This is a clear indication that since the termination of the last glaciation there was a time when the seas of the Cape were warmer than at present.” In his opinion the *P. commersonnii*

obtained by early humans “were likely killed by onsets of cold water” or upwelling events as occur in the southern Cape today.

### Some climate change conclusions

As estuaries are transition areas between rivers and the sea, and are influenced by changes in freshwater, terrestrial and marine conditions, climate change is likely to have a large impact on these ecosystems (refer to Table 23 and Figure 201 for overviews). The more immediate effects of climate change on southern African estuaries and estuary-associated fishes will come from changes in rainfall, temperature and increased frequency of coastal storms. Local reduction in rainfall will result in a decrease in freshwater flow, and may cause estuaries to close more frequently and permanently open estuaries to become more constricted (and even close in the long-term). Estuary-associated fish species are known to be sensitive to reductions in the volume of freshwater runoff and this may reduce the abundance of these species which will also have fisheries implications





**Figure 201.** A summary of actual and potential climate change influences on the fishes of southern African estuaries (after James et al. 2013).

Changes in:

(a) freshwater, (b) terrestrial and (c) marine conditions will likely result in habitat loss, salinity and depth alterations, eutrophication and changes in estuarine water temperature, turbidity and nutrients, altered estuarine mouth dynamics, all of which will impact on estuarine fish communities.

Changes due to:

- (a) Alterations in rainfall, sedimentation, river water temperature, nutrient concentrations and hydrodynamics.
- (b) Changes in air temperature, sedimentation, organic and nutrient inputs.
- (c) Decreasing pH, increasing storm frequency, a change in wave climate and sea surface temperature, increasing sedimentation and sea-level rise.

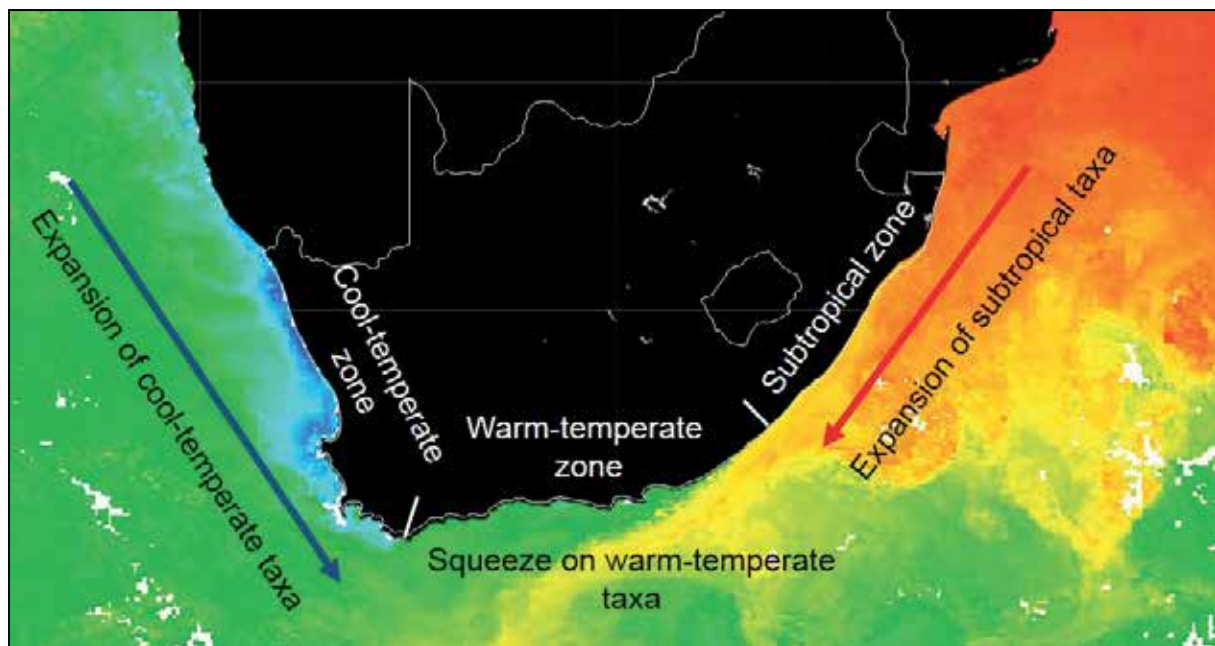
(James et al. 2013).

Reduction in freshwater flow will also reduce the quantity of nutrients entering estuaries, with a resultant impoverishment of the biota. Increases in extreme precipitation events projected for the east coast may result in increased freshwater flow and elevated delivery of sediment to estuaries as a result of runoff from land and river and stream channel erosion, which may significantly alter estuarine fish communities through the clogging of their gills, smothering of the benthos and create indirect impacts through elevated turbidity (e.g. prey detection and predator avoidance).

Like most parts of the world, there has been a general upward trend in air temperatures throughout southern Africa which has a direct influence on river and estuarine water temperatures, especially small temporarily closed systems. Changes in the coastal SST are, however, expected to be more heterogeneous, e.g. the mean SST increase of 0.25°C per decade is not uniform and there is evidence of cooling in some areas where strengthened upwelling occurs.

Increasing estuarine temperatures, together with future ENSO episodes, are predicted to result in shifts in species distributions, with tropical species moving south into estuaries dominated by more temperate taxa. Coastal cooling in some areas may, however, limit the ability of these species to shift their distribution westwards over long distances. Furthermore, it is unlikely that the cooling, associated with strengthened, sporadic upwelling will promote a movement of more temperate fish taxa beyond their existing range in a westerly direction. However, there is a very real threat that the range of certain temperate species may actually shrink due to the increasing water temperatures in most estuaries, particularly those occupying shallow closed systems which will respond rapidly to elevated air temperatures (James et al. 2013).

Shifts in species distribution and changes in temperature dependent processes such as growth, maturity and feeding will ultimately result in changes in community composition within estuaries, but this is very difficult to predict as different species will respond differently to warming.



**Figure 202.** Diagrammatic representation of the major distributional changes in marine and estuarine biota that are occurring in the three biogeographic zones along the southern African coastline (after Whitfield et al. 2016). The MODIS satellite sea surface temperature image is a 10 day average from February 2009.

Species less able to respond to changes in climate are likely to decrease in abundance and this may ultimately result in localized extinctions. Species with slow growth rates, and those reliant on more stable physico-chemical conditions, are likely to be less resilient to climate driven changes.

Many estuary-associated marine species are overexploited and there is evidence that the stocks of some species have collapsed (Whitfield & Cowley 2010). With the impacts of climate change likely to place additional stress on exploited species, the sustainability of estuarine fisheries may be further compromised, even if fishing pressure is reduced.

Available evidence suggests that the south-westward expansion of the subtropical zone down the east coast of southern Africa is gaining momentum (Figure 202), with strong evidence of pioneer mangrove, invertebrate and fish species now occupying Eastern Cape estuaries within the current warm-temperate biogeographic region. This is epitomized by the situation in the permanently open Kariega Estuary where mangrove flora (e.g. *Bruguiera gymnorhiza*) and fish fauna (e.g. *Periophthalmus argentilineatus*) are already showing an ability to establish isolated populations

within the existing saltmarsh habitats. Typical mangrove associated crab species (e.g. *Uca annulipes*) have also colonized this estuary in large numbers, a trend that is likely to be repeated in other permanently open Eastern and Western Cape estuaries (Whitfield et al. 2016). Once these founder populations are well established it is likely ichthyofaunal communities will be modified and that overall transformation of the ecosystem structure will accelerate.

Further global warming will result in the establishment of mangrove forests where saltmarshes currently exist, which will then be followed by an increase in dominance of invertebrate and fish assemblages that are characteristic of such habitats. By deduction, there will be a concomitant decline in saltmarsh plants and associated invertebrate species. The movement of tropical and subtropical fish species into the warm-temperate biogeographic region has been documented very clearly (James et al. 2008c) and is also likely to gain momentum as global warming continues. Some species are already common in the warm-temperate / cool-temperate transition zone where *Pomadourys commersonnii* and *Redigobius dewaali* have established robust breeding populations.

Other tropical taxa, not recorded in temperate estuaries as yet, may also appear in the region as global warming progresses.

In contrast to the expanding distribution by pioneer populations of tropical species into the warm-temperate zone, endemics within this zone are being subject to a temperature 'squeeze' from both the east and the west (Figure 202), with increased competition a likely outcome as tropical species become more abundant in the region and expansion by endemic taxa to the west is not possible due to predicted increased upwelling in this region (Rouault et al. 2010). Indeed, it is very likely that cool-temperate taxa will expand

eastwards as temperatures of coastal waters to the west of Cape Agulhas decline due to increased upwelling, which will further lower the temperatures in open estuaries in the south-western Cape. Water temperatures in TOCEs of this region are, however, likely to increase due to continental effects and the lack of marine influence. The extent to which such scenarios occurred in permanently open and temporarily open / closed estuaries during warming periods in the Holocene Climate Optimum is largely unknown but recent research in the Wilderness Lakes region is providing valuable insights in this regard (Wündsche et al. 2018).

### 5.3 FISH ASSEMBLAGES AND COASTAL CONNECTIVITY

Historical and recent connectivity with the marine environment in coastal and estuarine lakes and lagoons is a primary determinant of present day fish assemblages in these systems. Coastal lakes are isolated from the sea and estuarine lakes retain a permanent or intermittent connection with the marine environment. A small group of estuarine fish species have persisted in both types of lakes. These fishes are all small, estuarine resident species that are capable of completing their life cycles in both estuaries and isolated coastal lakes (Bruton 1979a).

The pelagic *Gilchristella aestuaria* and *Atherina breviceps*, inhabit coastal and estuarine lakes across the full biogeographic range within southern Africa. In subtropical lakes such as Sibaya some members of the families Gobiidae have also persisted, e.g. *Croilia mossambicus*, *Glossogobius giuris* and *Silhouettea sibayi*. These are all species with tropical affinities and an ability to breed in freshwater. However, their presence in these systems is mainly as a result of biogeographical factors rather than differences in the origin and evolution of coastal lakes along the coast. This hypothesis is supported by the successful establishment of *Oreochromis mossambicus* in temperate lakes. This cichlid occurs naturally in east flowing rivers down to the Bushmans in the Eastern Cape Province and is present in the lower reaches of almost all rivers and estuaries within its native

range. Upon introduction, this species readily established in the more temperate southern Cape coastal and estuarine lakes where it is now ubiquitous.

A euryhaline physiology, together with a reproductive style suited to establishment and proliferation in lentic environments, is important to the success of these estuarine fishes in coastal lakes. A study on the effect of propagule pressure on the establishment success of fishes in irrigation ponds in the Sundays River floodplain by Woodford et al. (2013) demonstrated that the most successful native colonizers were *Gilchristella aestuaria*, *Oreochromis mossambicus* and *Glossogobius callidus*. It is interesting to note that these three species are also well represented in the coastal lake ichthyofauna around southern Africa. Apart from the water chemistry, habitats within these coastal lakes closely resemble that of estuarine lakes in various ways, e.g. suitable bare sediment areas for nesting by *O. mossambicus* (Bruton & Boltt 1975) and the presence of submerged aquatic vegetation which is important for egg attachment by *Atherina breviceps* (Neira et al. 1988).

Estuarine spawning fishes that are absent from coastal lakes in southern Africa include *Ambassis ambassis*, a species that is common in the oligohaline waters of southern African subtropical temporarily open / closed estuaries (e.g. Mhlanga) and estuarine lakes (e.g. Amanzimnyama), but





**Figure 203.** Groenvlei was previously connected to sea via the Swartvlei Estuary but within the last 3 000 years has become completely isolated and lost its marine fish fauna (Photo: Alan Whitfield).



**Figure 204.** Aerial view of the winding Serpentine that currently links Eilandvlei, Langvlei and Rondevlei to the Wilderness Estuary, thus facilitating juvenile marine fish recruitment into these lakes (Photo: Alan Whitfield).

these fishes clearly require an intermittent connection with the sea or estuarine environment for long-term survival in freshwater systems. A similar situation exists for various eleotrid species in the subtropical systems of northern KwaZulu-Natal.

The loss of connectivity with estuarine systems has also impacted the diversity of marine fishes in all coastal lakes. No marine fishes are found where connectivity has been completely lost (e.g. Groenvlei, Figure 203). The extinction of marine fishes in these systems would have occurred gradually as their linkages with marine and estuarine environments became more constrained over time and salinity regimes shifted from estuarine to fresh. While most estuary-associated marine fishes in southern Africa are tolerant of low salinities rather than hypersaline conditions (Whitfield et al. 1981), relatively few inhabit completely freshwater areas as a matter of preference.

In systems that have retained tenuous linkages with the sea (e.g. Wilderness lakes, Figure 204) elements of the marine fish assemblage have persisted. Other marine spawning species in 'transitioning' estuarine lakes include known facultative catadromous species, such as *Pseudomyxus capensis* in the warm-temperate region and *Megalops cyprinoides* in the subtropical region. Additional marine species that typically occur in transitioning estuarine lakes include species that penetrate rivers elsewhere in southern Africa (e.g. *Mugil cephalus*). The numbers and types of marine species occurring in different systems depends upon the nature of the connection with the marine environment and the prevailing salinity regime. Thus, in Rondevlei and Langvlei where connectivity with the greater Wilderness lakes system has been retained and salinities are mesohaline, 16 marine and estuarine species occur, whereas in Verlorenvlei where connectivity is only established under flood conditions and salinities are lower, only three marine species occur. Marine fishes are a consistent component of the fish fauna of Lake Cubhu but in Lake Mzingazi they occur only irregularly and in low abundance as recruitment opportunity has been limited to sporadic extreme flood events.

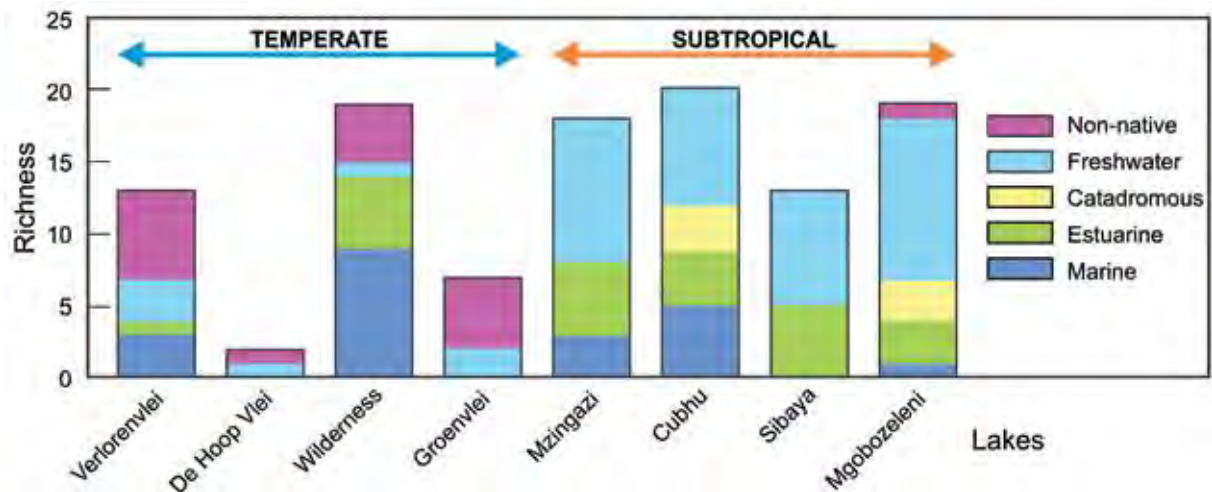
The Kosi segmented estuarine lakes system in

northern KwaZulu-Natal supports a fish fauna that is spatially distributed in a manner that reinforces our observations of fish assemblages in evolving lakes and lagoons elsewhere in South Africa, and illustrates the interplay of marine/estuarine connectivity and salinity effects. The mouth of Kosi Estuary, with near marine salinities, supports a rich diversity of more stenohaline marine fishes (Blaber 1978). Most of these do not penetrate the system beyond the estuary and species richness falls away quickly in the next two upstream estuarine lakes (Makhawulani and Mpungwini) which have polyhaline salinities. The fish here are dominated by estuarine-associated marine and estuarine resident species. Lake Nhlanga, 12 km from the mouth, and separated from the lower estuarine lakes by a long and narrow channel, has a fresh to oligohaline salinity regime and is dominated by estuarine resident fishes. Marine fishes still occur in high numbers but reduced diversity. Lake Amanzimnyama at the head of the system (20 km from the sea) is fresh, with the estuarine residents *Gilchristella aestuaria* and *Ambassis ambassis* dominating fish abundance. Marine species still occur, but these are rare and restricted to mainly catadromous taxa. Essentially the marine species are replaced by at least nine freshwater species which are the same as those that typically occur in other KwaZulu-Natal coastal lakes. Thus in one coastal system there is strong evidence of the combined effects of changing salinity and connectivity on fish composition as the compartments become increasingly freshwater dominated and less connected with the marine environment (Whitfield et al. 2017b).

Freshwater fish diversity in coastal lakes and lagoons is a function of historical and present biogeography and salinity. From a freshwater-biogeography perspective, the inflowing rivers of the four temperate systems reviewed here contain three or fewer native freshwater fishes, while the subtropical lakes are fed by river systems that can contain more than 40 freshwater fish species and are periodically connected to one another during times of flood.

As a result of limited tolerance to salinity, few freshwater fishes penetrate estuaries in southern Africa (Whitfield 2015). Those that do include





**Figure 205.** Fish species richness in four temperate and four subtropical coastal lakes/lagoons based on fish guild composition (after Whitfield et al. 2017b).



**Figure 206.** Lake Sibaya, an estuarine lake that has evolved into a coastal lake within the last 10 000 years, with major consequences for the associated ichthyofauna (see Whitfield et al. 2017b for details).

*Oreochromis mossambicus*, *Coptodon rendalli*, *Clarias gariepinus*, *Pseudocrenilabrus philander*, *Enteromeus paludinosus* and *E. trimaculatus*, all of which occur in KwaZulu-Natal coastal lakes within their natural biogeographical range.

Other freshwater species that occur in coastal lakes are invariably secondary freshwater fishes which have some tolerance of brackish water. As is characteristic for the Cape Fold Ecoregion (Ellender & Weyl 2014), rivers feeding Verlorenvlei, De Hoop Vlei, the Wilderness lakes and Groenvlei contain few native species. This, in conjunction with the relatively high salinities in some of these systems, explains the low representation of native freshwater fishes. The Verloren River for example, contains only the three native species that are represented in the lake.

Elevated salinity is also a likely key factor in the occurrence and distribution of freshwater fishes in De Hoop Vlei. Despite being connected to a relatively large catchment of approximately 1 200 km<sup>2</sup>, only *Sandelia capensis* occurs in the lake and only during oligohaline phases (Harrison 1957). In the Wilderness Lakes, the inflowing-river Duiwe River contains the barb *Pseudobarbus swartzi* but salinities of up to 8 are likely to be the primary factor preventing its occurrence in the floodplain lakes.

Subtropical coastal lakes in KwaZulu-Natal all have freshwater conditions or very low salinities (<1) and support a more diverse freshwater fish assemblages (10-12 species) compared to temperate coastal lakes (Figure 205). Historical connectivity to larger catchments may play a role in all three subtropical case studies. Lakes Cubhu and Mzingazi were both part of a larger Richards Bay system that was linked to the Mhlathuze River catchment, and Lake Sibaya (Figure 206) was previously connected to the large Phongola River before it was diverted northwards towards Maputo Bay.

Biogeographical considerations, however, are a more likely proximate reason why coastal lakes in KwaZulu-Natal support higher freshwater fish species diversity than do similar systems in temperate regions (Weyl & Cowley 2015). In both zoogeographical regions *Atherina breviceps* and *Gilchristella aestuaria* feature as relict

species capable of occupation of both estuarine and coastal lakes and lagoons. Although other estuarine spawning species such as *Croilia mossambicus* and *Glossogobius giuris* are also capable of making the transition during the evolutionary changes within these aquatic ecosystems, many marine and some estuarine taxa appear to rely on continued connectivity with the sea in order to persist within such water bodies. Such linkages are likely to play an important role in the spawning and /or early life stages of these particular taxa (Whitfield et al. 2017b).

Recent history has seen significant changes in the freshwater fish fauna of southern African coastal lakes, especially in the Western Cape systems that naturally support a very limited diversity of these fishes. These changes have been caused by translocations of subcontinental fishes beyond their natural distribution limits and the introduction of alien species. Some non-native fishes have persisted in most temperate lakes but they are generally absent from the subtropical systems. The reasons for this are unclear, but since there is evidence of the failed introduction of at least one species into Lake Sibaya, biotic resistance from the richer native fish communities is a possibility.

The impact of these introductions and translocations have not been studied in southern African estuarine and coastal lakes. In the latter closed systems it is probable that predation impacts on small estuarine fishes are significant. Predatory fishes have been observed feeding on native estuarine fishes (e.g. Weyl & Lewis 2006) but *Atherina breviceps* and *Gilchristella aestuaria* seem to have persisted in the presence of alien fishes for more than 80 years in Groenvlei. Indeed, the recent alien fish introductions is an example of the growing threats to these systems during a period when human activities have had significant negative impacts and show potential to match the changes recorded during the entire Holocene.

The historical changes in the fish faunas of estuarine and coastal lakes (e.g. Chater & van der Elst 1995, Cyrus & Wepener 1997, Vivier & Cyrus 2002) are examples of just one of the growing threats to these systems that are indicative of changes that have been introduced during a new

epoch, the 'Anthropocene', when human activities have become a significant impact on the Earth's geology, atmosphere and ecosystems. Impacts to southern African coastal lakes have become increasingly significant over the last 100 years, when agricultural development in the catchments of these systems has grown, with concomitant reductions in ground water levels and surface water inflows to coastal systems. This has affected salinity regimes in these systems, and has likely impacted both the flora and fauna of these lakes.

In KwaZulu-Natal, direct abstraction of freshwater occurs for municipal, industrial, agricultural and mining use. Extensive forestry development and direct abstraction from Lake Sibaya catchments has exacerbated the impact of prolonged droughts on the system. In 2016 the water level in Lake Sibaya was lower than previously recorded, to the extent that the system was divided into two basins separated by a dry sand spit. The installation of weirs in the coastal lakes in the vicinity of Richards Bay to increase abstraction yields has also caused barriers to fish migration and significantly impacted on the ability of marine fish faunas to enter or leave these lakes.

In the Western Cape Province, the introduction of alien and translocated fishes has been the overriding cause of changes in coastal lake fish faunas since the retreat of sea levels 3 000 to 4 000 years ago. It appears that these introductions have not led to localized extinctions of relict estuarine fish populations, but they have certainly placed pressure on them, through predation and /or competition for food resources.

In summary, the Holocene evolution of South African coastal lakes and lagoons has resulted in major changes in the composition of

fish populations over that period. Historical and current connectivity with riverine and marine environments are the primary determinants of present day fish assemblages in these systems (Whitfield et al. 2017b). A small and remarkably consistent group of relict estuarine species have persisted in these coastal lakes and lagoons.

The loss or reduction of connectivity with the sea has impacted on the diversity of marine fishes in coastal lake and lagoon systems, with no marine fishes occurring in those water bodies where connectivity has been completely broken (e.g. Sibaya, Groenvlei). In systems that have retained tenuous linkages with the sea (e.g. Verlorenvlei, Wilderness lakes) elements of the marine fish assemblage have persisted, especially the presence of facultative catadromous species.

Freshwater fish diversity in coastal lakes and lagoons is a function of historical and present biogeography and salinity. From a freshwater biogeographic perspective, the inflowing rivers of the four temperate systems reviewed here contain three or fewer native freshwater fishes, while the subtropical lakes that are fed by river systems contain up to 40 freshwater fish species. Thus the significantly higher fish species diversity in subtropical versus temperate coastal lakes and lagoons comes as no surprise (Figure 202).

Recent studies in Lake St Lucia provide additional evidence of what happens when marine connectivity is lost or severely reduced. Between June 2002 and May 2007 the fish fauna of the lake became progressively dominated by the freshwater *Oreochromis mossambicus* and estuarine *Ambassis ambassis* and *Hyporhamphus capensis*, with marine species making an insignificant contribution to the total (Vivier et al. 2010).

#### 5.4 FRESHWATER DEPRIVATION: A MAJOR THREAT

Much of southern Africa has a semi-arid climate with highly seasonal and variable rainfall. In addition, years of above-average rainfall frequently alternate with dry cycles, the latter often punctuated by heavy rains of varying magnitude and extent. These natural extremes provide the perturbations that contribute to the physico-chemical variability which, in turn, affects biotic processes in estuaries (Benson 1981, Forbes & Cyrus 1993).

Growing demand for fresh water in southern Africa has led to widespread impoundment and extraction of surface and underground water resources. In addition, invasive alien trees are having a considerable negative influence on the water yields from catchment areas (Dye & Poulter 1995). When river flow patterns are altered and the intensity and frequency of flood events are modified, these disturbances change natural fluctuations within the riverine and estuarine ecosystems. Smaller floods are commonly entirely removed from the river discharge spectrum and large flood events may be attenuated according to the available dam storage capacity

at the time of the flood (Adams & Talbot 1992). Imposition of these human disturbances often results in estuarine processes deviating from natural patterns, the implications of which need to be understood before effective management strategies can be devised to maintain the diversity of estuarine systems along the coast.

The combined average annual runoff of South Africa's rivers is estimated to be  $53\,500 \times 10^6 \text{ m}^3$ . In some areas the highly variable river flow can have periods of up to 10 consecutive years of less than average flow. Because of this variability and the high evaporation losses from storage, it is estimated that only about 62% of the mean annual runoff (MAR) can be exploited economically.

The largest users of fresh water in South Africa are farmers (Figure 207) and the demand for water is increasing due to growing human populations, together with a rapid urbanisation process and increased access to water reticulation schemes. Based on projected demand, it has been estimated that all surface water resources will be fully utilized by the year 2020 (Davies & Day 1986).



**Figure 207.** Extensive sugar cane cultivation on the Mfolozi floodplain – part of the reason why Lake St Lucia is currently regarded as a freshwater deprived estuarine system (Photo: Ricky Taylor).

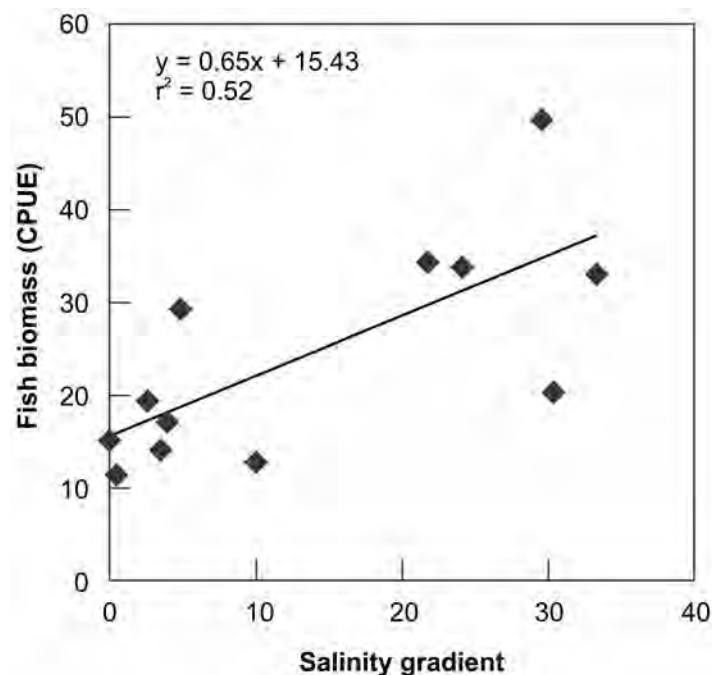
### Freshwater requirements of estuaries

An important aspect of the South African National Water Act of 1998 requires the implementation of Resource Directed Measures (RDM). The main aim of the RDM is to determine the 'Ecological Reserve', which is the water quantity and quality required for the protection of the basic needs of aquatic systems. The needs are defined as the quality and quantity of water required to maintain a desired level of ecological structure and function, or quality, of a specific section of the aquatic system (e.g. river reach, estuary, coastal lake).

Using a variety of sources, Whitfield & Bruton (1989) synthesized some of the principal effects of freshwater deprivation on the physical and biotic components of estuaries in the Eastern Cape Province. These authors emphasized that one of the main effects of impoundments is to reduce the incidence and amplitude of minor floods/pulses in rivers and estuaries. Floods are a critical determinant of the physical structure, functioning and evolution of estuaries, and a change in the pattern and magnitude of floods can lead to an alteration in sedimentary processes,

depth profiles, mouth configuration, duration of the open phase and tidal prism within an estuary. Since both river floods and the physical variables described above have a direct and indirect effect on the estuarine biota (e.g. McLachlan & Grindley 1974, Marais 1982, Talbot et al. 1990, Whitfield & Paterson 1995), future research in this field should be directed at elucidating these complex short and longer term interactions.

Indications are that estuaries with strong freshwater inputs are attractive to subadult and adult marine fishes because data presented by Marais (1988) showed that gill net catches in Eastern Cape Province estuaries are positively correlated with increasing longitudinal salinity gradients (Figure 208). In addition, he also determined that there was a highly significant positive correlation ( $r=0.46$ ,  $p<0.001$ ) between estuarine fish abundance and catchment size, as well as between overall fish biomass and catchment area ( $r=0.59$ ,  $p<0.001$ ), both trends being a probable consequence of increased river inflow associated with increasing catchment area. The higher run-off from larger catchments almost invariably



**Figure 208.** Relationship between longitudinal salinity gradient, which is the difference in mean salinity between the tidal head and mouth of an estuary, and gill net fish biomass (CPUE) in a range of permanently open estuaries along the warm-temperate Eastern Cape coast (data from Marais 1988).



leads to positive estuarine salinity gradients and increased nutrient inputs, together with higher fish abundance (Whitfield et al. 1994).

#### Effects of impoundments on estuaries

The effects of freshwater deprivation will vary according to estuary type and locality. Estuaries in regions of low rainfall and high evaporation rates are more likely to be adversely affected by excessive freshwater abstraction than similar systems in higher rainfall areas. This is reflected in the virtual absence of hypersaline conditions in KwaZulu-Natal estuaries when compared with the more frequent occurrence of such conditions in estuaries from semi-arid regions where annual precipitation is lower and evaporation higher.

Successionary trends in estuaries can be reversed or changed by episodic events, e.g. river flooding. In addition, the frequency and intensity of episodic events within a single estuary vary, thus producing a range of possible trajectories. The effects of certain human perturbations (e.g. dams) are to hasten the succession along trajectories which often result in the temporary or permanent disruption of certain estuarine functions. In instances where freshwater pulses are prevented from reaching estuaries due to dam

development, the natural sequence of estuarine biota responses is altered, and small scale successions become less frequent (Wooldridge & Melville-Smith 1979).

Long-term freshwater deprivation can lead to a complete restructuring of energy flow within the affected estuary. In general, a high proportion of primary production in those southern African estuaries which receive adequate riverine input is contributed by phytoplankton. Conversely, when riverine discharge into an estuary has been drastically curtailed, food webs usually centre on benthic primary production (Allanson & Read 1995).

How differing riverine inputs may be reflected in estuarine system properties can be illustrated by a comparison of the Swartkops and Kromme estuaries (Table 26). Both have similar physical dimensions, lie in the same climatic region, but differ in the amount of riverine input by an order of magnitude, a reduction solely due to impoundments in the catchment (Schlacher & Wooldridge 1996b). The resulting shifts in ecosystem properties (Table 26) suggest that river flow is vital to both pelagic productivity and the maintenance of a range of food chains within estuaries. The increasing abstraction of fresh water from both

Table 26. Comparisons of some ecosystem properties between the Swartkops Estuary which receives moderate freshwater inflow and the Kromme Estuary where major dams in the catchment have severely reduced riverine inflow (data from Baird & Ulanowicz 1993).

	Swartkops	Kromme		Swartkops	Kromme
<i>Physico-chemistry</i>			<i>Net primary production</i>		
Area (km <sup>2</sup> )	4	3			
Temperature (°C)	13-26	13-28	Pelagic production (mg C m <sup>-2</sup> day <sup>-1</sup> )	319	28
Mean river flow (m <sup>3</sup> s <sup>-1</sup> )	0.6	0.06	Benthic production (mg C m <sup>-2</sup> day <sup>-1</sup> )	1 504	2 284
Salinity range	10-35	33-35	Pelagic: Benthic ratio	1:5	1:81
<i>Primary consumer biomass</i>			<i>Secondary consumer biomass</i>		
Suspension feeders (mg C m <sup>-2</sup> )	45 721	21 814	Suspension feeders (mg C m <sup>-2</sup> )	5 900	3
Deposit feeders (mg C m <sup>-2</sup> )	8 050	21 556	Deposit feeders (mg C m <sup>-2</sup> )	15 500	6 579
Suspension: Deposit	1:0.28	1:0.99	Pelagic: Benthic ratio	1:3	1:2193

large and small river catchments has had the effect of forcing certain southern African estuarine types into extreme states (Whitfield & Bruton 1989). In particular, pelagic productivity is adversely affected, resulting in major declines in the abundance of planktivorous fish species.

### Permanently open estuaries

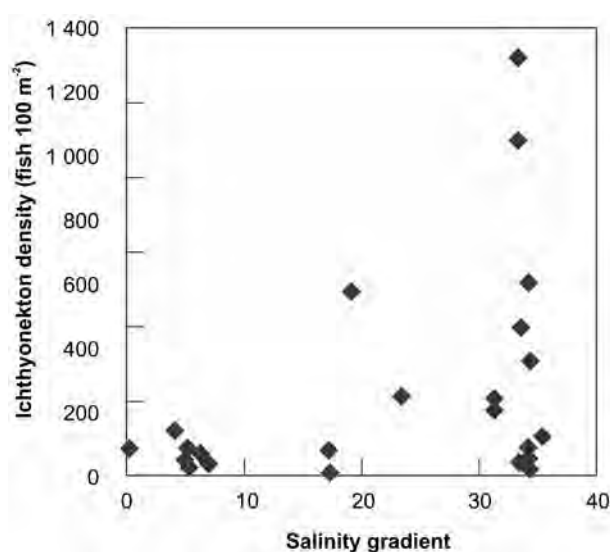
Fewer than 40 South African estuaries maintain permanent tidal inlets with the sea (Reddering & Rust 1990) and it is these systems that are most threatened by reduced freshwater inputs. The extent to which river water is impounded varies, but in some catchments the combined capacity of existing impoundments already exceeds the mean annual runoff of the river system, e.g. the Kromme system. Large episodic floods ( $>80 \times 10^6 \text{ m}^3$ ) can still flow over the walls of Kromme catchment dams, depending on water volumes held at the time of the flood. However, smaller floods do not reach the Kromme Estuary, with a resultant loss of nutrient and organic input to this system (Emmerson & Erasmus 1987).

Where major impoundments prevent significant river flow into these estuaries, tidal mixing processes become dominant and temporarily change the estuary into an 'arm of the sea' (Whitfield & Bruton 1989). Hypersaline conditions ( $>40$ ), particularly during summer, have been recorded in the upper reaches of certain

permanently open estuaries deprived of freshwater inflow. Such conditions are most prevalent during extended droughts due to high evaporation rates and zero river inflow.

River flow into estuaries influences not only the salinity but also the biochemical properties of the water body, including the introduction of catchment olfactory cues to both the estuary and adjacent ocean. Fishes have a highly developed sense of smell and it is probable that olfactory cues, which can be of freshwater or estuarine origin, act as a guide to marine larvae and 0+ juveniles that are attempting to locate estuarine nursery areas (James et al. 2008a). Indirect evidence to support this view is provided by the high densities of estuary-associated marine fish larvae in the surf zone that were attracted to plumes of river water leaving the Seekoei Estuary (Strydom 2003).

Permanently open Eastern Cape estuaries with longitudinal salinity gradients  $>19$  have considerably higher densities of 0+ juvenile marine fishes (Figure 209) than those systems where salinity gradients are small or absent (Whitfield 1994a). A similar finding was arrived at by Martin et al. (1992) who found that the densities of post-larval marine migrants in the St Lucia Estuary increased markedly following an episodic flushing of that system. Although the inference from the above studies is that the salinity gradients are the attractant for these 0+ juvenile fishes, it is more



**Figure 209.** Relationship between longitudinal salinity gradient (which is the difference in mean salinity between the tidal head and mouth of an estuary) and postflexion marine fish recruits in three permanently open estuaries along the Eastern Cape coast (after Whitfield 1994a).

likely that the increased amounts of olfactory cues that are exported to the marine environment on each ebb tide are vital to the recruitment process. Loss of river inputs to permanently open estuaries will compromise that process.

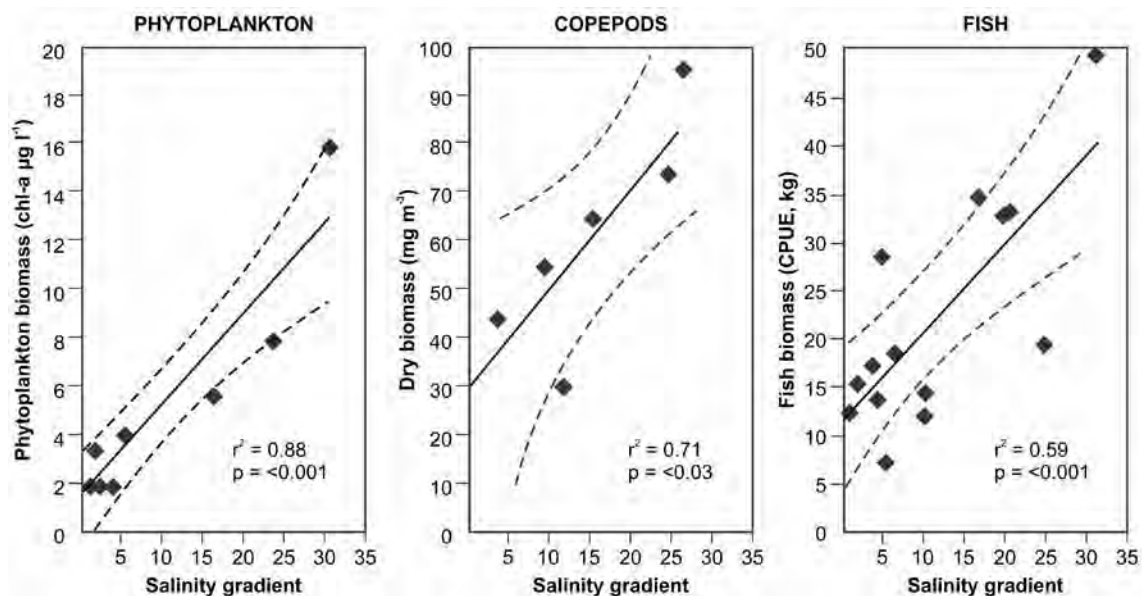
The biota of permanently open estuaries in the Eastern Cape Province undergoes several important changes following significant long-term reductions in riverine input. Primary food resources in the water column (e.g. phytoplankton and particulate organic matter) decline (Allanson & Read 1995, Grange & Allanson 1995) while macrophyte production increases due to the spread of marine plants such as *Zostera capensis* into the middle and upper reaches of such estuaries (Adams et al. 1992, Schlacher & Wooldridge 1996b). This expansion is primarily facilitated by the increased water transparency and reduced frequency of river pulses entering the estuary. The reduced dissolved nutrient levels in the water column do not have an adverse effect on submerged rooted plants since they can obtain the required nutrients directly from sedimentary sources.

Zooplankton abundance declines in association with reduced sestonic food availability (Grange & Allanson 1995, Baird & Heymans

1996) and the planktivorous fish community becomes less abundant. In essence, the estuary is left with a predominantly zoobenthic driven food web (Table 26).

The above findings are reinforced by the stable carbon isotope information documented by Paterson & Whitfield (1997) in the freshwater deprived Kariega Estuary, which showed that phytoplankton is relatively unimportant in the bionomics of this system. The positive effect of freshwater inflow on phytoplankton biomass usually involves two processes; firstly, the development of vertical stratification creates more stable hydrodynamic conditions which retain phytoplankton inside the estuary. Secondly, the bulk of inorganic nutrients in estuaries are allochthonous, and increases in river flow result in an increase in nutrient availability to estuarine primary producers.

The increased phytoplankton productivity is usually reflected in reduced submerged macrophyte cover and a higher zooplankton biomass (Grange & Allanson 1995) which, in turn, is able to support a higher fish biomass when compared to those estuaries where pelagic productivity is low. This is clearly shown in Figure 210, with



**Figure 210.** Relationship between biomass of different biota and the magnitude of freshwater inflow over a range of permanently open estuaries along the Eastern Cape coast. The measure of riverine inflow is reflected in the longitudinal salinity gradient which is the difference in mean salinity between the tidal head and mouth of an estuary. Each data point represents mean values for an estuary and the 95% confidence limits are shown by a dotted band on either side of each regression line (after Schlacher & Wooldridge 1996b).

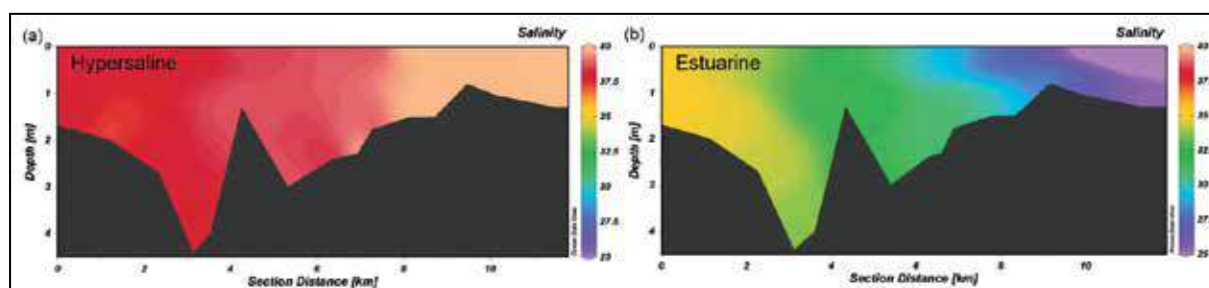
those Eastern Cape estuaries with little or no salinity gradient (poor or zero river flow) having a limited copepod biomass and this, in turn, being reflected by a reduced fish biomass (when compared to estuaries with a higher river flow).

A recent study in the Kariega Estuary has provided clear evidence of the medium-term benefits of episodic river flooding on estuarine fish assemblages (Nodo et al. 2018). This freshwater-deprived system experienced a major episodic river flood event in October 2012 when river flow was the highest ever recorded in almost 50 years. Sampling of demersal fish assemblages in the Kariega Estuary using a beam trawl between December 2013 and November 2014 provided an opportunity to document differences between fish composition and abundance under earlier negative salinity gradient conditions (Figure

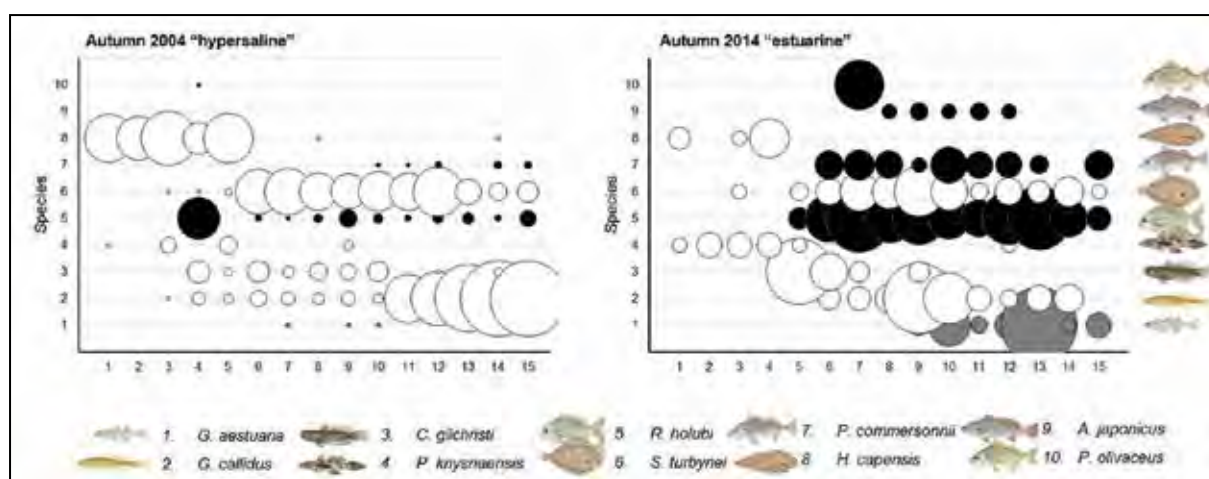
211a) when compared to fish assemblages under the subsequent positive salinity gradient conditions (Figure 211b).

Results indicated an increase in the abundance of benthopelagic marine migrant species such as *Rhabdosargus holubi* (Figure 212). In particular, the early juveniles of important fishery species such as *Pomadasys commersonnii* increased in abundance in the middle and upper reaches of the estuary when compared to the same stations under reversed salinity (freshwater deprived) conditions (Figure 212). The pelagic *Gilchristella aestuaria* was also significantly more abundant under estuarine than hyperhaline conditions (Nodo et al. 2018).

Similar to the above study, Vorwerk et al. (2009) also documented an increase in the abundance of both *Argyrosomus japonicus* and



**Figure 211.** Mean salinity recorded in the Kariega Estuary during (a) hypersaline and (b) estuarine conditions (after Nodo et al. 2018). The section distance is measured from the mouth to the head of the estuary.



**Figure 212.** Bubble plots showing the catch per unit effort (0.3-23 fish per haul) of the ten most abundant fish species caught at 15 sites during hypersaline (autumn 2004) and estuarine (autumn 2014) conditions in the Kariega Estuary (after Nodo et al. 2018). Pelagic species are shaded grey, benthic species white and benthopelagic species are black. Site 1 was near the mouth and Site 15 near the head of the estuary.

*Pomadasys commersonnii* following a far smaller spring river pulse in 2006. However, much smaller length classes were also recorded following the 2012 reset flood than following the more minor flood in 2006 (Nodo et al. 2018).

### Temporarily open /closed estuaries

Most of these systems have small river catchments (<500 km<sup>2</sup>) and extended periods when the river flow is minimal or even ceases altogether (Whitfield 1992). The magnitude of river flow into some of these estuaries has declined considerably in recent years as a result of the growing number of farm dams that retain increasing proportions of freshwater flow from the catchments. The effect of farm dams is most noticeable during and after prolonged periods of drought and at the beginning of the rainy season. The Seekoei Estuary in the Eastern Cape is a good example of how farm dams have had a major negative impact on the ecology of this TOCE.

Large amounts of sediment, which accumulate during the lagoonal phase (Cooper 1989), are removed from temporarily open estuaries during river flooding (Reddering & Esterhuysen 1987). Since mouth opening and closing of the above systems is directly linked to the amount of runoff feeding the inflowing rivers, impoundments within the catchment can have a major influence on the duration of the open and closed phases (Whitfield et al. 2012c). Reduced river inflow will lead to prolonged mouth closure and a shorter open phase, thus inhibiting invertebrate and fish migrations between the estuary and the sea (Forbes & Benfield 1986, Kok & Whitfield 1986, Wooldridge 1991).

In addition to its influencing mouth phase, freshwater deprivation during droughts can also lead to hypersaline conditions developing within closed systems. This can, in turn, result in the loss of major components of the food web, especially those species that are intolerant of hypersalinity. An extensive fish kill was recorded in the Seekoei estuarine lagoon when the salinity exceeded 95, whereas no fish kill was recorded in the adjacent Kabeljous system where the salinity was only 55. The Seekoei catchment, which is similar in size to that of the Kabeljous catchment, has more farm

dams than the latter system. The inference here is that abstraction of fresh water in the Seekoei catchment during the 1988/89 drought was sufficient to elevate hyperhaline conditions in this estuary, thereby resulting in the loss of a high proportion of the aquatic biota.

An increasing threat for many TOCEs is the excessive input of nutrients or even untreated sewage water from leaking or burst pipes in some municipal areas. These catchment inputs often create anoxic conditions due to elevated biological oxygen demand leading, in turn, to fish kills (e.g. Begg 1978).

### Estuarine lakes

Salinities in estuarine lakes are highly variable and depend on a variety of factors, the most important of which is the balance between freshwater input, evaporation, and water exchange across the mouth. Salinity variations in the St Lucia system can range from less than 5 to more than 100 (Day 1981c). Although salinity extremes have always been a natural feature of Lake St Lucia, the magnitude of the salinity peaks during the past half century has increased following the construction of impoundments in the catchment basin (Whitfield & Taylor 2009). Unless freshwater supply can be assured, the amplitude and temporal scale of the salinity fluctuations within this estuarine system are likely to increase in the future, i.e. hypersaline conditions will be higher and last longer than under natural conditions. The adverse impact of salinities above 50 on both the flora and fauna of Lake St Lucia has been well documented (e.g. Figure 213, Bolt 1975, Wallace 1975a, Adams et al. 2013) and management strategies aimed at reducing the magnitude of future hypersaline conditions are being investigated.

A major step forward towards increasing the freshwater supply to Lake St Lucia was taken within the last decade by Ezemvelo KwaZulu-Natal Wildlife and the iSimangaliso Wetland Park Authority, a move that was fully supported by scientists working on the system (Whitfield et al. 2013). This new initiative involves the relinkage of the Mfolozi River to the lower St Lucia Estuary directly behind the north/south primary sand berm. This management strategy has a major



challenge in the form of reducing the influence of the high sediment load on the estuary and Narrows, whilst at the same time obtaining the benefits of freshwater inputs to the lake system.

Freshwater deprivation in Western Cape systems such as Swartvlei and Botrivier are unlikely to cause hypersaline conditions, but would result in prolonged mouth closure. These conditions favour estuarine animal species which can complete their life cycle in brackish waters, but would result in a decline in marine dependent invertebrate and fish populations due to natural mortality and a breakdown in natural recruitment processes (Bennett et al. 1985, Wooldridge 1991). Long term freshwater deprivation would also lead to a reduced nutrient input, with concomitant declines in primary production within these nutrient poor estuarine lakes (Howard-Williams 1977). Declining water quality in some of these systems is also cause for concern.

#### Estuarine bays

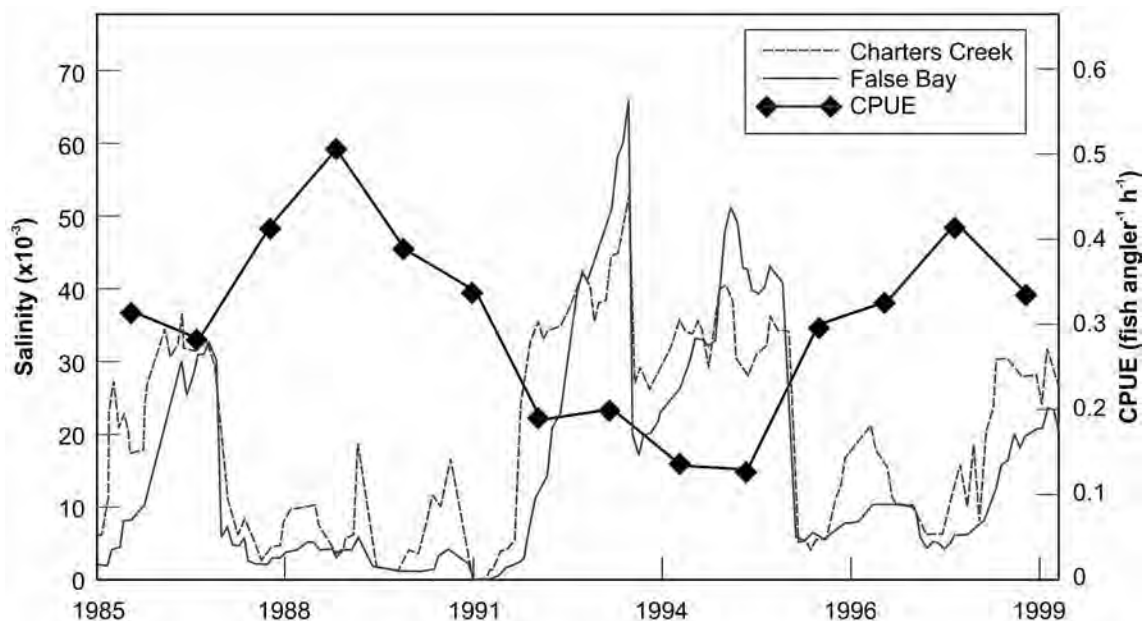
Increased freshwater abstraction from inflowing rivers would result in an increase in salinities in the upper reaches of these systems, but little change would be recorded in the lower and middle reaches due to strong tidal exchange patterns.

Water temperatures in these reaches are strongly influenced by marine conditions and these would tend to extend further up the estuary if river flow ceased.

The fauna and flora of estuarine bays are dominated by marine species (Day & Morgans 1956, Viljoen & Cyrus 2002) which are unlikely to be adversely affected by a reduction in freshwater input. However, loss of river flow into an estuarine bay would have a negative impact on oligohaline and migratory species (e.g. freshwater prawns *Macrobrachium* spp. and the freshwater mullet *Pseudomyxus capensis*) which utilize the riverine portions of these systems (Bok 1979, Reavell & Cyrus 1989). Overall primary productivity would be adversely affected by a reduction in river flow, especially in the upper reaches.

#### River mouths

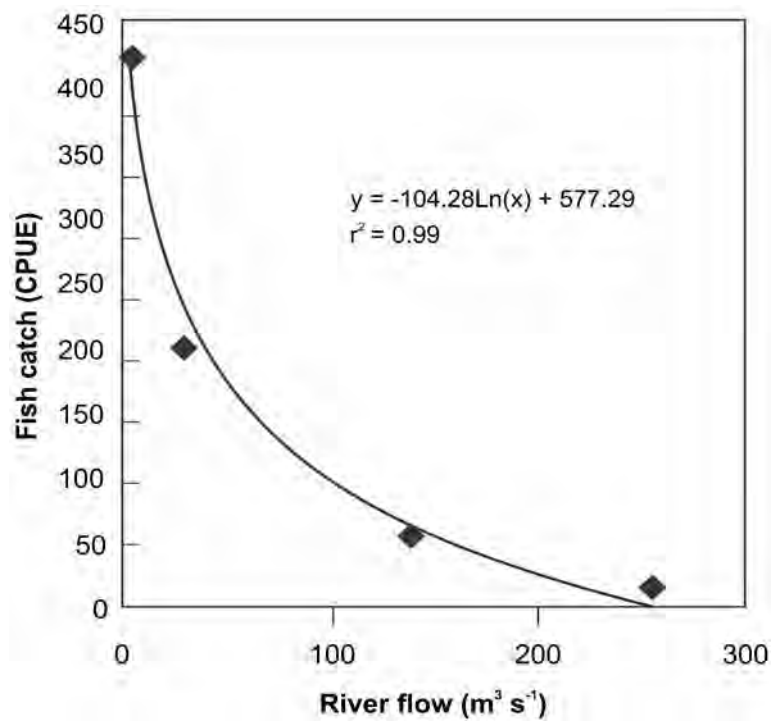
Freshwater deprivation in these systems would lead to saline conditions extending higher up the estuary, provided that the mouth remained open during the low river flow conditions. If the mouth closed, oligohaline conditions are likely to prevail behind the sand bar during the lagoonal phase (which is likely to be of short duration due to the large catchment size of such systems).



**Figure 213.** Increases and declines in angler's fish catches at Lake St Lucia in relation to prevailing salinity regimes within the system. Note that the lowest catches coincided with a period (1993-1995) when hypersaline conditions prevailed over much of the lake area (after Mann et al. 2002).



**Figure 214.** Loss of major riverine inputs to the Orange Estuary over extended periods has resulted in strong marine inflows to this system on flood tides. Note the absence of turbid river water in the mouth of the Orange Estuary in this picture (Photo: Steve Lamberth).



**Figure 215.** Seine net fish catches in the Thukela Estuary under four different river flow regimes (after Whitfield & Harrison 2003).

Freshwater and estuarine biota tend to dominate river mouths (Day 1981c). Marine and estuarine organisms are usually confined to the lower reaches (Brown 1958), extending upstream during periods of reduced freshwater input. In general, river mouths have a relatively depauperate aquatic biota, including fishes, with a surprisingly low freshwater faunal representation. Under high river flow conditions, the estuarine zone may even be pushed out to sea, thus limiting the usefulness of this type of system to most estuary-associated fish species.

A reduction in river flow into this type of system would probably be beneficial to both estuarine and marine fish species usually found in estuaries. This would apply particularly if the mouth remained open during low flow conditions and salinities within the estuary increased as a result of greater upstream tidal penetration (Figure 214). In the Thukela system there was an inverse relationship between the CPUE of fishes within the estuary and river flow, i.e. highest fish densities were recorded when river flow was low and vice versa (Figure 215).

## 5.5 MORTALITIES OF FISHES IN ESTUARIES

### Abiotic factors influencing mortalities

Fishes of southern African estuaries are adapted to highly variable conditions, and individual species can usually tolerate wide ranges of salinity, temperature, turbidity and dissolved oxygen. Indeed, Bennett (1985) expressed a view that, if changes of equivalent magnitude to those recorded in estuaries were to occur at sea, massive mortalities of marine life would be the end result.

Mass mortalities of fishes in estuaries are usually triggered by extreme and infrequent external changes such as floods, droughts, cold snaps and pollution events impinging on the aquatic environment. A review of the documented causes of southern African fish kills may assist in the prediction of future mortalities in estuaries, and highlight research areas that need to be explored if we are to understand the physiological basis for the species responses observed.

#### Salinity

Detailed information on the salinity tolerance of fishes on the subcontinent is limited to a few species, e.g. see Blaber's (1973b) laboratory study on *Rhabdosargus holubi*. Field records on the occurrence of fishes in different salinities are extensive (e.g. Whitfield 1996a) and indicate that not all species found in estuaries are adapted to the same extent. This would account for the fact that certain fish species are recorded in fish kills on certain occasions but absent at others.

Mass mortalities of fish in southern African estuaries are mostly associated with a combina-

tion of low salinities ( $<3$ ) and low water temperatures ( $<14^{\circ}\text{C}$ ). More than 100 000 fish belonging to at least 11 species were recorded dying in subtropical Lake St Lucia during June 1976 when the salinity declined below 3 and the water temperature decreased to  $12^{\circ}\text{C}$  (Blaber & Whitfield 1976). Examination of dead and dying fish during the winter of 1976 revealed skin lesions and haemorrhaging over large areas of the body, although most commonly encountered around the caudal peduncle, fin bases, opercula and mouth. The large mortality was probably due to either a lethal combination of low salinities and sudden low temperature leading to osmoregulatory failure, or to fungal infection of the skin lesions which usually follows severe osmoregulatory stress. The disorientation shown by dying fish in the lake was symptomatic of osmoregulatory failure (Blaber 1974a). Although Lake St Lucia is linked to the sea by the Narrows, the relatively uniform salinity conditions prevailing over the entire system may have prevented the marine fish species from returning to sea before critical physiological conditions developed.

A similar mass mortality was recorded in the warm-temperate Botrivierlei during October 1981. Salinity concentrations in the lake declined to 2-3 and the temperature was less than  $18^{\circ}\text{C}$  when at least 7 000 fish belonging to nine species died in the system (Bennett 1985). Indications that all the species killed were avoiding the lowest salinities is provided by the fact that

most dead fish were found in the southern areas of the estuarine lake where readings were highest (salinity = 3). It should be emphasized that the marine fish killed in October 1981 had survived salinities <8 for four months, and 3 for at least two weeks prior to the mortality. If the duration of exposure had been shorter or the water temperature higher, these species might not have succumbed. Another factor that may have played a role was the age of the fish. All the fish that died in the Bot system were estimated to be older than three years, indicating that juveniles may be more tolerant of low salinities than subadult and adult fish (Bennett 1985).

Mass mortalities under hypersaline conditions appear to be less frequent than under oligohaline conditions, and such kills usually occur when fish are trapped in an estuary that lacks freshwater inflow for prolonged periods. During April 1989, the temporarily closed Seekoei Estuary on the Eastern Cape coast experienced salinities above 90 as a result of a protracted drought and excessive freshwater abstraction by agriculture in the catchment. More than 6 000 juvenile and adult fish, belonging to at least 11 species (comprising both marine and estuarine taxa), were recorded dying in the estuary.

Freshwater fish species associated with estuaries such as *Clarias gariepinus* can also undergo mass mortalities, e.g. at St Lucia where this species was exposed to mesohaline waters arising from wind-induced seiches entering inflowing rivers (Blaber 1981b).

Temporary beneficiaries of fish kills in estuaries are some of the piscivorous birds, and especially scavenging species such as the gulls (Figure 216) and certain large crabs (Figure 217). In addition, there are isopods such as *Cirolana fluviatilis* that gather in their thousands and collectively consume large dead fish in a matter of hours (Newman et al. 2007).

### Water temperature

As discussed above, water temperature often plays an important role in determining the salinity extremes tolerated by both marine and freshwater fish species. Under normal circumstances fish can escape temperature extremes by either moving

from the littoral zone into deeper offshore waters or vice versa.

In very shallow systems such as Lake St Lucia, with high surface to volume ratios, this is often not possible. A fish kill involving an estimated 250 000 estuarine, marine and freshwater teleosts was noted during the winter of 1987 at Lake St Lucia (Forbes & Cyrus 1993). A sudden cold snap during mid-June 1987 was listed as the primary cause of the above mortality, with salinities at the time (29-33) being euhaline (Cyrus & McLean 1996). The majority of the 21 species recorded dying during the above event were small species, with taxa of tropical origin being most affected.

Low water temperatures in estuaries have been directly linked to the mass mortality of adult *Oreochromis mossambicus* in the Kasouga Estuary during July 1979 (Jubb 1979). Winter mortalities of *O. mossambicus* have also been recorded in both the St Lucia and Wilderness lakes systems when temperatures declined below 14°C. Conversely high water temperatures were the probable cause of fish mortalities in the Kosi Estuary (Kyle 1998).

Cold upwelling events along the southern Cape coast can cause mass mortalities of marine fishes, some of which are often washed into estuaries on the flood tide. Dead specimens of 14 marine fish species were recorded in the mouth region of the Storms River Estuary following an upwelling event which resulted in sudden water temperature declines from 21°C to 11°C (Hanekom et al. 1989). Large shoals (200-3 000 individuals) of marine fish frequently take refuge in estuaries along the Tsitsikamma coast when upwelling occurs.

High littoral water temperatures of up to 32°C resulted in the death of at least 3 000 *Hippocampus capensis* and several hundred *Syngnathus temminckii* in the marginal areas of the Swartvlei Estuary (Russell 1994). These fish were presumably trapped in overheated macrophyte beds by receding water levels after the estuary mouth had opened in February 1991. More mobile species, which are also associated with aquatic plant beds in estuaries presumably escaped the warmer littoral areas. *Rhabdosargus holubi* is abundant in the Swartvlei Estuary (Whitfield 1988a) and cannot



**Figure 216.** The grey-headed gull *Larus cirrocephalus* at Lake St Lucia, one of the scavenging bird species in southern African estuaries (Photo: Alan Whitfield).



**Figure 217.** The crab *Scylla serrata* is a common inhabitant and scavenger of dead fish in most warm southern African estuaries (Photo: Alan Whitfield).



survive in water temperatures above 30°C (Blaber 1973b). However, if acclimated more slowly to higher water temperatures, then 34°C is the upper limit (van der Vyver et al. 2013).

### Dissolved oxygen

The first record of a mass fish mortality attributed to low concentrations of dissolved oxygen was at Rondevlei, an estuarine lake which is part of the Wilderness system. In March 1993, hundreds of dead *Rhabdosargus holubi* (324-410 mm FL) and *Lithognathus lithognathus* (713-778 mm FL) were observed in shallow water along the western side of the lake (Russell 1994). Physico-chemical measurements taken when the mortality was first noted revealed that temperature, salinity and concentrations of suspended solids were within ranges previously recorded. However, dissolved oxygen levels in the water column were 0.1-0.7 mg l<sup>-1</sup>, far below the normal range of 4-14 mg l<sup>-1</sup> for Rondevlei. Concentrations of less than 1 mg l<sup>-1</sup> persisted for at least five days and may have resulted from the senescence of a dinoflagellate /algal bloom (Russell 1994). Despite these low dissolved oxygen levels, pelagic schools of *Atherina breviceps* and *Gilchristella aestuaria* were observed in the lake and appeared unaffected.

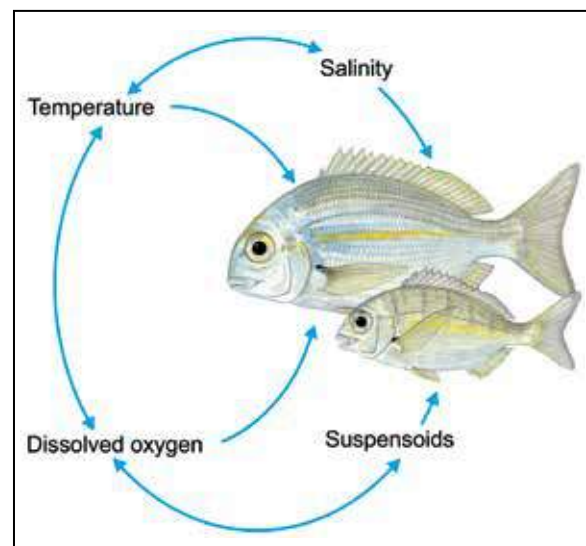
Fish mortalities, probably caused by low concentrations of dissolved oxygen arising from treated sewage effluent inputs and other types of pollution, have also been recorded in the subtropical Tongati Estuary in November 1981 (Blaber et al. 1984). Surface water had oxygen saturation levels of less than 25% in November 1981, and no fish were recorded in the system between July and October 1981 when bottom waters also had oxygen concentrations less than 25% saturation. Fish kills in the Sezela Estuary on the KwaZulu-Natal south coast in April 1977 were probably also linked to near-zero dissolved oxygen values (Begg 1978). According to Ramm et al. (1987) the deposition of untreated sugar mill waste into the Sezela system resulted in extensive anoxic sludge deposits, which then used up the available oxygen within the water column.

Toxic sulphide-rich marine waters have been recorded entering the Berg Estuary (Lamberth et al. 2010) and are often also associated with

anoxic conditions in certain meromictic southern African estuarine lakes such as Swartvlei (Allanson & Howard-Williams 1984) and Lake Mpungwini (Ramm 1992). Mixing of high concentrations of these free sulphides into Mpungwini surface waters during periods of turbulence or upwelling always had the potential to cause mass mortalities of fish and other biota. During the spring equinox tides of September 1989, thousands of fish, representing all the major species in the central Kosi system, died as a result of toxic concentrations of sulphides (>10 mg l<sup>-1</sup>) being upwelled into surface waters of Lake Mpungwini (Ramm 1990a).

### Suspended sediment

High riverine silt loads have previously been associated with fish kills in southern African freshwater systems, but it was only in January 1995 that a large-scale mortality of fish in the Sundays and Great Fish estuaries was attributed to this particular source (Whitfield & Paterson 1995). A total of 16 fish species, belonging to marine, estuarine and freshwater taxa, was recorded dying in the Sundays Estuary during this event. Both juvenile and adult fish appeared to be affected by the high levels of silt and clay carried by the floodwaters.



**Figure 218.** Diagrammatic representation of environmental factors and the major interactions influencing fish mortalities in southern African estuaries (after Whitfield 1995a). Small-scale interactions between salinity and suspensoids, dissolved oxygen and salinity, and suspensoids and water temperature are also possible.

Although available evidence suggests that clogging of the fish gill filaments by suspended sediments was primarily responsible for the mass mortalities, osmoregulatory and other stress factors may also have contributed to the fish kill (Figure 218).

### Mouth breaching

A final cause of mass mortality in some estuaries relates to the trapping of fishes in vegetated shallows as the lagoon water level rapidly declines following mouth breaching (Figure 219). This type of mortality is most unusual but can occur in certain TOCEs with extensive submerged plant beds and a very slight littoral gradient (Figure 220). A wide variety of fish species of different sizes can become trapped in the rapidly draining plant beds and associated habitats during the TOCE outflow phase (Whitfield & Cowley 2018). In addition, burrowing gobies such as *Croilia mossambica* can

become stranded when TOCEs breach and burrows are exposed for a prolonged period (Harrison pers. comm.).

### Some conclusions

A striking feature of most fish kills in estuaries is the range of species affected in the same manner, despite their differing physiological tolerances to particular conditions. In many cases, mass mortalities of fish have been linked to a single dominant factor but, in reality, a combination of factors precipitates a mass mortality event. The most frequently interacting factors in a southern African context appear to be salinity and water temperature, dissolved oxygen and water temperature, and suspensoids and dissolved oxygen (Figure 218). In some cases more than two factors may be in operation simultaneously, thus creating an environment unsuitable for the survival of the ichthyofauna.



**Figure 219.** Fish, mainly *Pomadasys commersonnii* and *Rhabdosargus holubi*, trapped and dying in shallow littoral areas, an event that was triggered by a rapid decline in the water level of the West Kleinemonde Estuary following mouth opening in November 2017 (Photo: Paul Cowley).



## Biotic factors influencing mortalities

### Piscivorous fish

Piscivorous fish assemblages in southern African estuaries are diverse in terms of composition, size, foraging behaviour and prey preference. The three most important species found in all types of estuaries are *Argyrosomus japonicus* (Sciaenidae), *Elops machnata* (Elopidae) and *Lichia amia* (Carangidae), all of which are pursuit predators (Figure 221). The size composition of fish prey consumed by piscivorous fishes is dominated by small pelagic fish species (e.g. *Gilchristella aestuaria*) or the 0+ juveniles of larger species, especially mugilids (e.g. *Mugil cephalus*) (Marais 1984). Although the juveniles of most piscivorous fish species often have a high proportion of their diet comprising nektonic invertebrates (e.g. penaeid prawns), as these individuals develop into subadults, they depend increasingly on fish as the main food (Blaber & Cyrus 1983).

In Lake St Lucia, where a wide size spectrum of fishes were available to the many piscivores in this system, >90% of the prey were <8 cm SL, with the peak for *A. japonicus* being 6-7 cm SL and for *E. machnata* the peak was 3-4 cm SL (Whitfield & Blaber 1978a). Despite the preference by these two piscivores for small zooplanktivorous fish species (*Thryssa vitrirostris* for *A. japonicus* and *Gilchristella aestuaria* for *E. machnata*), a wide variety of prey fishes were consumed which appeared to be correlated with the composition of these species in seine net catches from the lake. Overall, estuarine resident rather than marine migrant taxa were targeted by these piscivores.

The relationship between the relative densities of *A. japonicus* and *E. machnata* in relation to the relative densities of their dominant prey (*G. aestuaria* and *T. vitrirostris*) was also strongly correlated, e.g. 30% of *A. japonicus* and *E. machnata*, and 34% of *G. aestuaria* and *T. vitrirostris* were captured in South Lake, whereas 70% of



**Figure 220.** A view of a section of the lower reaches littoral of the West Kleinemonde Estuary, showing fish trapped by the rapidly receding littoral waters following mouth opening (Photo: Paul Cowley).



**Figure 221.** A shoal of *Argyrosomus japonicus*, very efficient piscivores under low light conditions or in turbid estuaries (Photo: reeplifesurvey.com).



**Figure 222.** A large shoal of subadult and adult *Caranx ignobilis* in the upper reaches of the subtropical Mtentu Estuary (Photo: Ben Pretorius).

*A. japonicus* and *E. machnata* and 66% of *G. aestuaria* and *T. vitrirostris* were captured in False Bay (Whitfield & Blaber 1978a). This indicated that piscivorous fish species at Lake St Lucia, which were dominated by the above two predators, were feeding in a mostly density dependent manner.

There were, however, two fish species which were not consumed by piscivores in proportion to their relative abundance, namely *Oreochromis mossambicus* and *Rhabdosargus holubi*. The juveniles of these two species remain in shallow littoral waters and in association with submerged macrophytes respectively, thus avoiding large piscivorous fishes but, in the process, coming into contact with wading piscivorous birds in the shallows. In contrast, the two major planktivorous fish species *G. aestuaria* and *T. vitrirostris* were not confined to littoral waters and tended to avoid macrophyte beds, thus overlapping their distribution with that of their major predators, namely *A. japonicus* and *E. machnata* (Whitfield & Blaber 1978a).

There are also indications that demersal piscivores take a higher proportion of demersal fish as prey when compared to pelagic piscivores, e.g. the three major prey species of the benthic dwelling *Muraenesox bagio* were *Solea turbynei*, *Johnius dorsalis* and *Leiognathus equula* all of which are demersal taxa. In contrast, the three major prey species of the pelagic *E. machnata* were *G. aestuaria*, *T. vitrirostris* and *Hyporhamphus capensis*, all of which are pelagic taxa at St Lucia (Whitfield & Blaber 1978a).

The swimming speed of piscivores may also be a factor in determining which fish prey species form part of the diet. Fast swimming predators such as *Sphyraena barracuda*, *Lichia amia* and *Caranx ignobilis* (Figure 222) appear to have a higher proportion of fast swimming mullet in their diet than do slower swimming or sedentary piscivores such as *Otolithes ruber*, *Platycephalus indicus* and *Muraenesox bagio* (Whitfield & Blaber 1978a).

Very little quantitative information is available on actual mortalities generated by piscivorous fishes in estuaries. One of the few datasets available is that provided by Cowley & Whitfield (2002) who estimated a mean monthly consumption of fish by *Lichia amia* in the small

East Kleinemonde Estuary at 58 kg per month, which equated to approximately 1% of the total fish biomass present in that system per month. Unfortunately, without a detailed analysis of the diet of *L. amia* from the East Kleinemonde, the mortality rates imposed on particular prey species is unknown.

### Piscivorous birds

The diverse array of piscivorous birds are very effective predators of fishes in estuaries (Figures 223 and 224). This is because the three major groups of birds, wading, diving and aerial predators, cover estuaries spatially and are able to target a wide range in fish sizes. They also have the ability to quickly detect prey fish abundance and vulnerability to predation, and to alter their behaviour accordingly, e.g. breeding white pelicans *Pelecanus onocrotalus* at Lake St Lucia are known to forage mainly on the Phongolo pans more than 100 km away due to the concentration of fish in the rapidly evaporating pan system (Whitfield & Blaber 1979b).

Conversely, during July 1994, thousands of Cape cormorants *Phalacrocorax capensis* invaded estuaries along the south-eastern Cape coast due to a shortage of an important prey fish species in the marine environment. The predatory impact of this invasion on the fishes of the East Kleinemonde Estuary was quantified and it was estimated that Cape cormorants consumed 2 878 kg of fish in this system during 1994 compared to 1 536 kg by all other avian piscivores in the same year (Cowley et al. 2017).

The sizes of fish consumed by piscivorous birds follow the spatial foraging patterns of the species, e.g. little egrets consume prey mainly <5 g, great egrets <50 g, grey herons <110 g and goliath herons <300 g (Whitfield & Blaber 1979a). Amongst the diving birds, the reed cormorant consumes fish mainly <20 g, white-breasted cormorant <200 g and white pelicans also <200 g (Whitfield & Blaber 1979a). The same size related prey preference was shown by the aerial piscivores, with the pied kingfisher targeting fish <15 g, Caspian tern <200 g and African fish eagle <1 500 g (Whitfield & Blaber 1978d).

The fish species targeted as prey by birds are





**Figure 223.** A variety of tern species make use of sand bars in the mouth region of estuaries for roosting after foraging in estuaries and/or the sea (Photo: Tris Wooldridge).



**Figure 224.** The colourful half-collared kingfisher *Alcedo semitorquata* is often associated with quiet areas in the middle and upper reaches of small Eastern Cape estuaries (Photo: Tris Wooldridge).

often not the same as those favoured by predatory fish. As has already been mentioned in the previous section, the major prey species for piscivorous fishes at Lake St Lucia were the estuarine residents *Gilchristella aestuaria* and *Thryssa vitirostris* (Whitfield & Blaber 1978a). In contrast, the freshwater *Oreochromis mossambicus* and a variety of marine fish taxa, especially mugilids, were targeted by piscivorous birds at the lake (Whitfield & Blaber 1978d, 1979a, 1979b). The available evidence suggests that birds are major predators of fish in estuaries and that the impact is greatest in small TOCEs (Cowley et al. 2017, Table 27).

### Fish parasite loads

A number of preliminary studies in southern African estuaries have shown that some fish carry high parasite loads which may affect not only fitness but also the survival of the host, e.g. 63% of the needlefish *Strongylura leiura* examined in Lake St Lucia were found to have intestinal infestations of adult *Ptychobothrium belones*, some with as many as six cestodes in a single fish

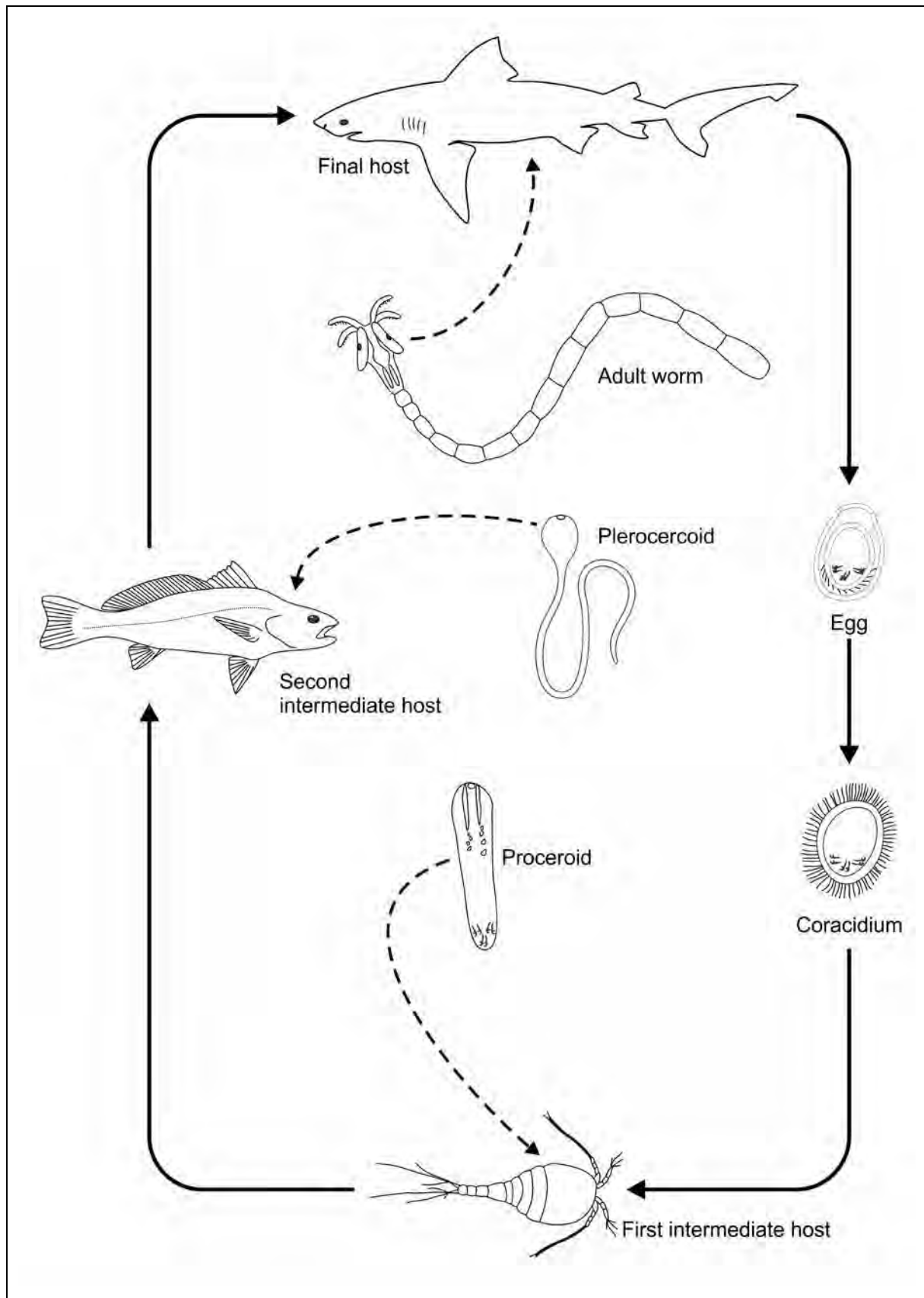
(Whitfield & Heeg 1977). The second intermediate host of this parasite is probably the halfbeak *Hyporhamphus capensis* which feeds on copepods, among which the first intermediate host is likely to be found.

A similar life cycle is found in the cestode *Grillotia perelica*, the plerocercoids of which infect at least eight mullet species in southern Africa, with *Mugil cephalus* achieving a 40% infestation rate in the Mntafufu Estuary (Schramm 1991). The large size of *G. perelica* plerocercoids makes it likely that small infected mugilids would die before becoming available to the final host. Consequently, the pattern of infestation of the mullet is such that there is rising prevalence and intensity of infection with increasing fish size.

The final hosts of *Grillotia perelica* have been identified by Schramm (1991) as the bull shark *Carcharinus leucas* and sandbar shark *Carcharinus plumbeus*, both of which feed on mugilids. One *C. leucas* caught in the mouth of the Mbhashe Estuary contained six *G. perelica* in its intestine. *Carcharinus leucas*, along with the blacktip shark *Carcharinus limbatus*, is also the final host of the

Table 27. Piscivorous bird species mean daily count, individual body mass per species, and total estimated annual fresh matter intake (FMI) per species at the East Kleinemonde Estuary during 1995/6. Bird species in the table are ranked according to FMI over 12 months (after Cowley et al. 2017).

Species	Common name	Mean daily bird count	Individual bird body mass (g)	Total FMI per annum (kg)
<i>Phalacrocorax africanus</i>	Reed cormorant	13.16	538	782.95
<i>Phalacrocorax carbo</i>	White-breasted cormorant	4.47	1 904	712.99
<i>Anhinga melanogaster</i>	African darter	3.22	1 326	356.12
<i>Ardea cinerea</i>	Grey heron	2.03	1 436	235.62
<i>Sterna hirundo</i>	Common tern	3.30	138	93.95
<i>Egretta garzetta</i>	Little egret	1.43	480	78.81
<i>Ardea alba</i>	Great egret	0.46	1 100	44.83
<i>Ceryle rudis</i>	Pied kingfisher	2.79	77	43.79
<i>Haliaeetus vocifer</i>	African fish eagle	0.15	3 092	29.62
<i>Megaceryle maxima</i>	Giant kingfisher	0.35	361	15.84
<i>Ardea purpurea</i>	Purple heron	0.04	920	3.45
<i>Phalacrocorax capensis</i>	Cape cormorant	0.02	1 231	2.39
<i>Alcedo semitorquata</i>	Half-collared kingfisher	0.02	39	0.20



**Figure 225.** Typical trypanorhynch cestode *Poecilancistrum caryophyllum* life cycle, with the dusky kob *Argyrosomus japonicus* as the second intermediate host and the bull/Zambezi shark *Carcharinus leucas* as the final host (after Schramm 1989).

cestode *Poecilancistrum caryophyllum* which has the dusky kob *Argyrosomus japonicus* as its second intermediate host (Figure 225). Both *C. leucas* and *A. japonicus* are associated with turbid waters in large subtropical estuaries. The leervis *Lichia amia*, which is also a piscivore, has been found to harbour *Callitetrarhynchus gracilis* plerocercoids (Schramm 1991) but the final host of this parasite has yet to be identified.

Parasitic nematodes belonging to the genus *Contracaecum* occur in the mesenteries of a number of marine fish species in Lake St Lucia. Percentage infestation of estuary-associated marine taxa ranged from 3% for *Elops machnata* to 19% for *Platycephalus indicus* (Whitfield & Heeg 1977). The final hosts are piscivorous birds, and adult *Contracaecum spiculigerum* and *C. microcephalum* were identified from the regurgitated pellet contents of the whitebreasted cormorant *Phalacrocorax carbo* and regurgitated stomach contents of the white pelican *Pelecanus onocrotalis* respectively. The cichlid *Oreochromis mossambicus*, which had a *Contracaecum* infestation rate of 15%, is a likely intermediate host for one or both of the above species because it is common to the diets of all piscivorous birds at Lake St Lucia (Whitfield & Heeg 1977). *Strongylura leiura*, which was the only piscivorous fish species in the St Lucia system parasitized by adult cestodes, was also the only piscivore in the lake not to be found infested by parasitic nematodes.

Known ectoparasites on fishes in southern African estuaries include Isopoda, Copepoda, Hirudinea and Branchiura. The site of attachment varies according to the type of parasite and its method of feeding on the host. Ectoparasitic isopods (e.g. *Anilocra capensis*) infest fishes such as *Pomadasys commersonnii*, *Pomadasys olivaceum*, *Rhabdosargus holubi* and *Rhabdosargus sarba*, usually attaching themselves to the side of the head immediately above and behind the eye (Figure 226). Several isopods may parasitize a single fish, often comprising a male and female combination, with each parasite opening up a small wound from which the blood and body juices are drawn.

*Rhabdosargus sarba* is also vulnerable to the parasitic copepod *Lernanthropus sarbae*. This copepod seems to parasitize mainly sparids because

it has also been found attached to the gills of *Rhabdosargus holubi* in Lake St Lucia (Olivier & van Niekerk 1995). Similarly the parasitic copepod *Mugilicola smithae* has been recorded attached to the gills of at least four mugilid species, as well as the gills of the eel *Anguilla mossambica* (Kruger et al. 1997). The use of oligohaline and mesohaline upper reaches of estuaries by fishes to get rid of gill and other parasites is a topic of research that has recently commenced, with the parasites of *Argyrosomus japonicus* currently under investigation.

In contrast to the location of isopods and copepods (Grobler & Cyrus 2003, Grobler et al. 2003), parasitic leeches in subtropical Lake St Lucia have been found attached to the inside of the mouth of fishes such as *Elops machnata*, *Rhabdosargus sarba* and *Terapon jarbua*, as well as externally on species such as the *Acanthopagrus vagus*, *Chelon dumerili* and *Pomadasys commersonnii*. The same fish species in the more temperate regions of the subcontinent do not appear to be parasitized by leeches, probably due to this parasitic group being restricted mainly to warmer waters.

Branchiurans belonging to the genus *Argulus* are also found on fish in estuaries (van As et al. 2001), with the most recently discovered species *Argulus kosus* being documented on *Sarpa salpa* in the Kosi system (Avenant-Oldewage 1994). An example of *Argulus* sp. parasitism on other estuary-associated fish species is shown in Figure 227.

### Fish pathogens

Bacterial and other diseases can, through natural mortality, be a significant factor driving the population dynamics of fishes (Loch & Faisal 2015). Fish culture operations involving artificially high teleost densities can lead to the proliferation of pathogens, sometimes causing widespread fish mortalities (Pulkkinen et al. 2010).

*Aphanomyces invadans* is a pathogenic water mould that causes lesions and mass mortalities in wild and cultured fish populations, a disease known as Epizootic Ulcerative Syndrome (EUS). This pathogen was first reported in Africa from the Zambezi Basin in 2006, thereafter in the





**Figure 226.** A pair of parasitic isopods *Anilocra capensis* on the head region of two host sparid species (Photos: Wikipedia and Alan Whitfield).



**Figure 227.** Parasitic branchiurans (*Argulus* sp.) on the head of *Lichia amia* from the Knysna Estuary (Photo: Leslie Ter Morshuizen).



Palmiet River (Western Cape Province) in 2011 (Huchzermeyer & van der Waal 2012).

The first estuarine occurrence of *A. invadans* in southern Africa was verified in the cool temperate Palmiet Estuary during the autumn of 2015 where it was responsible for a mass mortality of the barehead goby *Caffrogobius nudiceps*. During 2015 it was also suspected as being responsible for mass mortalities of marine fish such as the robust mullet *Osteomugil robustus* and estuarine bream *Acanthopagrus vagus* in the subtropical Mgobezeleni Estuary at Sodwana Bay (Whitfield et al. 2016).

### Invasive organisms

The susceptibility of estuarine systems to biological invasions is poorly understood, although indications are that estuaries under stress are more susceptible to invasive plant and animal species than less disturbed systems. A good example is the freshwater snail *Tarebia granifera* that has invaded many KwaZulu-Natal estuaries, especially those in a degraded state (Appleton et al. 2009). The apparent concentration of recorded estuarine invasions within degraded estuaries located on the east and north-east coast (Mead et al. 2011) is in contrast to the lower levels of documented invertebrate invasions in the less human-impacted estuaries along the south-east and southern coasts of South Africa.

To date, 15% of the known invasive introductions reported are within southern African estuaries, the majority of which are invertebrate species (Mead et al. 2011). Interestingly, only two invasive fish species have been reported entering the upper reaches of certain estuaries, namely the common carp *Cyprinus carpio* and largemouth bass *Micropterus salmoides*. Both species are not euryhaline and therefore have limited ability to penetrate most southern African estuaries.

The impact of invasive species on indigenous estuary-associated fish species is largely unknown and in need of further research (Magoro et al. 2015). Such studies need to focus on the impact of invasive invertebrates on the food resources of fishes in estuaries. For example *Tarebia granifera* populations in Lake St Lucia are often much higher than that of indigenous gastropods in the

same trophic level (Miranda & Perissinotto 2012). According to these authors the lack of fish and bird predation, as well as the absence of trematode parasites from this invasive species, may facilitate the spread of this mollusc in subtropical estuaries on the subcontinent (Appleton et al. 2009).

Perhaps one of the most obvious potential impacts on indigenous fish populations comes from Groenvlei, a now isolated coastal lagoon in the southern Cape. Only *Gilchristella aestuaria* was sampled in the early 1900s in Groenvlei, leading to the conclusion by certain freshwater ichthyologists and fishery management authorities that the introduction of non-native recreational fish species would be appropriate. Subsequent intensive fish sampling of Groenvlei showed that a second indigenous fish species, *Atherina breviceps*, was also abundant in the lagoon and that both *A. breviceps* and *G. aestuaria* were recently genetically differentiated from other estuarine populations of these species to such an extent that the Groenvlei stocks deserve special conservation attention (Phair et al. 2015).

Unfortunately formal fish stocking of various inland waters with non-native freshwater fish species was encouraged by provincial conservation departments in South Africa during the early and mid-1900s, with 15 largemouth bass *Micropterus salmoides* (Figure 228) being introduced into Groenvlei in 1934. This successful introduction of *M. salmoides*, and the perceived vacant ecological niches available for other non-native fish species, provided momentum for the introduction of additional alien fishes, primarily as fodder fish for the largemouth bass.

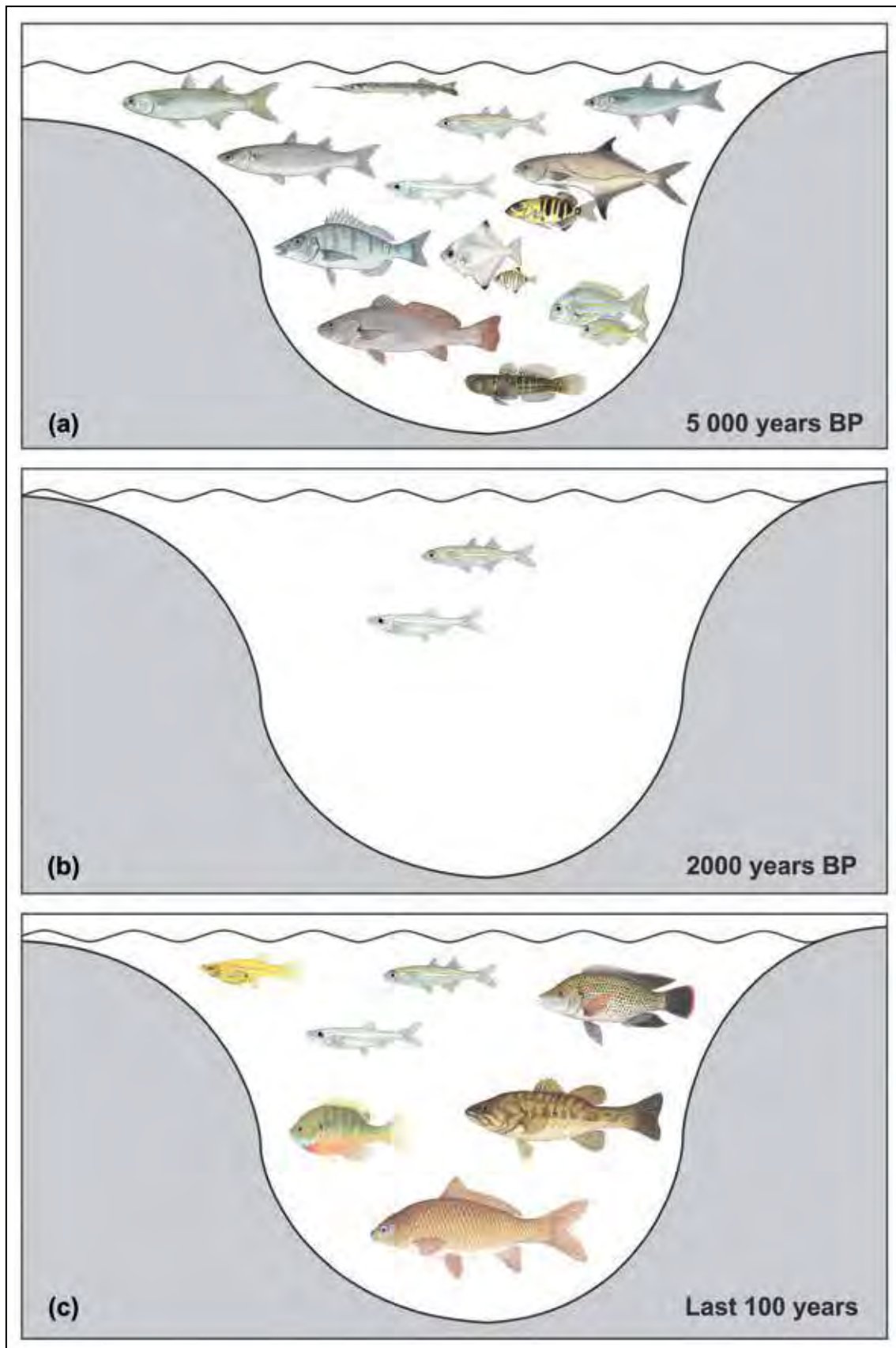
Bluegill *Lepomis macrochirus*, Mozambique tilapia *Oreochromis mossambicus* and western mosquitofish *Gambusia affinis* were introduced into Groenvlei during the 1940s. Following on from these government approved fish introductions to the system, an illegal introduction of the common carp, *Cyprinus carpio*, (Figure 229) occurred in about 1990. All five non-native species of fish have successfully established in Groenvlei (Figure 230c, Weyl et al. 2015), and some have also been successfully introduced to the nearby Wilderness Lakes system (Olds et al. 2016). The impact of these fish on indigenous taxa is unknown.



**Figure 228.** The alien largemouth bass *Micropterus salmoides* is known to sometimes occupy the headwaters of certain southern African estuaries (e.g. Kowie), where it preys on indigenous estuary-associated fish species (Photo: Fishinpedia).



**Figure 229.** The invasive mirror carp *Cyprinus carpio* has escaped from catchment farm dams and now occupies the oligohaline headwaters of certain southern African estuaries, e.g. the specimen shown here was captured in the upper reaches of the Mbashe Estuary (Photo: Alan Whitfield).



**Figure 230.** (a) Probable fish species in the Groenvlei estuarine lagoon about 5 000 years BP. (b) Fish species remaining in the Groenvlei coastal lagoon about 2 000 years BP. (c) Changes in fish species assemblage in the Groenvlei coastal lagoon during the last 100 years, driven by non-native introductions (after Whitfield et al. 2017b).



## Human factors influencing fish mortalities

### Recreational and subsistence fisheries

Recreational anglers catch a wide variety of fish species, e.g. a total of 34 species (17 families) were reported in the Kosi fishery between 1986 and 1999 (James et al. 2001). Declining CPUE levels for *Acanthopagrus vagus* and *Lutjanus argentimaculatus* in the above study (Figure 231) indicate declining populations of these species and imply that recent fishing levels are not sustainable. This view is reinforced by the findings of James et al. (2008b) who estimated that *A. vagus* in the Kosi system had been reduced to 24% of its unfished level based on a spawner biomass per recruit model. The causes of the fishing mortality on this and other marine fish species in the Kosi system were a combination of traditional traps and gillnets, together with recreational angling using rod and line (Kyle 1993, 1999, 2013).

A similar analysis of recreational anglers' catches in Lake St Lucia between 1986 and 1999 (Mann et al. 2002) revealed a total of 55 species (27 families) being utilized. Three dominant fish species featuring in the catches of the anglers were *Argyrosomus japonicus* (42 247), *Acanthopagrus vagus* (28 195) and *Pomadasys commersonnii* (26 465). The annual CPUE data for *A. japonicus* indicated an overall downward trend but the regression analysis for *P. commersonnii* exhibited a slight upward trend over the same period (Figure 232), suggesting that either the former species is more heavily targeted by anglers or the latter species is more resilient to fishing pressure.

A gill net fishery in Lake St Lucia revealed substantial impacts by these nets on already heavily exploited estuary-associated marine fish species (Crook & Mann 2002). Of the top four fish taxa sampled by 30 legal gill nets in the lake between March 1995 and 1996, 4 524 were *Pomadasys commersonnii*, 2 643 were *Acanthopagrus vagus* and 2 179 were *Argyrosomus japonicus* (Mann 1996). All three of these fish species are already heavily targeted by recreational fisherman and research has shown that *A. japonicus* is severely over-exploited (Mirimin et al. 2016), with a spawner biomass per recruit level estimated at only 2% of the pristine state (Griffith 1997).

Clearly the recreational and subsistence fisheries in Lake St Lucia are unlikely to be sustainable at these rates of exploitation. The illegal gill net fishery in North Lake and False Bay has been transformed into a commercial operation and its impact on already overexploited marine fish populations is likely to increase in the future.

The question whether angling or netting in any form should be permitted in a World Heritage Site arises and there is also the common property resource problem presented by community gill netting rights that will be very difficult to solve (Crook & Mann 2002). Indeed it has been shown that the conservation benefits of no-take MPAs can be nullified if illegal exploitation of fishes occurs (Venter & Mann 2012).

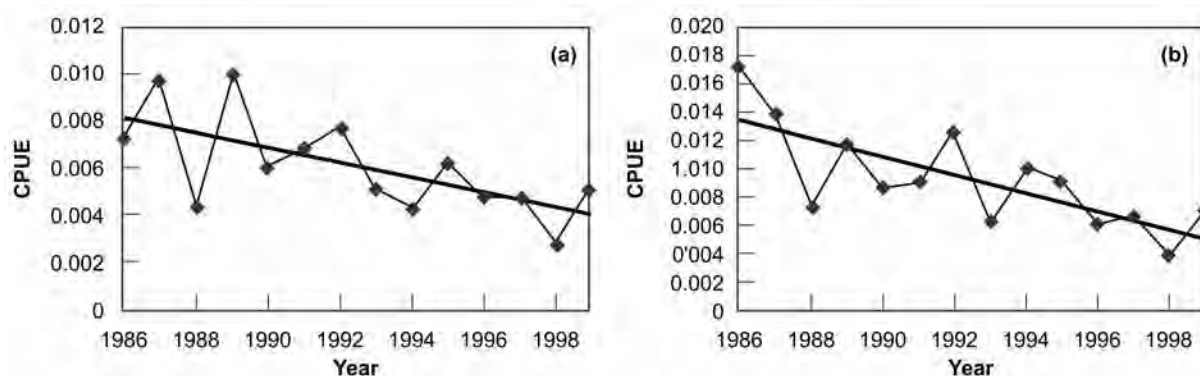
In the same way that fishery mortalities in estuaries influences marine fish stocks (Parker et al. 2017), so will fishing of estuary-associated marine fish in the sea have an influence on the numbers found in estuaries. The elf *Pomatomus saltatrix* accounts for up to 80% of the annual shore angling catch in KwaZulu-Natal (Maggs et al. 2012). The removal of more than 1.5 million *P. saltatrix* over three decades from this coastline alone must have had a major influence on egg and larval production and therefore the numbers of juveniles of this species entering southern African estuaries. This is likely to have a negative impact on the ecology of estuaries due to reduced recruitment levels of *P. saltatrix* and other targeted estuary-associated marine species.

All targeted estuary-associated fish species are under pressure from subsistence and recreational anglers. An example of the decline in the numbers of *Lichia amia* is provided by the work of Maggs et al. (2016) which showed that the shore and boat based fishery, and shore and boat-based spear fishery for this species all showed considerable declines between the 1980s and from 2 000 onwards. These data strongly suggest that traditional management strategies have failed to slow down the decline in catch per unit effort of *L. amia* and that spatio-temporal closure of estuaries to fishing and the promotion of catch and release policies are urgently required for this species.

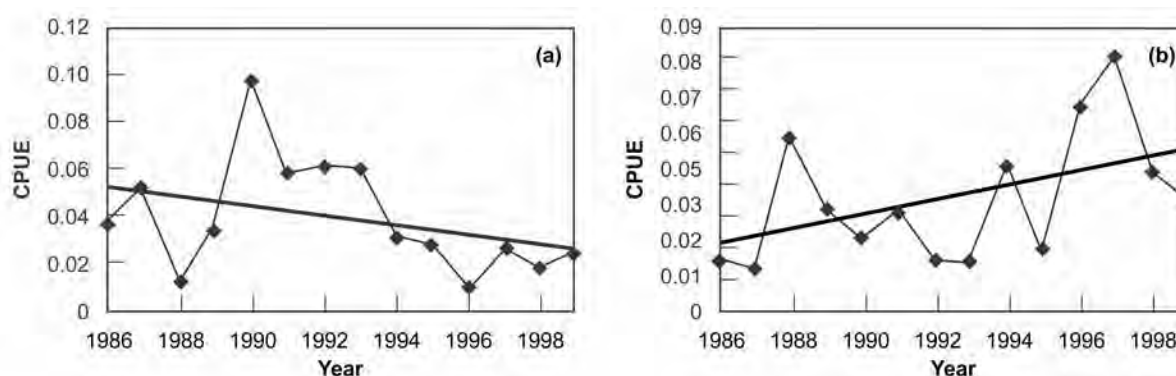
Fishing mortalities of estuary-associated marine species are usually not the same in estuaries

when compared with the sea. An example of this difference has been highlighted by James et al. (2004) who calculated that fishing mortalities for *Rhabdosargus sarba* were much higher in estuaries than the adjacent coast (Figure 233), mainly due to increased angler access to estuaries. Thus the spawner biomass per recruit model indicates that

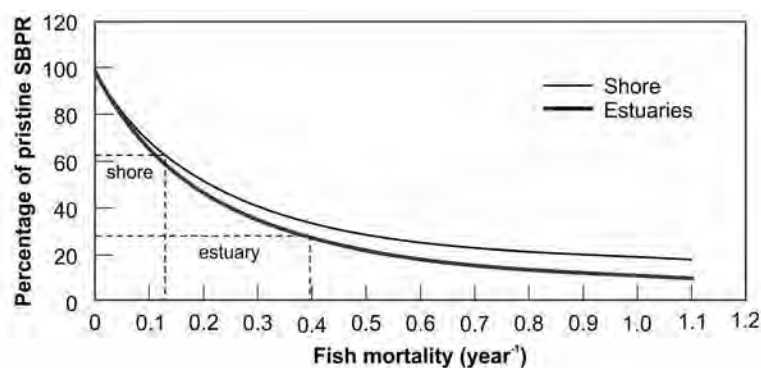
*R. sarba* is more than 60% of its unfished level for coastal marine stocks and only about 30% of its unfished level in estuaries. This finding strongly supports management action to provide additional protection for estuarine representatives of marine fish species (Figures 234 and 235) when compared to those in the sea.



**Figure 231.** Annual CPUE trends in fish per angler per hour of (a) *Lutjanus argentimaculatus* and (b) *Acanthopagrus vagus* from the Kosi system between 1986 and 1999 (after James et al. 2001).



**Figure 232.** Annual CPUE trends in fish per angler per hour of (a) *Argyrosomus japonicus* and (b) *Pomadasys commersonnii* from the St Lucia system between 1986 and 1999 (after Mann et al. 2002).



**Figure 233.** Spawner biomass per recruit ratio for *Rhabdosargus sarba* in the KwaZulu-Natal Province. Dotted lines indicate the percentage pristine spawner biomass per recruit ratio (SBPR) at historic levels of fishing on the sea shore was approximately double that found in estuaries (after James et al. 2004).





**Figure 234.** Individually, estuarine recreational anglers have little impact on targeted fish species, but collectively the 20 boats and associated anglers shown here in the Gamtoos Estuary will have a major impact on fish stocks (Photo: Paul Cowley).



**Figure 235.** Consistent overfishing of targeted species such as the dusky kob *Argyrosomus japonicus* in the past and present has led to a decline in both the average size and abundance of these taxa in estuaries.

### Weirs, causeways and marinas

It has long been recognised that weirs and causeways were a major barrier to the upstream movements of juvenile freshwater mullet *Pseudomyxus capensis* and therefore a threat to the survival of this fish in Eastern Cape systems (Bok 1984). More recently it has become apparent that a much wider variety of estuary-associated fish species (e.g. *Mugil cephalus*) are involved in upstream migrations, mainly by juveniles (Wasserman et al. 2011).

An assessment of the distribution and abundance of migratory marine-spawned fish taxa in the lower reaches of the Sundays Estuary revealed that only *P. capensis* and *Monodactylus falciformis* were capable of surmounting small instream barriers, with a larger number of estuary-associated marine species confined to the site directly below the first instream barrier (Wasserman et al. 2011). This suggests that even causeways can restrict access by estuary-associated fish species to upstream riverine environments and that large weirs

create a total barrier to both upstream and downstream movements of such species, with the exception of anguillid eels.

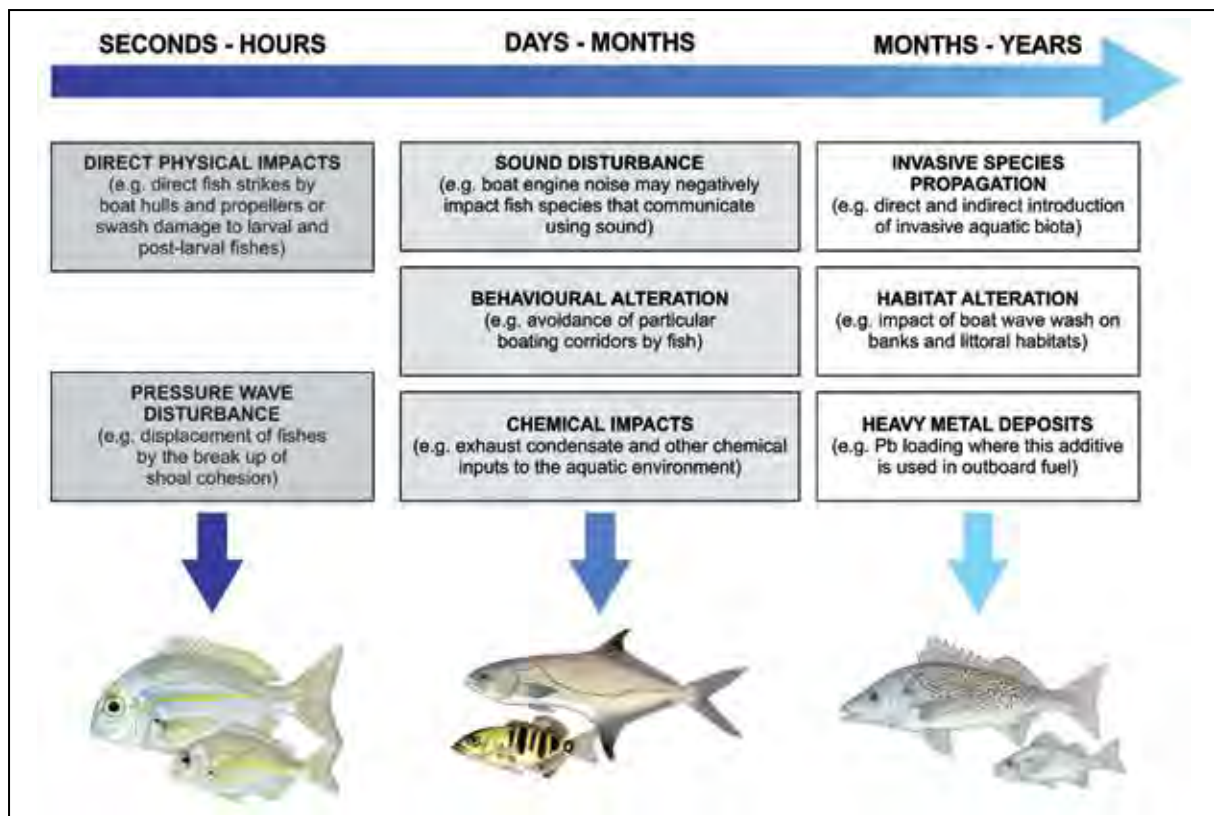
Although estuarine marinas may increase the available water area and volume to fishes, there is strong evidence to suggest that these structures are not conducive to the settlement of postflexion larvae and early juveniles due to the steep walls of the artificial channels and the consequent lack of gently sloping littoral habitats that provide refuge from large piscivorous fishes (Figure 236a and c) (Kruger & Strydom 2010).

In contrast, an earlier study on the Kromme system, that included both planktonic and nektonic components (Baird et al. 1981), suggested that the Marina Glades system (Figure 236b) did not have an adverse effect on the ecology of the estuary. In fact the authors concluded that the development actually increased the habitat area for plankton, benthic macro-invertebrates and fish.



**Figure 236.** Aerial view of (a) the Royal Alfred Marina on the Kowie Estuary, and (b) the Marina Glades on the Kromme Estuary, above a picture (c) of Port Alfred on the lower Kowie system (Photos: Harcourts South Africa).





**Figure 237.** Likely influences and impacts of power boating activities on fishes and their habitats, and the likely time frame over which the impacts may occur (after Whitfield & Becker 2014).

### Motor boats

The available evidence suggests that motor boats do have an impact on many aspects of the biology and ecology of fishes (Whitfield & Becker 2014, Figure 237). Multiple lines of evidence point to direct disturbance effects varying according to the species, and sometimes only certain size classes of fishes seem to respond to outboard powered craft. Alterations in the local wave climate and water turbidity brought about by boating activity may also influence fishes and their habitats, especially submerged plant beds that can be directly destroyed by propeller contact or adversely impacted by increased wave action and turbidity.

The sound generated by boat motors can also have a negative influence on the communication and behavior of certain species but others appear to be largely unaffected. Boat pollution arising from fuel (diesel or petrol) and antifouling paint used on boat hulls also has direct and indirect detrimental effects on fishes, although the elimination of lead (Pb) additives from petrol and the banning of TBT paints in many countries have

reduced the negative impacts of these particular management problems.

Finally, the use of boats as intentional and unintentional vectors of aquatic invasive organisms is very real and has created major problems to the ecology of freshwater systems in particular. Although boats in southern African estuarine waters are not implicated in fish introductions, the transmission of invasive molluscs is almost certainly inadvertently occurring along the coast and affecting fish ecology in the process.

The effects of passing boats on the abundance of different sized fish within the main navigation channel of the Bushmans Estuary was recently investigated, with both the smallest (100-300 mm) and largest (>500 mm) size classes having no change in their abundance following the passage of boats (Becker et al. 2013b). However, a decrease in abundance of mid-sized fish (301-500 mm) occurred following the passage of boats and was attributed to a number of possible factors, including noise, bubbles and the approaching boat itself.

## 5.6 FISHES AS ENVIRONMENTAL INDICATORS

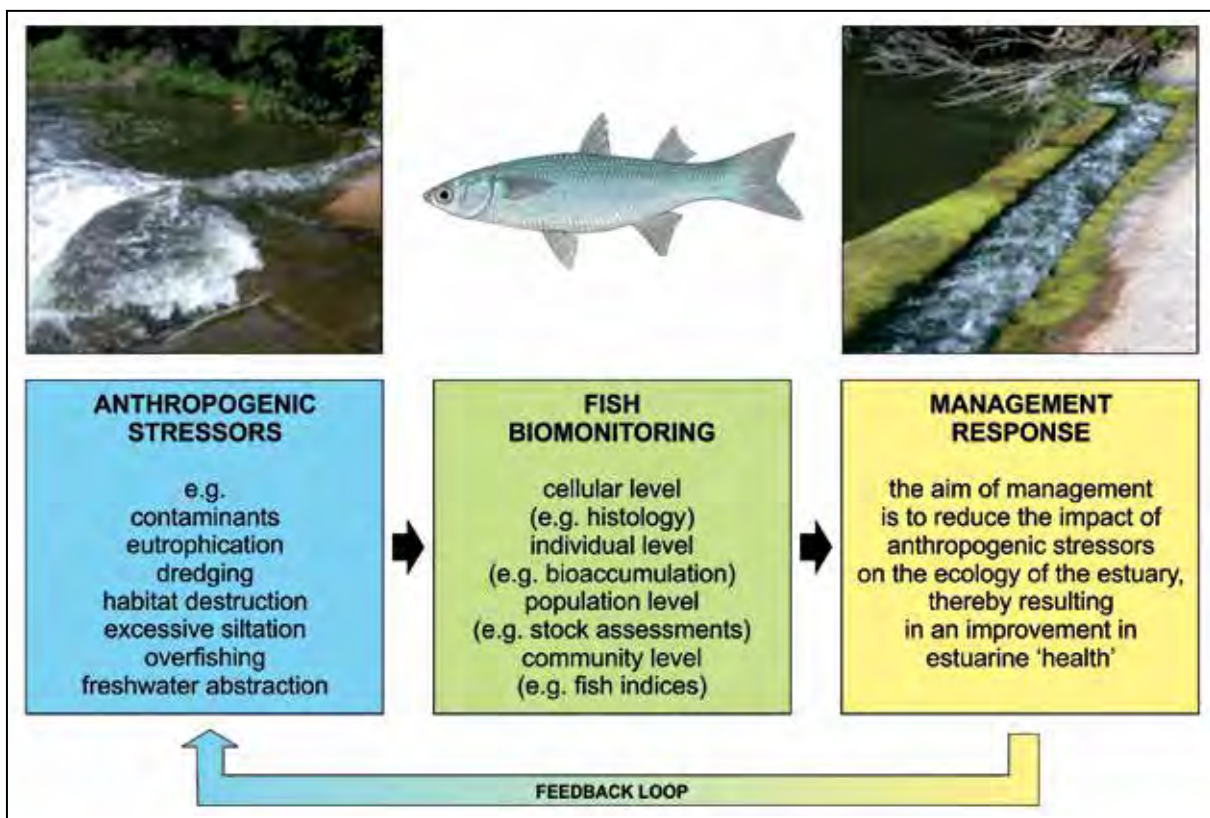
Environmental monitoring of estuaries used to be restricted to water-quality parameters but these measures often do not adequately reflect the condition of the ecosystem. This led to the development of biological monitoring tools and indicators. Aquatic biota, especially fishes, integrate the effect of a range of environmental factors, thereby creating a good indicator of aquatic ecosystem health. Furthermore, the biota may be the only practical means of evaluating certain impacts that are difficult to measure using purely physico-chemical measurements.

Biological monitoring studies should ideally determine stress at the ecosystem, community, population, individual, and cellular levels (Figure 238) using techniques that examine aspects such as fish cohort strength, community structure, toxicity bioassays, behavioral assess-

ments, bioaccumulation studies, and pathology (Whitfield & Elliott 2002). Pathology deals with causes, processes, and effects of disease and includes postmortems, histological examinations, parasitological examinations, and liver enzyme assays.

### Why use fish as biological indicators

The use of fishes as indicators of environmental health or biological integrity is based on the tenet that fish species or fish communities are sensitive indicators of the relative health of an aquatic ecosystem. Biological monitoring is preferred to chemical monitoring because the latter misses many of the anthropogenic-induced perturbations of aquatic systems, e.g. habitat degradation. This view is reinforced by Karr & Dudley (1981) who emphasized that physical and chemical



**Figure 238.** In the above example, the construction of a weir barrier (top left) just above the headwaters of the Kowie Estuary, prevented early juvenile freshwater mullet *Pseudomyxus capensis* (top centre) from moving from the estuary into river nursery areas in the lower catchment. The subsequent construction of a fishway on the side of the weir (top right) enabled the migration patterns of *P. capensis* to resume. In this case the management response was positive and the feedback loop worked by constructing a fishway to reduce the impact of the anthropogenic stressor, namely the weir.

attributes of water are unsuccessful as surrogates for measuring biotic integrity.

Bioaccumulation monitors the uptake and retention of potential toxicants (such as trace metals and pesticides) in the body of an organism. Studies have shown that there is a relationship between muscle and liver metal concentrations and the pathological status of fish in estuaries. Some scientists have even moved beyond fish *sensu stricto* and used fish parasites as indicators of environmental stress.

What is the current status of our knowledge concerning the use of fish as indicators of estuarine health in southern African aquatic ecosystems and how is this information being used? This section reviews the evidence, and examines how scientists and managers can incorporate biological and ecological data into decision support systems for estuaries on the subcontinent.

Fishes utilize a wide variety of habitats in both the marine and estuarine systems. These habitats, and consequently the fish assemblages associated with them, are potentially affected by a number of anthropogenic influences, some of which are depicted in Figure 239. In addition, some of these potential impacts can have a direct influence on the food resources, distribution, abundance, growth, survival and behaviour of fishes.

Within southern Africa, many groups of organisms have been proposed as indicators of ecosystem health and, although no single group is favoured by all biologists, it appears that fish and selected macro-invertebrates have received the most attention (Roux et al. 1993, Harrison et al. 1994).

Fish have numerous advantages as indicator organisms for biological monitoring programmes, including:

- Fish are typically present in all aquatic systems, especially estuaries and coastal lagoons, with the exception of highly polluted waters.
- There is extensive life-history information available for most species.
- When compared to invertebrates, fish are relatively easy to identify and most samples can be processed in the field, with the fish being returned to the water.
- Fish communities usually include a range of

species that represent a variety of trophic levels and include foods of both aquatic and terrestrial origin. They are therefore able to reflect the adverse effects of stresses on a variety of ecosystem components.

- Fish are comparatively long-lived and therefore provide a long-term record of environmental stress.
- Acute toxicity and stress effects can be evaluated in the laboratory using selected species, some of which may be missing from the study system.
- The general public are more likely to relate to information about the condition of the fish community than data on invertebrates.
- Societal costs of environmental degradation are more readily evaluated because of the economic and aesthetic values attached to fishes.

However, the use of fishes as indicators of biological integrity does have difficulties and problems, including the following:

- The selective nature of sampling gear for certain sizes and species of fishes can bias results.
- Sometimes substances physically or chemically harmful to other life forms do not have a detrimental effect on fishes.
- The mobility of fishes on seasonal and diel time scales can lead to sampling bias within and between estuaries.
- Diverse fish communities may exist in environments significantly altered by humans (Hocutt 1981). Indeed, the absence of fishes in a particular environment can be of far greater importance than their presence when assessing biological integrity.
- The number of technicians needed for ichthyofaunal field sampling is usually greater than that required for physical or chemical monitoring of the aquatic environment.

Many of the disadvantages described above are, however, out-weighed by the widespread advantages. In addition, it should be emphasized that a number of the negative aspects associated with using fish as bio-indicators would also apply to other taxonomic groups (e.g. invertebrates) which may also be used in biological monitoring of the aquatic environment. Inclusion of a variety



of physico-chemical parameters, together with biotic measurements of both fish and other taxonomic groups, is therefore strongly recommended when conducting a comprehensive analysis of the 'health' of an estuary.

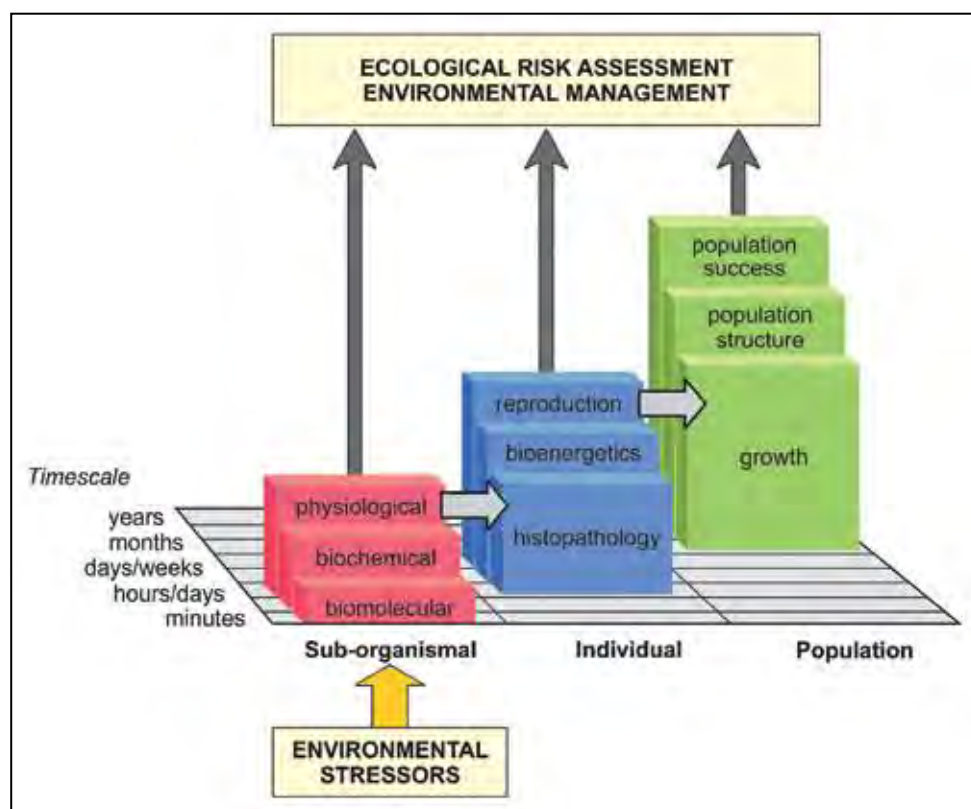
### Fish health studies and pollution

Fish health is strongly influenced by the accumulation of heavy metals and other toxins from polluted estuarine environments, e.g. industrial pollution of the Swartkops Estuary has led to arsenic, lead, mercury and cadmium being found in the juvenile stages of popular angling fish species within this system, with very high arsenic and cadmium levels recorded for large piscivorous fish such as *Argyrosomus japonicus* and *Lichia amia* (Nel et al. 2015).

Several studies have been conducted on the effect of various pollutants on estuarine fishes (e.g. Hemens et al. 1975, de Kock & Lord 1988). An example of how fishes can be used as indicators

of estuarine environmental abuse can be found in an early study by Blaber et al. (1984) which determined that Mugilidae from the Mdloti Estuary had average dieldrin levels of  $49 \text{ mg kg}^{-1}$  at a time when dieldrin was a banned substance for use on agricultural land in South Africa (van Dyk et al. 1982).

The use of DDT in agriculture ceased in 1976, but according to Davies & Randall (1989) approximately 121 tonnes were still being used annually for malaria control in 1985. Fish samples collected from the Kosi estuarine system in 1976 all had DDT in both the muscle and liver, with the flathead mullet *Mugil cephalus* having DDT concentrations of  $400 \text{ mg kg}^{-1}$  (wet mass) in the muscle and  $860 \text{ mg kg}^{-1}$  (wet mass) in the liver (Butler et al. 1983). The health authority responsible for the anti-malarial spraying operations in the area subsequently instituted stricter control of the procedures used, and samples of the same fish species collected in 1981



**Figure 239.** Diagrammatic representation of the hierarchical responses of fishes along a time-response scale to environmental stressors. Notice that lower-level (sub-organismal) responses are early warning indicators of stress while higher-level (individual, population) responses reflect the ecological significance of environmental stressors and perturbations (modified from Adams 2005).

revealed a decline in DDT values to  $<0.05 \text{ mg kg}^{-1}$  (wet mass).

Although chemical analyses of estuarine waters may highlight the presence or absence of potential pollutants at the time of sampling, bio-monitoring tends to integrate past exposures and thus identify potential stressors that require further detailed investigation (Richardson et al. 2010).

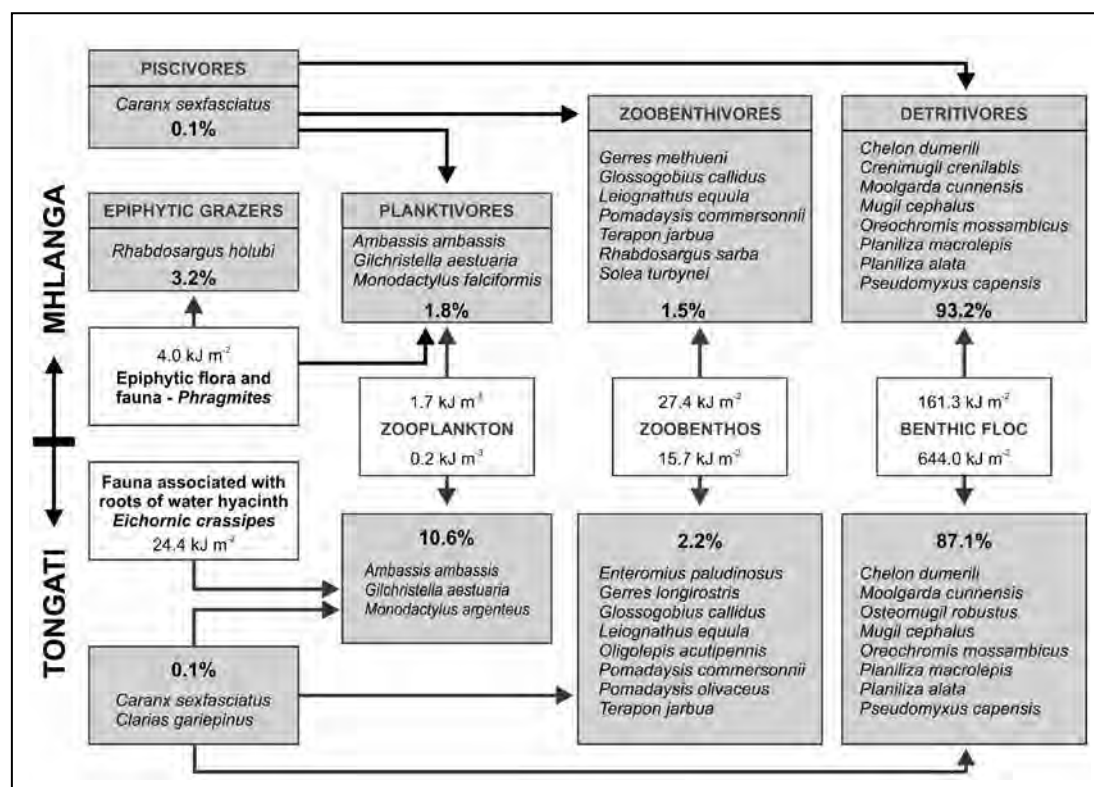
Direct and indirect pollution of southern African estuaries is on the increase (Moldan et al. 1979) and numerous reports exist documenting metal and other pollution levels in estuaries. However, very little published information is available on the impact of pollutants to fish species or assemblages (Mzimela et al. 2003, Nel et al. 2015). Indeed, one could successfully argue that this field of research has major repercussions for the health of both the ichthyofauna and people, and therefore requires considerably more funding attention going forward.

One of the earliest studies to tackle this topic was a comparison between the trophic structures of fish communities of a degraded TOCE and a

nearby one in a more natural state (Figure 240). The Tongati Estuary was affected by sewage effluent, industrial waste and agricultural run-off; consequently there was very limited epifauna or flora within its emergent *Phragmites* reed beds and almost no zooplankton (Blaber et al. 1984). Much of the water surface was also covered with the alien water hyacinth *Eichornia crassipes*.

In contrast, the more natural Mhlanga Estuary had an abundant *Phragmites* epifauna and flora and ten times the biomass of zooplankton (Whitfield 1980b) found in the Tongati Estuary. Surprisingly, the planktivores in Tongati comprised a greater proportion of the overall fish biomass than they did in Mhlanga despite the paucity of zooplankton. However, a more detailed analysis of the dietary components of the planktivores in the Tongati revealed that they had switched to feeding on the abundant epifauna associated with suspended *Eichornia* roots, an aquatic invasive plant in this system, rather than typical zooplankton prey.

Zoobenthos in the Tongati was less diverse and abundant than in the Mhlanga but poly-



**Figure 240.** Simplified trophic structure of the semi-natural Mhlanga Estuary and degraded Tongati Estuary in terms of fish biomass (percentage) and standing stock (energy) of the aquatic food resources. Data from Blaber et al. (1984) and Whitfield (1980a).

chaetes and chironomid larvae were still present and supported a low biomass of zoobenthivorous fishes (Blaber et al. 1984). Both the Mhlanga and Tongati systems were dominated by detritivorous fishes, illustrating the resilience of detritus food chains to abiotic stresses, and the stability that this provides to the functioning of estuarine ecosystems.

### **Fish communities as bio-indicators**

Fish abundance and species diversity can both provide managers with a good indication of the 'health' of a particular system. For example, Guastella (1994) found that the catch rate of anglers in Durban Bay declined between 1976 and 1991, and attributed this decrease to factors such as loss of habitat, poor water quality, disturbance by harbour traffic and possible over-exploitation of fish stocks. He concluded that careful management and efficient policing of the harbour are essential prerequisites to ensure a healthy aquatic environment and sustainable catches in the future. The extent to which marine overfishing of adult fish stocks, and the degradation of estuary nursery areas elsewhere on the KwaZulu-Natal coast, affect estuary-associated marine fish species in Durban Bay is unknown.

Fish species health and composition in an estuary can also assist in the evaluation of the condition of a system (Figures 241 and 242). Results of ichthyofaunal surveys are generally presented as lists of species and their relative abundances, which require specialist interpretation and are usually beyond the comprehension of most coastal managers and planners (Cooper et al. 1994). A method of condensing this data into a more functional format is essential if this information is to be used in any planning or management process. Communication of environmental issues such as estuarine health to the public are becoming increasingly important and indicators therefore need to be easily understood by this sector.

A standard method of condensing biological community information is through the use of an index. The Community Degradation Index (CDI) developed by Ramm (1988) is based on a comparison of the biological community present within an aquatic system, to the community that

would exist in the absence of, or prior to, degradation (Figure 242). The index assumes that differences between the potential community and the present assemblage are due to habitat degradation and not a result of natural variation.

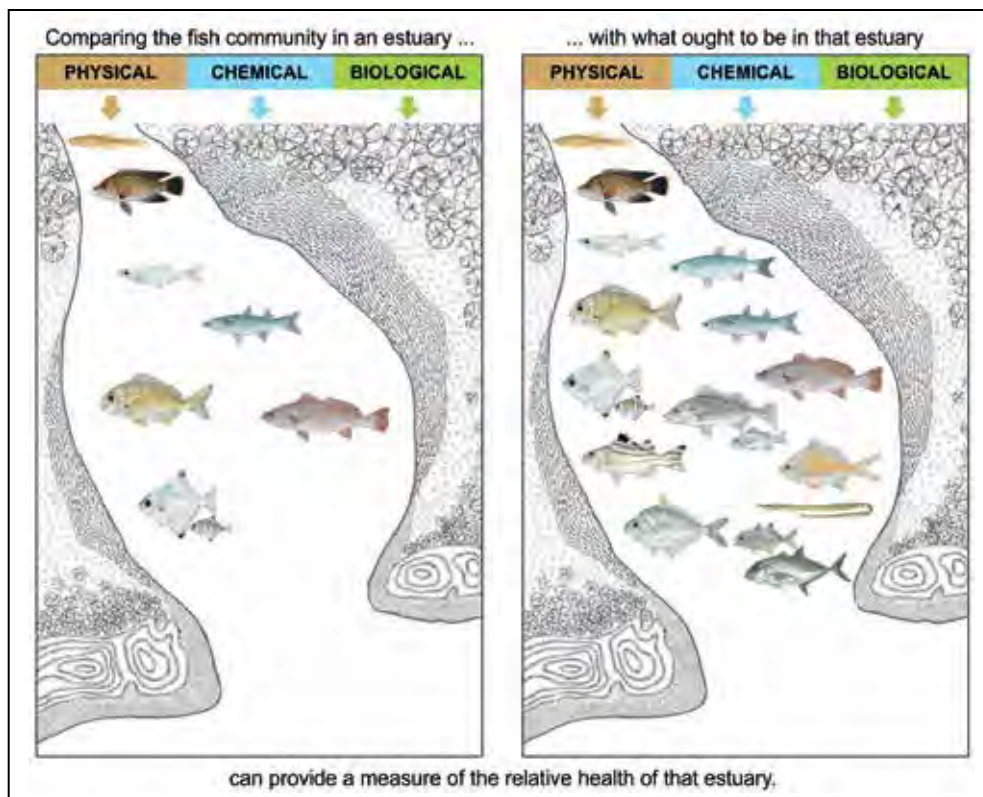
The Community Degradation Index (CDI) has been applied to numerous KwaZulu-Natal estuaries (Ramm 1990b). A total of 62 systems were first classified into six groupings based upon eight physical /hydrological parameters. This classification procedure involved the use of detrended correspondence analysis, two-way classification techniques and principle components analysis. Since the entire biological community could not be sampled, the fish assemblage of each estuary was selected (for reasons outlined previously) to represent the overall community in the analysis. Reference ichthyofaunal lists were developed for each of the physical groupings, and CDI values were calculated for each system by comparing the reference faunal list with a species list from biological surveys on that particular estuary (Ramm 1990b). Computed CDI values for KwaZulu-Natal estuaries ranged from 0.2 (undegraded) to 8.2 (severely degraded). In many respects, the CDI was a forerunner for the more comprehensive Biological Health Index (BHI) developed by Cooper et al. (1994).

Begg (1978) described the Sezela Estuary as the most severely polluted estuary in KwaZulu-Natal, mainly as a result of sugar cane fibre being deposited by a factory directly into the estuary. The system was essentially devoid of fish life and consequently had a CDI of 9-10 (Ramm 1990b). Concerted efforts to correct the problems in the estuary between 1982 and 1984 enabled recovery of the aquatic community to commence.

By 1984, biological surveys of the Sezela Estuary indicated a CDI of approximately 8, and by early 1986 the CDI had improved to about 6. In 1987 the CDI had improved to approximately 5 (Ramm 1990b) which clearly demonstrated the advantage of using this method to monitor the recovery of an estuary. On the same basis, the CDI could be used to document the faunistic degradation of an estuary over time and therefore assist in the identification of types of estuaries where the fish communities are most



**Figure 241.** The apparent near pristine Old Woman's Estuary was shown by Richardson et al. (2010) to suffer from probable insecticide and herbicide pollution from a nearby golf course, and that this impacted negatively on the health of the associated fish population. Although the fish indicated there was a pollution problem, actual water column analyses failed to reveal the presence of any potential contaminants (Photo: Alan Whitfield).



**Figure 242.** Conceptual diagram showing how the fish community in an estuary is dependent upon the physical, chemical and biological environment and, using a reference fish assemblage, can be used as a basis to determine a health index for these systems.

threatened. The CDI was only applied to estuaries in KwaZulu-Natal and was never extended to other estuaries on the subcontinent.

Using species diversity, or any other traditional index method, one could conclude that in 1987 the Sezela Estuary (19 species) was as degraded as the Mvoti Estuary (17 species). This would clearly have been inappropriate, as the comparison involves two systems which are physically very different. The Mvoti Estuary is a river mouth type system which has a naturally low diversity of fish species. The CDI, however, accommodates this incongruity and reflects an improvement in the Sezela Estuary during the period 1982-1987 from severely degraded to moderately degraded status (Ramm 1990b). The CDI measures the degree of dissimilarity between the potential community and the actual community (Ramm 1988).

A new Biological Health Index (BHI) was developed by Cooper et al. (1994) that modified the CDI to incorporate a measure of the degree of similarity between the potential community and the actual community. The formula for calculating the BHI is:  $BHI = 10(J)[\ln(P)/\ln(P_{max})]$ , where J is the number of species in the system divided by the number of species in the reference community, P is the potential species diversity (number of species) of each reference community and P<sub>max</sub> is the maximum potential species diversity from all the reference communities. The index ranges from 0 (poor) to 10 (good).

Reference communities are usually determined by establishing the normal range of fish community components such as presence /absence of taxa in the most unimpaired waters representative of the area. If a 'pristine' estuary is present in the region then that system could be used as a reference. Unfortunately very few pristine estuaries exist today and, even those that appear natural, have had marine fish recruitment processes affected by overexploitation of fish stocks elsewhere. An alternative method for determining the reference community is to compile a list of fish taxa from the complete suite of appropriate estuaries in the region under consideration.

In a study by Harrison et al. (1994), estuaries on the west coast of South Africa were classified

into groups of similar systems based upon a variety of physical-geological factors, and the resulting groupings were then treated as regions of ecological similarity. Reference ichthyofaunal lists, based primarily on biological surveys, were then drawn up for each physical group of estuaries under consideration. Freshwater fish species, stenohaline marine taxa and alien fishes were excluded from the lists. On comparing the relative biological health of the 21 estuaries on the Western Cape coast, eight (38%) systems were considered to be in a relatively poor condition, ten systems (48%) were considered to be in an acceptable or average condition, and three systems (14%) were in a relatively good condition.

The BHI has also been used to monitor the state of a particular system over time. The Damba Estuary was sampled over a two year period and the biological (fish community) health of the system calculated after each sampling event. Despite the dynamic nature of estuaries, the results were fairly consistent, with the same biological index value (2.58) being obtained on five of the eight sampling occasions (Cooper et al. 1994). This reproducibility further highlights the sensitivity and usefulness of the index as a monitoring tool.

In the late 1990s it was realized that the data existed to develop a multimetric fish index, the Estuarine Fish Community Index (EFCI), that could be applied to estuaries over the entire South African coastline. Thus the EFCI was developed and tested using fish catch data collected by a CSIR national project for most estuaries on the subcontinent (Harrison & Whitfield 2004). The EFCI is based on 14 metrics (Table 28) that represent four broad fish community attributes, namely species diversity and composition, species abundance, nursery function, and trophic integrity. Reference conditions and metric thresholds were derived from fish community data collected during an extensive national study.

The individual metrics were evaluated using data that were collected on an estuary that was degraded and in which rehabilitation measures had been implemented that were apparently successful. The recovery of EFCI evaluation in parallel with the improved estuarine condition demonstrated



that the selected metrics adequately measure the conditions of separate but related components of estuarine fish communities and that these do reflect environmental condition.

At about the same time that the South African EFCI was published, there was an upsurge in interest around fish community based indices for use in European transitional waters (= estuaries). As was the case with the EFCI, most of the fish indices for UK and Irish transitional waters (as part of the European Water Framework Directive) were based on metrics developed in South Africa. The dominant metrics used in these fish community indices are species richness /composition, habitat use and trophic guilds (Coates et al. 2007, Harrison & Kelly 2013).

In 2006, the EFCI was applied to data collected for some 190 South African estuaries (Harrison & Whitfield 2006). Its application spanned three biogeographic regions and included three distinct estuarine typologies. Metric reference conditions and scoring criteria were

developed for each estuary type within each zoogeographic region separately. The EFCI was applied to each estuary by comparing its fish community with the appropriate reference.

A comparison of the EFCI with independent measures of estuarine condition revealed that the index was able to effectively differentiate between poor- and good-quality systems (Figure 243). Applying the EFCI to estuaries in which multiple samples were taken showed that the index is reproducible, with 36 out of 44 multiple sample ratings (88%) having consistent poor to moderate, or good to moderate ratings (Figure 244). It was also found that the EFCI is both a robust and sensitive method for assessing the ecological condition of southern African estuaries. In addition, a major strength of the index is that it is an effective communication tool for converting ecological information into an easily understood format for managers.

One of the areas requiring further attention is repeated testing of the sensitivity and robustness

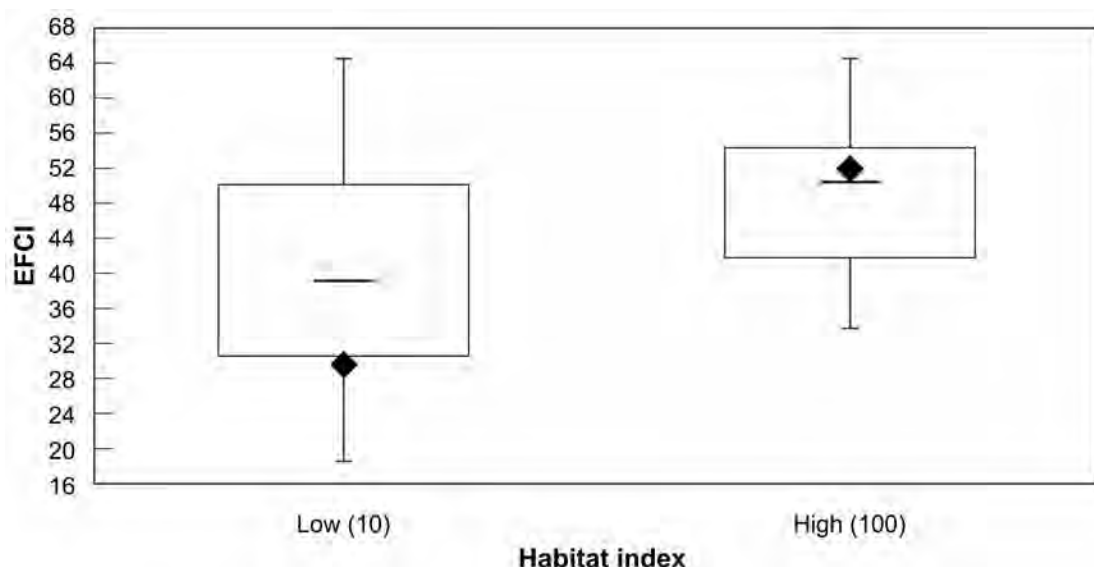
Table 28. Metrics used in the Estuarine Fish Community Index (EFCI) and fish responses to environmental stress (modified from Harrison & Whitfield 2004).

Fish community index metric	Response to stress
<i>Species diversity and composition</i>	
1.. Total number of taxa	Reduced
2. Rare/threatened species	Absent
3.. Exotic/introduced species	Present
4. Species composition (relative to reference assemblage)	Reduced
<i>Species abundance</i>	
5. Species relative abundance (relative to reference assemblage)	Reduced
6. Number of species that make up 90% of the abundance	Reduced
<i>Nursery function</i>	
7. Number of estuarine resident taxa	Reduced
8. Number of estuarine-associated marine taxa	Reduced
9. Relative abundance of estuarine resident taxa	Very low or very high
10. Relative abundance of estuarine-associated marine taxa	Very low or very high
<i>Trophic integrity</i>	
11. Number of zoobenthivorous fish taxa	Reduced
12. Number of piscivorous fish taxa	Reduced
13. Relative abundance of zoobenthivores	Reduced
14. Relative abundance of piscivores	Reduced

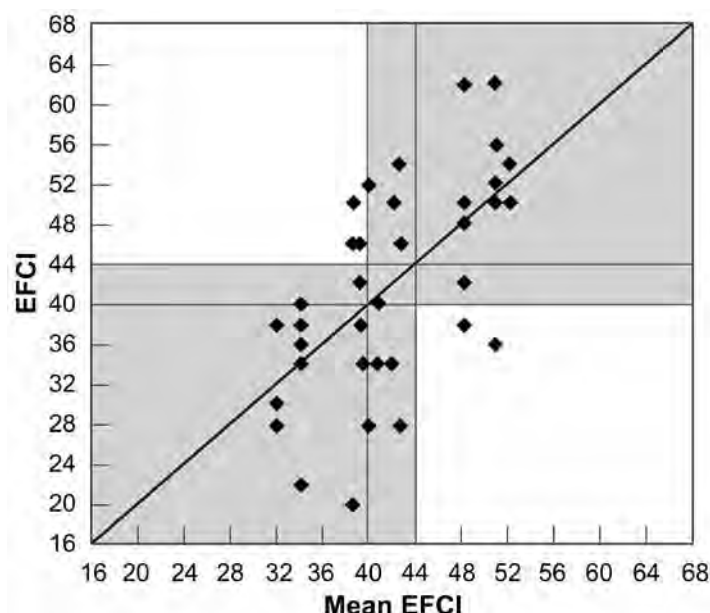
of indices, particularly the linking of natural and / or anthropogenic pressures with index responses. There have been innovative approaches in this regard, including that of Richardson et al. (2011), which used both stress responses at the individual fish level of biological organization and fish community level metrics to assess estuarine condition

in South African systems (Figure 245).

The prototype Estuarine Fish Health Index (EFHI) uses biological indicators from multiple levels of biological organization and integrates the well-established EFCI with stress responses measured at lower levels of biological organization at the individual species level. Four sub-



**Figure 243.** Comparison of EFCI values with independent measures of good-quality and poor-quality estuaries based on a habitat index (Turpie et al. 2002). Boxes include data within the first and third quartiles; vertical lines represent the range of EFCI values; horizontal bars represent the median, and solid diamond symbols represent modal values (after Harrison & Whitfield 2006).



**Figure 244.** Mean EFCI values versus EFCI scores for estuaries that were repeatedly sampled. Diagonal line represents the 1:1 EFCI score to mean EFCI relationship, vertical and horizontal lines represent the boundary of moderate EFCI ratings; shaded areas include EFCI ratings of poor-to-moderate and good-to-moderate (after Harrison & Whitfield 2006).

organism level biomarkers were used in the EFHI prototype by Richardson et al. (2011) on *Rhabdosargus holubi*, namely a liver histopathology assessment, lipid peroxidase and acetylcholinesterase assays, and an individual fish condition factor analysis. The data from these analyses and the results of the EFCI were integrated and showed that a combined index produces a more sensitive and predictive tool for assessing estuarine health than when used in isolation.

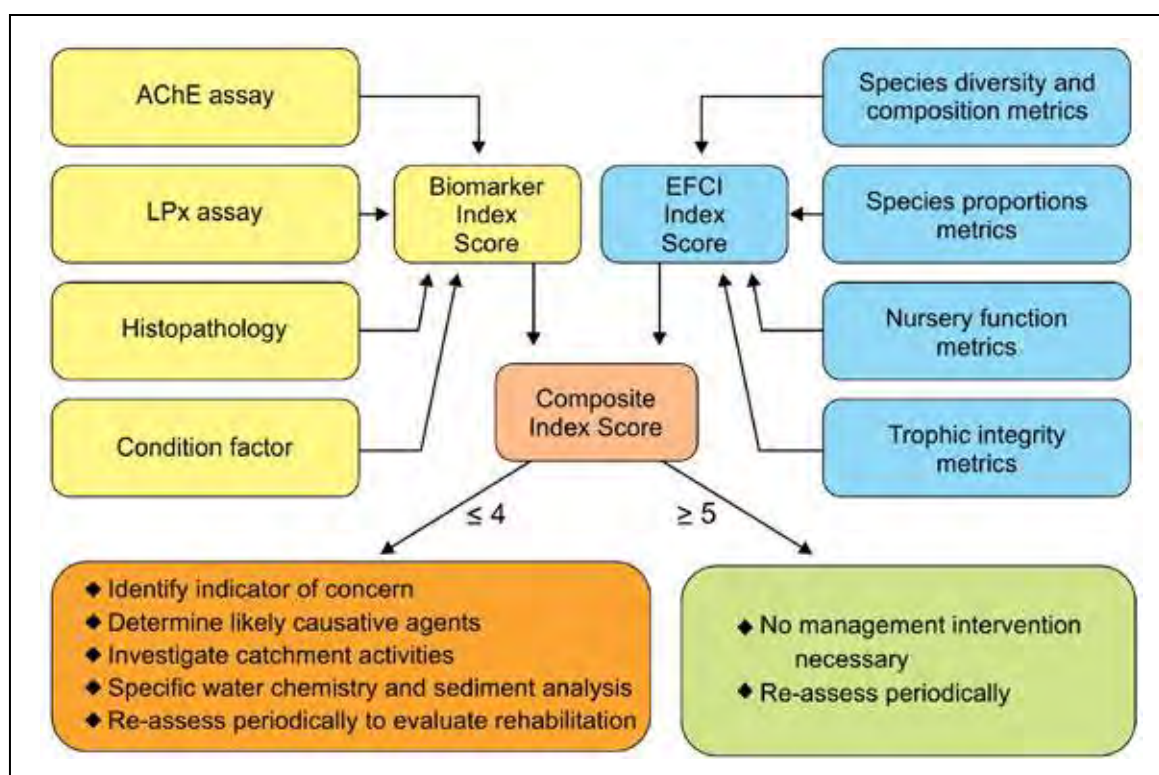
### Fish Recruitment Index

As the competition for scarce water resources increases, it is essential that the river flow requirements of estuaries are well articulated and that suitable methodologies are available to assist in determining the optimal scheduling of freshwater allocations. The development of a fish recruitment index that will adequately reflect the suitability of freshwater release policies for fish populations utilizing estuaries was perceived to be a major need that was addressed with the development by Quinn et al. (1999) of a Fish Recruitment Index (FRI).

A major requirement of the FRI was that it should be biologically meaningful and be readily understandable by biologists and water resource managers alike. A secondary objective was to make the best use of previous research and existing understanding and, in so doing, to provide guidelines for future research. New insights could then be adapted for use in the FRI.

The FRI is a biologically meaningful management index which is based on the integration of three key information sets. The first set is the current understanding relating to the importance or significance (dependency score) of marine fish species recorded in the estuarine environment and whether it is endemic to southern African waters or not. The second is the preferred timing of the immigration period for a particular species (optimal recruitment score). The third information set incorporates known environmental requirements for the recruitment by juvenile marine fish into southern African estuaries.

Details of the formula and practical application of the above index in a temporarily open / closed (Great Brak) and a permanently open



**Figure 245.** Schematic representation of the prototype Estuarine Fish Health Index (EFHI) which is a combination of the Harrison and Whitfield Estuarine Fish Community Index (EFCI) and the Richardson et al (2010). Estuarine Fish Biomarker Index (EFBI). Thresholds for possible management intervention are also indicated (modified from Richardson et al. 2011).

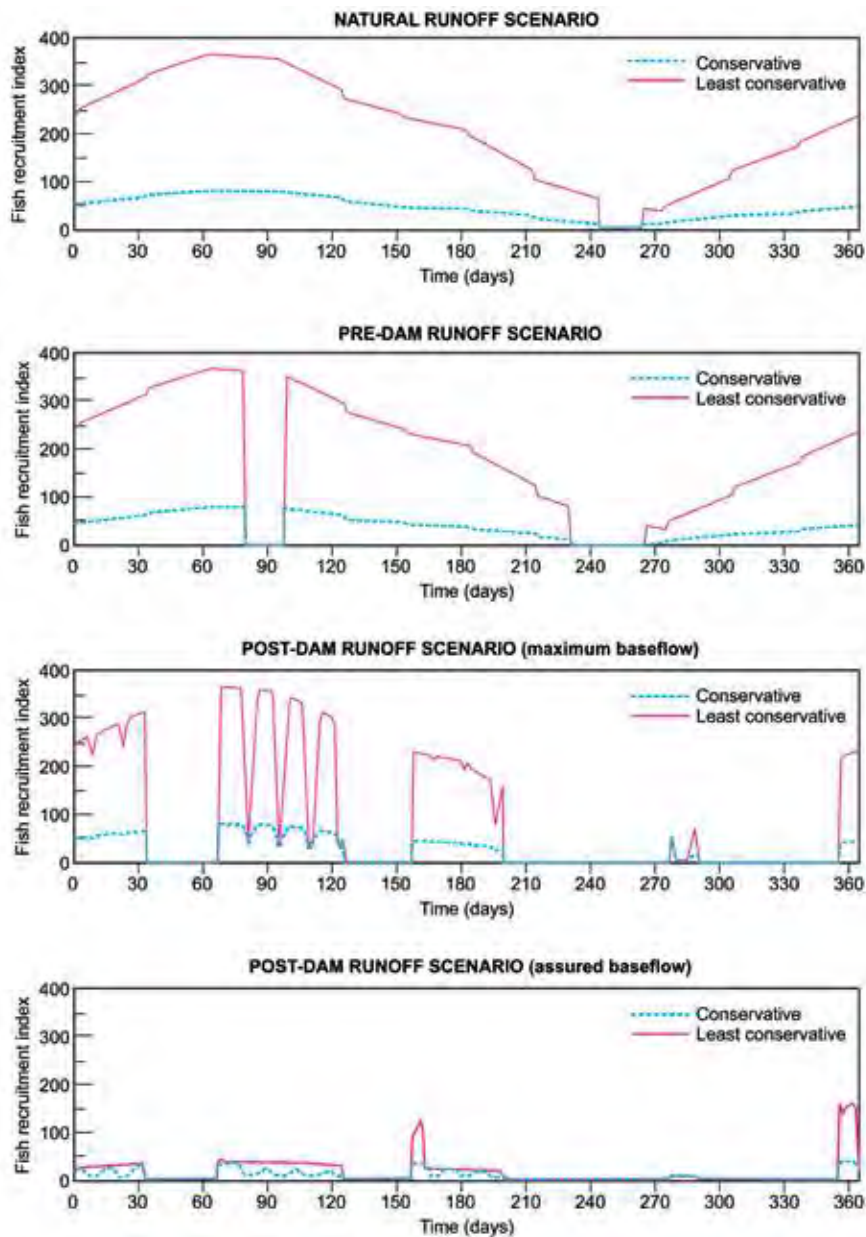
(Kromme) estuary are given in Quinn et al. (1998, 1999). In both these systems, a variety of river flow scenarios were examined and the predicted relative changes (on a daily basis) in the magnitude of marine fish recruitment assessed (Figure 246).

### Fish Importance Rating

A very relevant index for use in estuarine fish conservation, in particular the ranking of individual estuaries in terms of their value to fishes, is the Fish Importance Rating (FIR) index developed

by Maree et al. (2003). The FIR is based on a scoring system using both biotic and abiotic criteria that are considered to reflect the importance of individual estuaries to the estuary-associated ichthyofauna (Figure 247).

This prioritization exercise enabled South African estuarine systems to be ranked according to their importance to estuary-associated fish species based on estuary type, area, condition and degree of isolation (i.e. how isolated an estuary is in a coastal context).



**Figure 246.** Fish Recruitment Index (FRI) as applied to the Great Brak Estuary under a natural runoff scenario, pre-dam runoff scenario and two post-dam run-off scenarios of increasingly restricted river supply to the estuary (for details see Quinn et al. 1999).

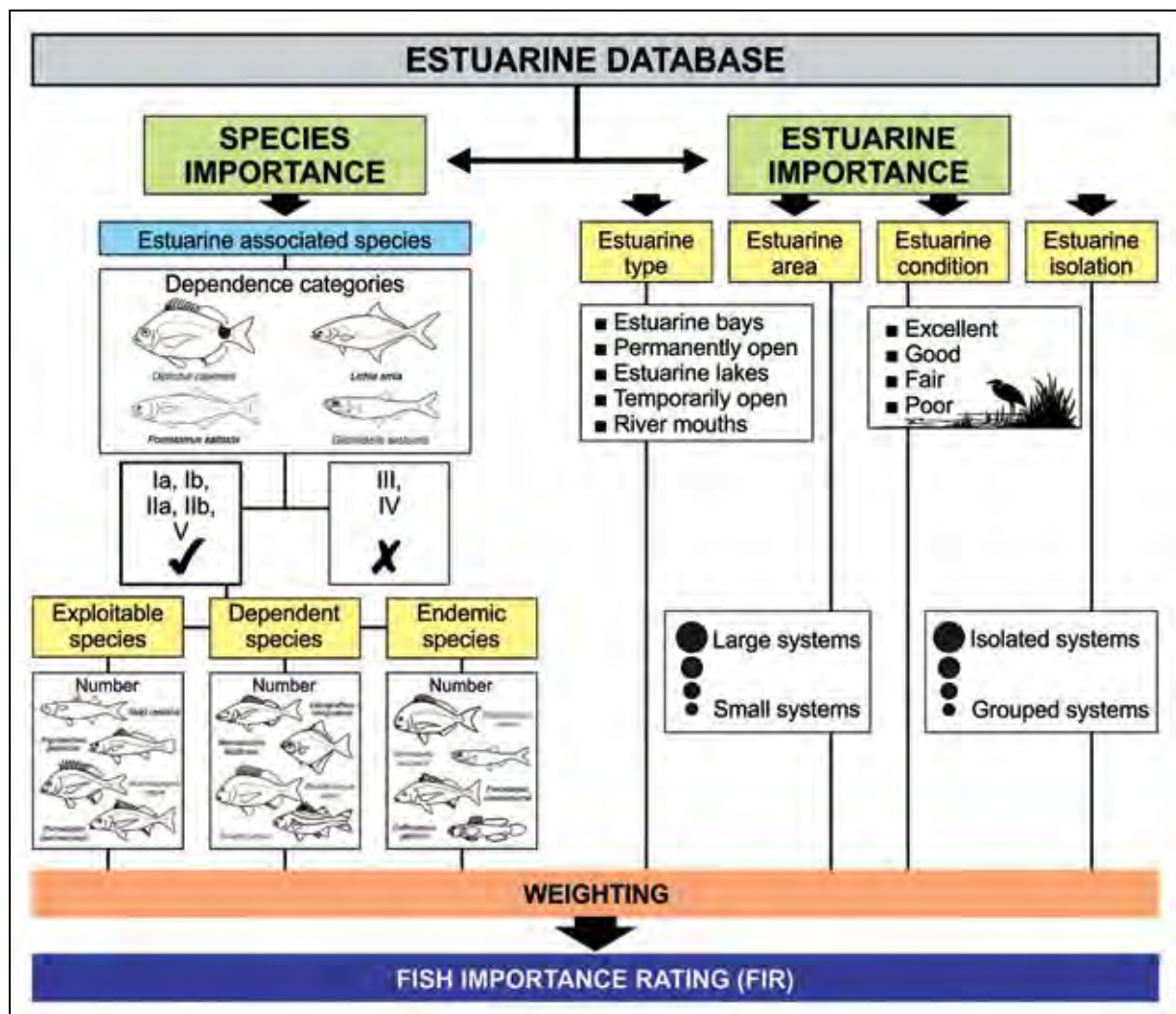


As expected, the large estuarine lakes such as St Lucia, Kosi, Klein and Swartvlei, and the estuarine bays including Durban Bay, Richards Bay, Mhlathuze and Knysna all featured in the top 10 South African systems from a FIR perspective. What was particularly surprising was the inclusion of the much smaller subtropical Matigulu /Nyoni and Mlalazi estuaries within this group (Maree et al. 2003).

By combining the importance of fish species found in particular estuaries, together with the value of those same systems (Figure 247), it was possible to identify those South African estuaries with a high conservation priority. This ranking can be presented in both a regional and country context, thus assisting conservation decisions on both a local and national scale.

### Some preliminary conclusions

The basis for using biological monitoring of fishes to assess environmental condition is that the relative health of a fish community is a sensitive indicator of stresses on the entire aquatic ecosystem. Ideally, studies should determine stress at the community, population, individual, physiological and subcellular level, using techniques such as production ecology, behaviour, physiology, pathology, biochemistry, bioaccumulation studies and genetics. The recommendation by Elliott et al. (1988) that fish studies should encompass a holistic approach to estuarine assessments, using chemical, hydrographical and other biological data to interpret the fish results, is endorsed but often not possible where limited budgets are available.



**Figure 247.** Diagrammatic outline of the Fish Importance Rating (FIR) process for South African estuaries (after Maree et al. 2003).



Within southern African estuaries a number of approaches have been adopted by scientists, led by Dr Trevor Harrison (Figure 248) and the Estuarine Fish Community Index (EFCI), with the Fish Recruitment Index (FRI) and Fish Importance Rating (FIR) addressing other estuary specific issues. In addition, monitoring of trends in anglers catches, documenting pollution events, sudden fish mortalities, etc. all provide insights into the health of these systems.

The importance of estuaries for fish has resulted in environmental quality objectives (EQO) being adopted to protect estuarine usage by fish and fish population health (Elliott et al. 1988). These fish orientated EQO include: (a) the water quality always allows the passage of migratory fish; (b) the estuary's residential fish community is consistent with the hydro-physical conditions; (c) the benthos and sediments are of sufficient quality to support the fish populations; and (d) the levels of toxic substances in the biota should be insignificant and should not affect predatory fish.

More recent developments in the EQO field are directed not only towards the maintenance of healthy estuarine fish populations, but also

incorporate the health of people. The adoption of a set of EQO for southern African estuaries, together with a system of appropriate environmental quality standards (EQS), is strongly recommended. Information from existing fish studies could be used in the preliminary formulation of both EQO and EQS for estuaries on the subcontinent. Further studies should then be initiated on those topics where current information is either inadequate or lacking altogether.

The search for improved fish indices to communicate the health of estuaries is ongoing. Examples from this century include South Africa (Harrison & Whitfield 2004), Belgium (Breine et al. 2007), Portugal (Vasconcelos et al. 2007), France (Delpech et al. 2010) and Australia (Hallett et al. 2012). An important point raised by Sheaves et al. (2012) is that indices have moved away from simple but effective composite measures towards more complex multivariate approaches. A slightly different perspective is expressed by Pérez-Domínguez et al. (2012) who suggested that most indices are developed for particular estuaries or regions and they therefore recommend a widening of the geographical relevance and functional attributes of future fish indices.



**Figure 248.** The ichthyologist primarily responsible for the development of the EFCI in South African estuaries, Trevor Harrison (Photo: Alan Whitfield).



## Chapter 6

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### Conservation of fishes in southern African estuaries

#### 6.1 INTRODUCTION

AQUATIC CONSERVATION, and the conservation of fish in particular, is an issue which should be important to all people. This view is highlighted by Bruton (1995) who states “The vital role of fishes in aquatic ecosystems, and of aquatic ecosystems in the physiology of the planet, make it essential that more attention is given for fish conservation, even if it is for the selfish motive of human survival”. As has been mentioned, estuaries are vital nursery grounds for many commercial, recreational and subsistence targeted fish species. Fishes are also very important in converting the elevated primary and secondary production within estuaries into high quality protein that is utilized by piscivores (including humans!) both in estuaries and the marine environment. The role of fish in nutrient recycling and carbon storage and transfer should also be emphasized.

The conservation of biodiversity has become a major national and international concern, and gained further momentum with the signing of the United Nations Convention on Biological Diversity. A major obligation of the signatories to the above convention is the development of national, regional and local strategies for the conservation and sustainable use of biodiversity. The planning of where priority conservation sites should be located and evaluating the various estuarine use options are essential components of such a strategy. Since fish are a dominant and economically valuable biotic component in most estuaries, and are also used by people for food and recreation, it would be wise to highlight the importance of this taxon in the above exercise.

Estuaries, like many other types of wetland worldwide, are under long-term threat of damage and destruction. As will be seen in the following section, a number of southern African fish species are dependent on estuaries for the maintenance of healthy populations. The viability of

estuaries as fish nurseries is directly related to the large amount of suitable food in these areas and this is dependent on the maintenance of natural aquatic processes. Factors that have caused fishes to become threatened are varied and often differ from one biogeographic area to another.

The negative factors influencing estuaries can include habitat degradation, disruption of essential ecological processes, hydrological manipulations, environmental pollution, over exploitation due to fishing activities, global effects, genetic contamination, and impacts of introduced aquatic animals. In southern African estuaries, habitat degradation through land use changes, and hydrological manipulations through excessive freshwater abstraction are important drivers of estuarine status. Less important at present, but showing increasing signs towards becoming a major problem in southern Africa is environmental pollution, especially organic and inorganic waste from industrial, agricultural and domestic sources.

Apart from public education and awareness, perhaps the most effective contemporary action that would have an immediate positive effect on estuary-associated fish populations would be the closure of selected estuarine systems to all forms of fishing (Figure 249). The existing legislation relating to bag and size limits is not working and the recent opening up of important MPAs (e.g. Dwesa and Tsitsikamma) to fishing is simply going to exacerbate the plight of targeted fish species that are already heavily overexploited. The next decade probably represents the last window of opportunity to reverse declining catch trends and the implementation of effective fish conservation measures. Failure to do so could result in the commercial and recreational ‘extinction’ of selected taxa that have already declined below the 5% level of original spawner stock biomass and are showing little or no sign of recovery.



**Figure 249.** Near natural estuaries (e.g. Ngoma) above with full protection as fish nursery areas are required to alleviate intense recreational and subsistence angling pressures elsewhere (Photo: Alan Whitfield).



**Figure 250.** Catch and release angling – an ideal way to ensure fish stock recovery and a sustainable recreational fishery in the future (Photo: Craig Thomassen).



Although many southern African anglers are quick to point fingers at the other known or suspected causes of declining estuarine fish stocks, the majority seldom consider their own role in the demise of targeted species. Offshore trawlers in particular are frequently cited as a proximate cause of the decline in coastal fishes (Kramer et

al. 2017), despite the fact that these commercial fishing operations target completely different species. Perhaps a major positive trend is provided by the growing contingent of 'educated' anglers who comply with fisheries legislation and also practise 'catch and release' fishing on a regular basis (Figure 250).

## 6.2 CONSERVATION OF THE PHYSICAL ENVIRONMENT

Only about 3% of the Earth's area is protected within refuges and most of these reserves are designed to cater for terrestrial rather than aquatic conservation. Even if the total area under protection were to be doubled or tripled, the Earth's biodiversity would still be threatened (Moyle & Leidy 1992). This applies particularly to fishes in estuaries which are highly mobile and cannot be confined to the boundaries of a particular reserve. In addition, the linear nature of most estuaries, and their high degree of linkage with freshwater and marine ecosystems, makes estuarine habitats highly vulnerable to external perturbations.

Many issues and developments, such as the siting of industries and recreational facilities, are subject to government control, consent or guidance. Ichthyologists are committed to supporting the appropriate and sustainable use of estuaries without prejudicing the fish resources. Unfortunately research funding for biological and ecological studies is declining as these resources are diverted to projects with a strong socio-economic bias. However, a 'sustainable development' approach is particularly relevant to estuaries, since it presupposes that risks of damage to the environment will be anticipated and avoided, and this approach requires ecological inputs.

Most estuaries in southern Africa are being subjected to varying degrees of catchment land-cover transformation. Natural landscapes and hydrological functions are integral to the functioning of estuaries. A recent study of the relationship between catchment land-cover and the health of the East Kleinemonde Estuary was investigated using Geographic Information System (GIS) techniques to delineate and quantify land-cover characteristics at different scales (Masefield et al. 2014). Preliminary results indicated that there was

a relationship between catchment land-cover and estuarine health within all of the assessed catchment delineations. Unsurprisingly, natural land-cover was determined to be the best predictor of estuarine health for the above system.

Research projects within southern Africa are contributing to the establishment of minimum standards for important environmental assets, and the environmental accounting by the state for those assets. With the South African Government having signed the Rio Convention on Biological Diversity, there is a national and international obligation to maintain estuarine habitats and their biota in a healthy state for all citizens of the country, an approach that is also emphasized by van Niekerk & Turpie (2012).

### **Maintaining estuarine productivity**

Estuaries are usually more productive than adjacent seas or inflowing rivers, and the maintenance of that productivity is important for any conservation measures that are proposed. Unfortunately the high primary and secondary productivity of estuaries on the subcontinent is seldom taken into account when assessing the value of these systems. The viability of estuaries as nurseries and feeding grounds for fishes is directly related to the accessibility and productivity of these systems. An indication of the importance of estuarine productivity is provided by Lamberth & Turpie (2003) who highlighted the economic value of fish stocks associated with South African estuaries.

Most fish species in estuaries on the subcontinent are adapted to normal tidal salinity fluctuations, and can even tolerate prolonged oligohaline or hypersaline conditions, provided these changes occur gradually over an extended period. Although salinity extremes are a natural feature





**Figure 251.** Impact of freshwater deprivation on Lake St Lucia. The Landsat image on the left shows a compartmentalised system towards the end of a prolonged drought (February 2016) whereas the one on the right (May 2017) shows a near full system following excellent rainfall and significant inputs from the reconnected Mfolozi River.

of certain estuarine systems, the levels attained by the salinity peaks have increased following the construction of impoundments in catchment basins. Unless alternative sources of fresh water can be found, salinity peaks within these estuaries are likely to increase in the future to the extent that such systems do not function at their full potential.

A good example of how the most important estuarine system in southern Africa has become dysfunctional has been documented by Whitfield & Taylor (2009). The St Lucia system has lost most of its freshwater supply (Figure 251) and no longer functions as the most important fish nursery area on the subcontinent (Cyrus & Vivier 2006). Hypersaline conditions result in the loss of species which cannot tolerate particular salinities and it has also resulted in a decline in available fish food resources (Whitfield 2005).

A holistic approach to ecosystem productivity (Bird et al. 2016, Ortego-Cisneros et al. 2016) and management is urgently required. Mismanagement of either the river catchments or their adjacent estuaries leads to impoverished systems which are then of little value to aquatic organisms or people. In this context 133 of the approximately 280 functional estuaries along the South African coast have been assessed as being in a poor or fair condition (Table 29). The situation is even worse when estuarine health is assessed using the percentage of total estuarine habitat, resulting in only 15% of the area being in excellent or good condition, and 85% in fair to poor condition (van Niekerk & Turpie 2012).

### Reducing estuary mouth manipulation

The majority of southern African estuarine systems are naturally closed off from the sea for varying periods, and in the past this has led to actions by poorly informed land owners and local authorities attempting to maintain open mouth conditions (Begg 1984b). Legislation and information dissemination has drastically curtailed the ad hoc breaching of estuarine sand bars, but existing housing and agricultural developments on adjacent floodplains have necessitated the continued premature opening of a large number of temporarily closed estuary mouths (Huizinga & van Niekerk 2001). This has a negative influence on effective sediment scour by the released lagoonal waters and hence the duration of the open phase, both of which impact on fish populations in South African estuaries (James et al. 2007).

The species composition, size distribution and abundance of marine fishes within estuaries undergo seasonal variations that are directly related to migration patterns (Wallace 1975a). Recruitment of most species into Eastern and Western Cape Province estuaries reaches a peak during early summer, which coincides with maximum food resource availability and corresponds to the time when systems along this section of the coast are normally open to the sea (Whitfield & Kok 1992). In addition, the prolonged recruitment periods of most fish species into estuaries provide a buffer against the variability in mouth opening and other short-term extremes in the aquatic environment, e.g. nearshore upwelling (Schumann et al. 1982).

Table 29. A composite analysis of the 'condition' of South African estuaries in each biogeographical region (data from Whitfield & Baliwe 2013).

Estuarine condition	REGION							
	Cool-temperate		Warm-temperate		Subtropical		South Africa	
	No.	%	No.	%	No.	%	No.	%
Poor	9	35	6	5	24	19	39	13
Fair	9	35	37	29	48	38	94	34
Good	7	27	71	56	40	31	118	42
Excellent	1	4	13	10	15	12	29	10
<b>Total</b>	<b>26</b>	<b>100</b>	<b>127</b>	<b>100</b>	<b>127</b>	<b>100</b>	<b>280</b>	<b>100</b>

Artificial winter opening of southern Cape estuary mouths has occurred in the past and has generally led to the premature closure of these systems, to the detriment of juvenile marine fish recruitment (Whitfield & Kok 1992). In addition, the larvae of several spring and summer recruiting species are absent from the nearshore marine environment during winter (Whitfield 1989c). Loss of the 'head' of water accumulated during the winter rains effectively reduces the chances of a spring or early summer opening, thereby denying certain fish species access to estuarine nursery areas.

### **Catchment conservation**

Mismanagement of catchments is probably the single most important factor accounting for the loss of estuarine habitat within southern Africa and will reduce the feeding grounds available to estuary-associated fish species. Ultimately the negative impact of this degradation will be felt more widely since, for several estuary-associated species, there is a close relationship between the availability of estuarine nursery areas and adult abundance in the marine environment (Mann & Pradervand 2007).

Catchment management should take into account the vital role that fresh water plays in the functioning of estuaries (Morant & Quinn 1999) and therefore the long-term conservation and health of fishes in these systems. The 1956 South African Water Act did not legally recognise the freshwater requirements of natural ecosystems and consequently many large dams were built without any environmental water release policy in place. However, the new National Water Act of 1998 promotes the concept that the ecological requirements of aquatic systems, including estuaries, need to be catered for by legislation. Under this new Act the quantity and quality of river water to be supplied to an estuary is investigated by experts and a dedicated allocation is then made by the Department of Water and Sanitation (Adams et al. 2002). Although freshwater allocations have been determined for a number of southern African estuaries, the promulgation and implementation of these recommended allocations has generally been lacking.

The transformation of estuaries into less suitable habitats for fishes has accelerated rapidly within the last century. Begg (1984) quotes numerous examples of systems in KwaZulu-Natal to illustrate this deterioration, e.g. the Mzumbi Estuary is described as having been reduced to "a shallow sheet of fresh water gravitating towards the sea over a bed of sand". This transformation has been caused by extensive catchment deterioration, floodplain cultivation and canalization, all of which have increased the sediment load that is transported downstream. Additional evidence of serious catchment mismanagement affecting estuarine fish stocks comes from the poorly managed Mbhashe system. Plumstead (1990) found that a barrage constructed on the Mbhashe River in 1984 was associated with a decline in both the abundance and diversity of fish species in the downstream estuary, as well as a rapid filling of the waters upstream of the barrage with eroded sediments.

The catadromous anguillid eels are particularly vulnerable to human manipulations of inland waters due to their obligate migrations. The construction of impoundments and excessive abstraction of fresh water has reduced eel habitat availability in rivers, as well as introducing barriers to migration. Glass eel migrations through estuaries and into fresh water occur mainly during summer but differ in magnitude between years (Bruton et al. 1987). Maximum eel recruitment into Eastern Cape estuaries and river systems occurs during above-average river flow following a flood, especially if the flooding event coincides with the spring tidal cycle. Clearly, the capture of freshwater pulses by large impoundments will reduce olfactory cues and other migratory stimuli entering estuaries and the sea, with a concomitant decline in the number of glass eels entering suitable river catchments. Similarly, downstream migrations by adult eels to marine spawning grounds are prevented by large dams that seldom overflow.

### **Coastal developments and pollution**

Approximately 40% of South Africa's population resides within 100 km of the coast. Given the rugged nature of this coastline, sheltered estuarine environments are the focal points for human

settlement, resulting in substantial pressure from a wide range of industrial, commercial, residential, tourism and recreational activities (Morant & Quinn 1999). Recent changes in economic conditions, such as increased consumer spending power and increased mobility of people, have witnessed a substantial increase in development activities in certain coastal areas, notably the Eastern Cape Province. Increased human habitation and development on or near estuaries will increase the demand for land, fishery resources and fresh water, and ultimately impact heavily on estuary-associated fishes.

Almost all of South Africa's estuaries have been degraded to a greater or lesser extent (Cooper et al. 1994). A number of these systems are fringed by residential, tourism-related and industrial developments that have directly impacted on estuarine landscapes, including their natural functioning. Bridges, roads and other bank and channel stabilizing structures not only influence the state and functioning of estuaries but also their biodiversity (Morant & Quinn 1999). Residential development projects such as marinas, in particular, have led to direct floodplain habitat loss and conversion of natural shorelines and other habitats in many South African estuaries.

Increased nutrient loads due to groundwater seepage from septic tanks into estuaries are a major cause for concern. For example, Baird & Pereyra-Lago (1992) revealed that inorganic nutrient and coliform bacterial concentrations in a marina canal system on the Kromme Estuary were higher when compared to other Eastern Cape estuaries and were one to two orders of magnitude higher during the December holiday season. Extreme cases of allochthonous nutrient loading in certain intermittently open estuaries such as the Hartenbos and Mdloti may lead to hyper-eutrophic conditions and ultimately the loss of aquatic biota (Figure 252).

Unlike the recycling of organic pollutants (e.g. nitrogen) via natural processes, heavy metal pollutants entering estuaries tend to become incorporated into the bottom sediments where they come into contact with both epibenthic and infaunal invertebrates, as well as demersal and benthic dwelling fish species. Consequently, low

level discharges that meet existing water quality criteria, may pose significant threats in the long-term. Indeed, Binning & Baird (2001) showed that the highest heavy metal concentrations in the Swartkops Estuary were recorded at points where runoff from informal settlements and industry entered the system. These authors also showed that the recorded contamination levels were remarkably higher than those documented by a similar survey 20 years earlier. Unfortunately, many human-induced impacts are often difficult to distinguish from natural variability in the short term, which emphasizes the need for long-term monitoring programmes (Allanson 2001).

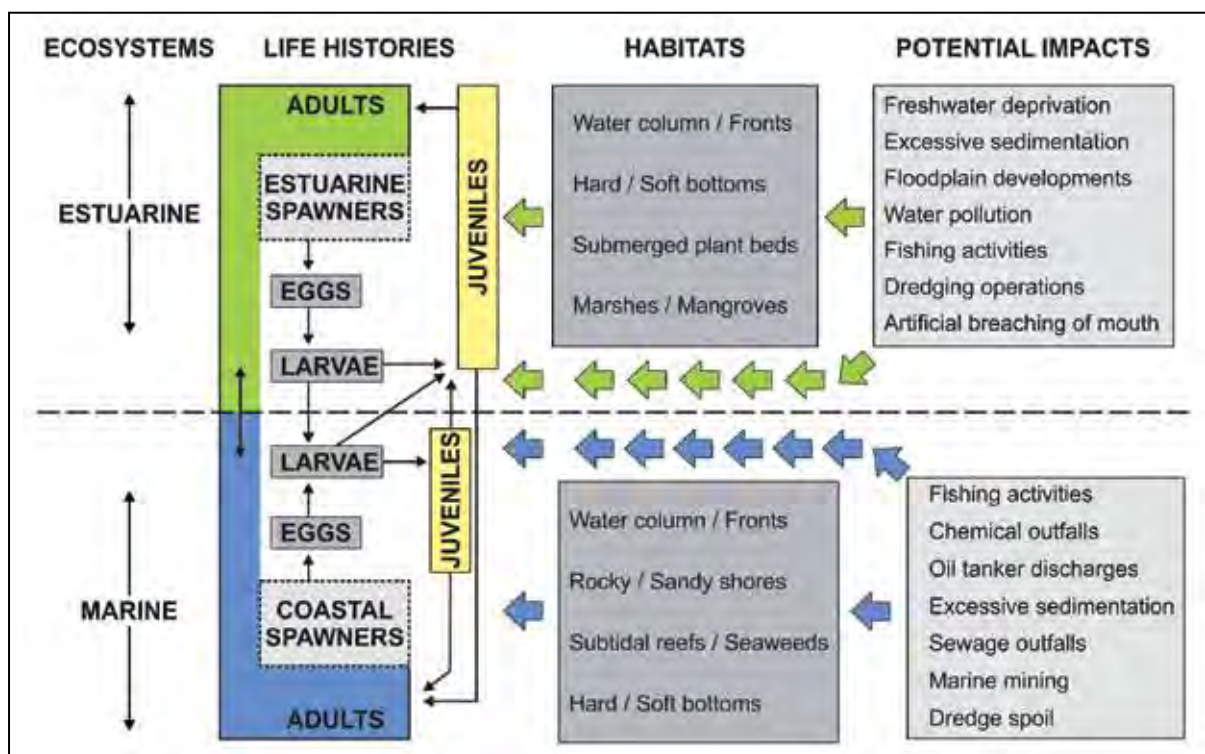
Estuarine aquaculture developments pose a major conservation threat in many parts of the world. However, due to the relatively small size, fluctuating abiotic conditions, and microtidal characteristics of southern African estuaries, aquaculture developments are limited to relatively few systems and currently do not pose a significant threat (Cowley et al. 1998). However, significant pressures on government departments to promote aquaculture and mariculture initiatives in estuarine environments could be translated into negative consequences for resident and migrant fish species in estuaries on the subcontinent in future.

Development and population growth have associated political and socio-economic pressures that need to be considered holistically within management arrangements to ensure sustainable coastal development. The National Environmental Management: Integrated Coastal Management Act (No. 24 of 2008) makes provision for integrated coastal management and sustainable use of resources. The Act also calls for the implementation of Estuary Management Plans that must be integrated into regional and local planning initiatives (i.e. Integrated Development Plans). This legislation is designed to support the considerable value, function and services provided by coastal and marine ecosystems (including estuaries) and to maintain their production potential over the long-term. However, in order to ensure that this goal is attained, it is essential that management authorities are resourced with sufficient capacity and funding to implement and enforce the regulations.





**Figure 252.** A large-scale fish kill documented at the temporarily closed Mdloti Estuary in February 2004, prior to the controlled artificial breaching of the mouth which was directed at flushing the anoxic waters out of the estuary. Note the presence of *Salvinia* and *Pontederia* invasive floating plants in the picture, nourished by the eutrophic conditions prevailing in this estuary (Photo: Nicolette Forbes).



**Figure 253.** Diagram showing potential environmental modifications to fish habitats and life-history stages brought about by global change in the southern African coastal region (after Whitfield 1996d).



### 6.3 INFLUENCE OF GLOBAL CHANGE

Climate change, is likely to produce profound modifications to the structure and functioning of estuaries which will, in turn, have a range of implications for the conservation of fishes in southern African estuaries. Already there are strong indications of increased land and sea surface temperatures in the region (Kruger & Shongwe 2004, Schleyer & Celliers 2003) and shifts in the distribution of individual species are already taking place in the Eastern Cape in response to these events (James et al. 2008, 2013).

As climate change gains momentum it can be expected to have an increasing impact on the distribution and abundance of all estuary-associated species, but particularly those temperate taxa that are sensitive to increased water temperatures. This is because of the shape of the South African coastline, which results in a reduction in the number and extent of warm and cool-temperate estuaries as the tropical and subtropical zones expand towards the south and southwest, creating a 'coastal squeeze' in the temperate region.

Global change, including changing rainfall patterns and amounts, also has the potential to bring about major changes in the way that coastal systems, including estuaries, function. This in turn influences conservation efforts aimed at estuary-associated fish species that often occupy both estuarine and coastal marine habits during different phases of their life cycle (Figure 253). In particular, an alteration in the frequency and duration of estuary mouth opening events for TOCEs will have major implications for fishes in these systems.

Another example of global change that has already occurred is provided by the Richards Bay system that was transformed from an estuarine lake (Figure 254) into two estuarine bays (Figure 255). Unfortunately insufficient research was conducted on the pre- and post-impacted system to quantitatively assess what the exact consequences were for Richards Bay as a major nursery area for both fishes and penaeid prawns. What we do know is that virtually every single one of the potential impacts listed in Figure 253 for estuaries has transpired, the only exception being artificial breaching of the new mouths. This is due to the fact that

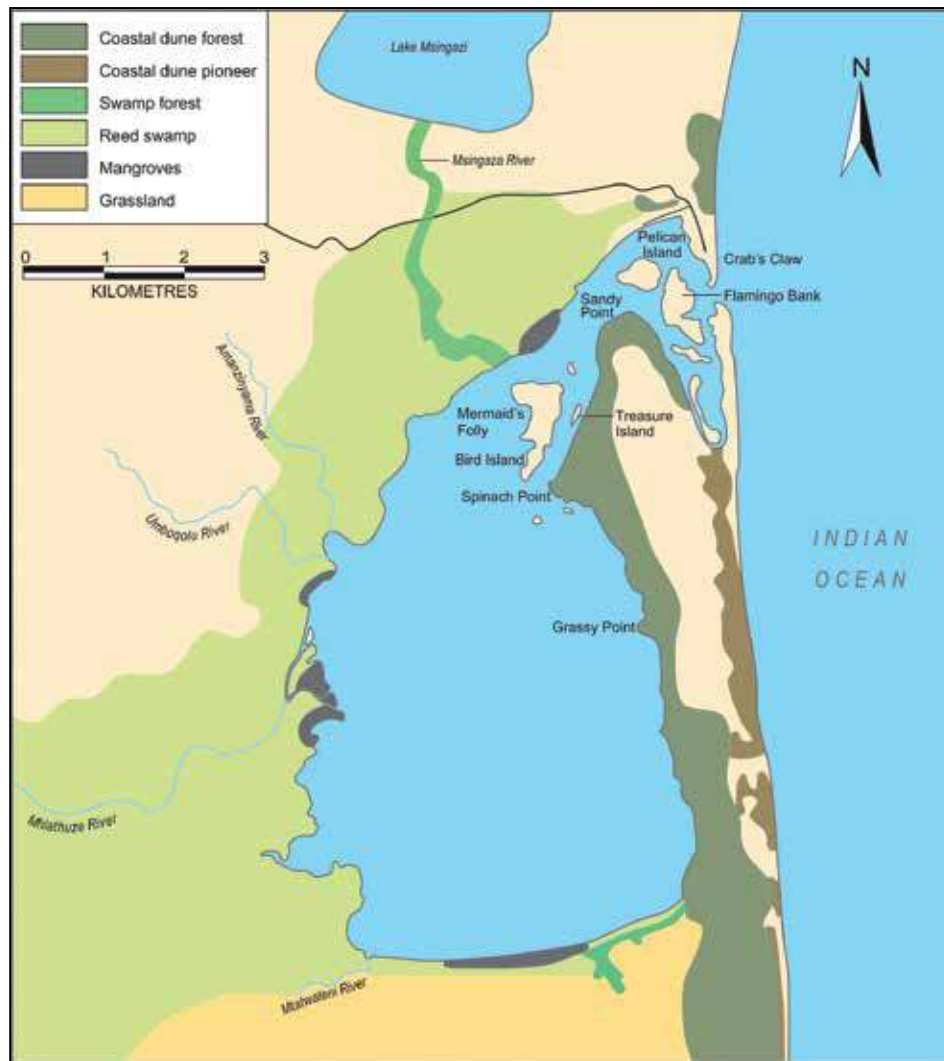
both the Richards Bay and Mhlathuze Estuary mouths remain permanently open.

#### **Lake St Lucia as a conservation case study**

With a surface area of approximately 35 000 ha, St Lucia is one of the largest estuarine water bodies in Africa and a declared Ramsar and World Heritage Site. Despite this elevated conservation status, Lake St Lucia has been subjected to a series of freshwater supply constraints over many decades that now threaten its rich biodiversity. The ability of the system to act as the single most important nursery area for estuary-associated fishes and invertebrates in southern Africa, and largest protected estuarine habitat for hippos, crocodiles and aquatic birds on the continent, is being compromised.

Constraints to the functioning of the ecosystem began as early as 1914 with the commencement of draining and canalization of the Mfolozi Swamp to open up the swamp and river floodplain for sugar cane cultivation. Warner's Drain was completed in 1936 and the sediment filtering capability of the swamp on river floodwaters was effectively removed. This resulted in exceptionally high sediment loads from the Mfolozi River entering directly into the St Lucia system and causing major shallowing in the estuary and Narrows. The river was therefore diverted southwards and provided with a separate estuary mouth (Taylor 2013), thus resulting in a complete loss of Mfolozi freshwater inputs to the St Lucia system.

During the past 60 years, increasing freshwater abstractions from its catchment rivers have further contributed to the increasingly severe salinity extremes experienced by Lake St Lucia. In the past decade, desiccation of large areas of False Bay, North and South Lake have occurred, due primarily to natural estuary mouth closure in combination with a prolonged drought and unnaturally low freshwater inflows during the closed phase. These events have pushed the system into an extreme state that has not been recorded previously and would not have occurred if Mfolozi River water had been available to the St Lucia system over this period (Whitfield & Taylor 2009).



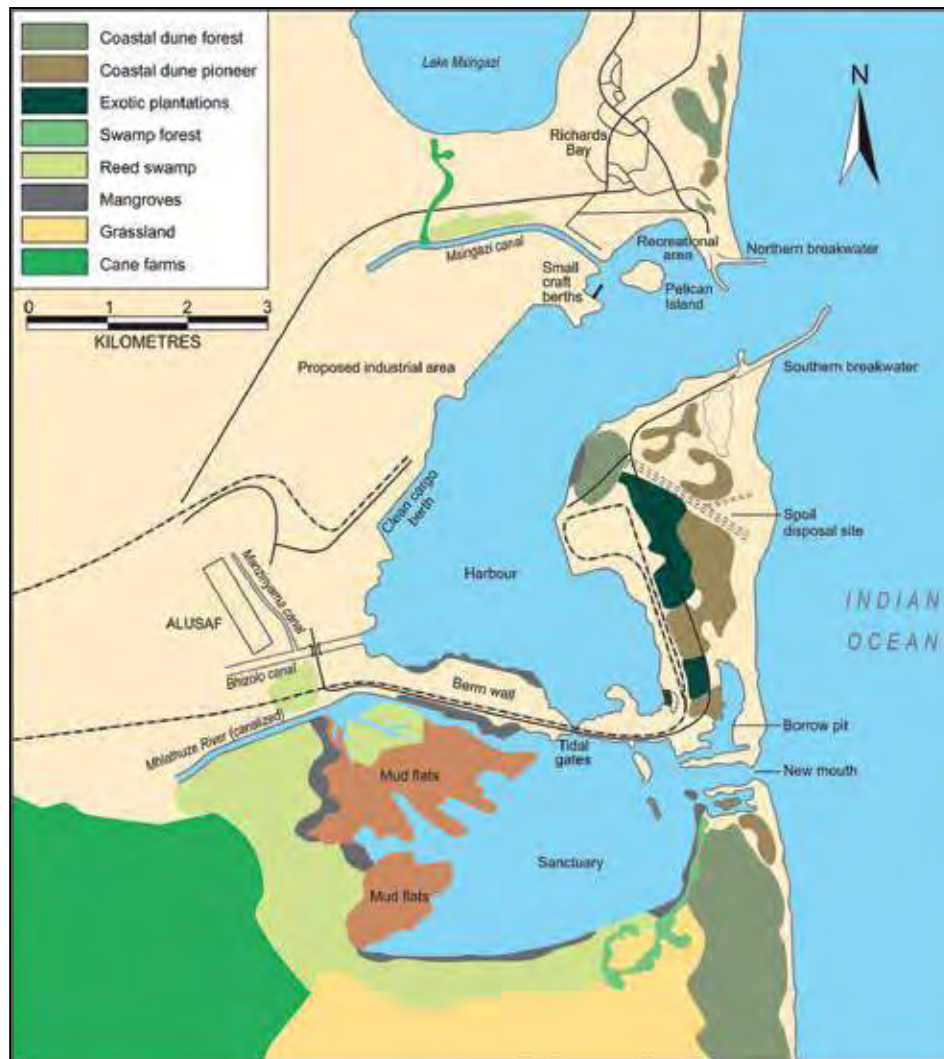
**Figure 254.** Richards Bay pre-harbour development (1964) showing an estuarine lake system.

Forestry plantations in some of the lake catchment areas further exacerbated the freshwater supply situation, although recent removal of pine plantations on the eastern and western shores of the lake have helped restore groundwater flows to the system from these areas. St Lucia, even in its degraded state (i.e. without the Mfolozi link, Figure 256), was still rated as one of the most important estuaries in South Africa but it is not functioning at anything near its full potential. Without water from the Mfolozi River being deflected into St Lucia during drought periods (Figure 257), and without the flushing that happens with natural breaching of the mouth, it cannot consistently operate as the most important estuarine system in South Africa.

Indeed, the extended closure of the St Lucia system during the first decade of this century

impacted recreational and subsistence fisheries along the southern African coastline, e.g. a decline in the catch per unit effort by anglers of *Rhabdosargus sarba* between 2001 and 2005 along the KwaZulu-Natal coast was attributed to prolonged closure of the St Lucia Estuary mouth and the lack of subadults and adults leaving the estuary for the marine environment (Mann & Pradervand 2007). In addition, this mouth closure also led to the collapse of the Thukela Banks prawn fishery. Therefore, without the Mfolozi River water, St Lucia will always be highly stressed and have highly compromised functioning during extended droughts.

St Lucia, and the sugar cane farmers on the Mfolozi floodplain, are also facing the effects of global change. It is predicted that the sea will rise by approximately 50 cm in the next 100 years and



**Figure 255.** Richards Bay post-harbour development (1976) showing two estuarine bays. (after Begg 1978).

that rainfall along the KwaZulu-Natal coast will increase by between 5% and 10%. If these predictions eventuate then St Lucia will benefit, as the system will then be buffered to some extent from droughts and extreme hypersalinity, and the increased water level will be partial compensation for the shallowing caused by sediment accumulation. But these predictions will impact negatively on farming activities on the Mfolozi floodplain and in the Mkhuze swamp area. Sea level rise and the compaction of deep wetland sediments, which is a response to the drainage of cultivated fields, will result in the low-lying farms on the Mfolozi floodplain becoming more susceptible to flooding and hence the cultivation on some of these farms will become difficult without extensive engineering structures to protect them.

The St Lucia system is resilient and recovers rapidly once the rivers start flowing again (Taylor 2013). However, there is increasing evidence that the system is being forced into extreme states such that it is unable to attain full recovery during intervening wet periods. Prolonged droughts during this century saw the temporary disappearance of more than 90% of St Lucia's water area, with concomitant devastation to the aquatic flora and fauna. Although many marine fish taxa lost during the drought will return over time, there may well be some organisms that are permanently lost to the system. There are also indications that recovery of the aquatic flora and fauna is much slower (and possibly incomplete) when there is a high salt load in the system that first has to be flushed out before biotic recovery can occur.



**Figure 256.** Aerial view of the St Lucia Estuary in the foreground and Mfolozi system in the background. These two systems have now been linked by removing the accumulated dredge sediments shown by the arrows in the centre of the picture (Photo: Ricky Taylor).



**Figure 257.** Partial removal of the artificial sand berm in 2012 has allowed Mfolozi River water to flow northwards into the St Lucia Estuary once again (Photo: iSimangaliso Wetland Park Authority).



## 6.4 FISH CONSERVATION ISSUES AND NEEDS

### Threats to fishes in estuaries

In southern African estuaries, habitat degradation through land use changes, hydrological manipulations through excessive freshwater abstraction, and natural resource overexploitation are the most important adverse factors affecting estuarine fish conservation (Table 30). Less important at present, but showing increasing signs towards becoming a major problem in the future is environmental pollution, especially organic and inorganic wastes from industrial, agricultural and domestic sources (Table 31). Although legislation exists to control environmental pollution of rivers and estuaries, there are disturbing signs that the implementation of that legislation is being compromised due to a variety of factors, including the lack of financial resources in environmental law enforcement agencies and a shortage of skilled human resources to document and prosecute guilty parties.

Cyrus (1991b) lists 20 'problems' arising from anthropogenic activities "which could lead to the periodic or permanent elimination of estuarine-dependent fish species from individual systems". These include increased siltation, loss of certain habitat types, hypersaline conditions, fish mortalities due to pollution and prolonged mouth closure. According to Cyrus (1991b) virtually every 'pressure' that estuaries face can be considered under the heading of habitat destruction (Figure 258), which can be divided into three subcategories, viz. physical, chemical or biological in origin. He goes on to suggest that the mounting pressures facing southern African estuaries and the consequent problems that arise, indicate that the fish fauna is under severe threat.

One of the major findings of a recent National Biodiversity Assessment for South Africa's estuaries (van Niekerk & Turpie 2012) was that while a large number of these systems were still in an 'excellent' to 'good' condition, they represented mainly very small systems, while the larger, more important fish nursery systems were predominantly of 'fair' to 'poor' quality. Altogether, 79% of the South African estuarine area is under threat, with 83% of the total estuarine area in the country

having little or no formal protection (van Niekerk & Turpie 2012).

Although major threats to fishes are usually linked to environmental degradation, there is also evidence that the stocks of certain fish species are overexploited or collapsed. According to Gilchrist (1918) the sparid *Lithognathus lithognathus* formed an important component of angler's catches in the Swartkops Estuary during the early part of the 20<sup>th</sup> century. However, monitoring of angling in the Swartkops Estuary during the 1970s (Marais & Baird 1980b) suggested a dramatic decline in the abundance of this species and its replacement by the haemulid *Pomadasys commersonnii* as the prime angling species. Sampling information during the 1980s and 1990s showed an almost complete absence of *L. lithognathus* from gill net catches in the Swartkops Estuary (Baird et al. 1996), with exploitation pressures in estuaries and along the coast being identified as a primary cause of the depleted stocks. Fortunately the closing down of large beach seine netting operations in False Bay that targeted adult *L. lithognathus* has provided some reprieve for this threatened fish species.

High levels of fishing mortality, particularly in estuarine nursery habitats, have resulted in the collapse of the South African sciaenid *Argyrosomus japonicus* stock (Griffiths 1997). A recent acoustic telemetry study in the Great Fish Estuary showed that juveniles of this species are extremely dependent on estuarine nursery habitats and that 41% of the tagged juvenile *A. japonicus* were captured in the estuarine fishery in less than a year and long before attaining sexual maturity (Cowley et al. 2008). If these statistics are similar in other large Eastern Cape estuaries, the future of this species is very bleak indeed.

Invasion by alien aquatic taxa is a major threat to freshwater fish species (Table 30) in South Africa (Marr et al. 2009). Although certain alien freshwater fish species (e.g. carp *Cyprinus carpio*) have been recorded in selected oligohaline estuarine systems, these taxa tend to be restricted both





**Figure 258.** The Lovu Estuary showing habitat alteration due to agriculture, urban development, road and rail linkages, and excessive sedimentation (Photo: Jacques Panfili).

in estuarine distribution and abundance. An exception to this rule is the mosquitofish *Gambusia affinis* that has been widely introduced to coastal lakes and lagoons with the goal of controlling mosquito populations within these areas. The impact of this invasive species on indigenous fish in these coastal systems is unknown.

More information is available concerning predation on estuary-associated marine fish species by alien largemouth bass *Micropterus salmoides* (Wasserman et al. 2011, Magoro et al. 2015), a fish that successfully preys on juvenile *Pseudomyxus capensis*, *Rhabdosargus holubi* and *Monodactylus falciformis* in the estuarine headwaters and rivers of the Eastern Cape Province, e.g. Kowie system. Largemouth bass are capable of tolerating the low-salinity conditions of estuarine

upper reaches for extended periods, particularly during periods of high river flow when salinities in the upper Kowie Estuary become oligohaline (Murray et al. 2015). Alternatively they prey on the juveniles of facultative catadromous species such as *P. capensis* as they enter the lower river system which used to have no piscivorous fishes prior to the introduction of the alien *M. salmoides*. (Weyl & Lewis 2006).

Genetic contamination of indigenous marine and estuarine fish stocks through hybridisation has not been documented but the cichlid *Oreochromis mossambicus*, a freshwater migrant into southern African estuaries, is currently under major threat of extensive hybridization by the invasive cichlid *Oreochromis niloticus* (van der Bank & Deacon 2007).

Table 30. Estimates of the relative importance of current major fish conservation issues in (a) freshwater, (b) estuarine and (c) marine ecosystems in South Africa (– = not significant, + = insignificant, ++ = slightly significant, +++ = significant, ++++ = highly significant) (after Whitfield & Cowley 2010).

Conservation issue	Freshwater ecosystem	Estuarine ecosystem	Marine ecosystem
Habitat alteration	++++	+++	+
Fish exploitation	++	++++	++++
Alien invasives	++++	++	+
Translocation	+++	++	–
Genetic contamination	++	+	–
Parasite translocation	++	+	–

Table 31. Some likely consequences of anthropogenic disturbances on the South African estuarine environment and fishes within these systems (modified from Whitfield 1998).

Feature	Expected environmental effect	Probable impacts on estuary-associated fishes	
		ADVERSE	BENEFICIAL
Excessive soil erosion in catchment	Sediment reduces estuarine water volume; increased turbidity	Smothering of benthic flora and fauna; decrease in aquatic habitat for fishes	Expansion of reed beds and mangroves may increase shallow water nursery habitat for fishes
Dredging of estuary	Increased tidal exchange; substratum disruption; increased turbidity	Decreased primary and secondary production; loss of certain zoobenthic prey for fishes	Deepened areas may offer refuge to certain large fishes but deep holes can become anoxic
Destruction of marginal vegetation	Bank erosion and shallowing of estuary profile	As above; reduction in deeper habitats for larger fishes	None
Disruption of wet-land functions	Reduced dry season flow; increased sedimentation	As above; loss of certain upstream detrital sources	None
Estuary canalization	Reduction in range and amount of estuarine habitat	Major decline in productivity and biodiversity will impact negatively on the estuarine fish community	None
Dam construction	Modification of river flow giving rise to mouth closure	Impeded migrations of both estuary-marine fishes and invertebrates	None
Bridges and associated embankments	Fixing of channel position and modification of flood scouring processes	Reduction in tidal exchange, altered nutrient balance and primary production will affect fish food web	None

Table 31 (continued). Some likely consequences of anthropogenic disturbances to the southern African estuarine environment and fishes within these systems (modified from Whitfield 1998).

Feature	Expected environmental effect	Probable impacts on estuary-associated fishes	
Weir construction	Altered water levels, salinity regime and circulation	Barriers to fish and invertebrate movements between estuary and river and trapping of organics	None
Mouth manipulation	As above; reduced scouring of sediments arising from premature mouth breaching	Premature mouth closure reduces potential marine fish and invertebrate recruitment	None
Nutrient or sewage pollution	Eutrophication and/or excessive biological oxygen demand	Low dissolved oxygen levels can cause fish kills when algal blooms senesce and/or organic loading is too high	None
Industrial pollution	Deterioration in water quality; presence of toxic compounds	Modification of species composition and abundance; mass mortalities if pollution levels are high	None



**Figure 259.** Subsistence fishing in southern African estuaries is growing exponentially and requires appropriate controls to limit overexploitation and promote sustainability (Photo: Alan Whitfield).



## Fish conservation issues

There are a number of issues that influence fish conservation in South African estuaries. Most of these issues relate to the maintenance of ecological processes within the catchments and recipient estuaries, but they extend also to other more specific areas such as fishing pressures and legal aspects, all of which contribute to the success or failure of estuarine fish conservation.

### Fishery resource exploitation

Fishing methods practiced within South African estuarine environments include hook and line fishing, net fishing (cast and hand nets) and traditional spear and trap fishing. Recreational hook and line fishing (requiring a permit) is a very popular pursuit in most estuaries along the south and east coasts of southern Africa, but is limited on the west coast due to a lack of suitable angling species.

Subsistence fishing is more active in rural areas (Figure 259), particularly along the south-east coast. Traditional fishing practices are restricted to the fish traps in the Kosi estuarine lake system in northern KwaZulu-Natal (Figure 260). No commercial hook and line fishing is permitted in estuaries, while commercial gill netting effort, only permitted in selected west coast estuaries, is currently being reduced.

The catch composition of estuarine fisheries differs around the South African coast, following biogeographical changes from the cool-temperate region on the west coast through to the subtropical north-east coast. Approximately 80 species of estuarine and estuary-associated fishes are captured in South African fisheries, with an estimated total annual yield of 28 000 tonnes (Lamberth & Turpie 2003). Due to overlapping areas of operation, species captured in both estuarine and



**Figure 260.** The Kosi Estuary is well known for the traditional Tsonga fish traps in the lower reaches. However, the large increase in the number of traps built during the 1990s converted this sustainable fishery into a semi-commercial operation that is no longer sustainable (Photo: Alan Whitfield).

coastal fisheries are currently managed as single stocks within a multi-species hook and line fishery.

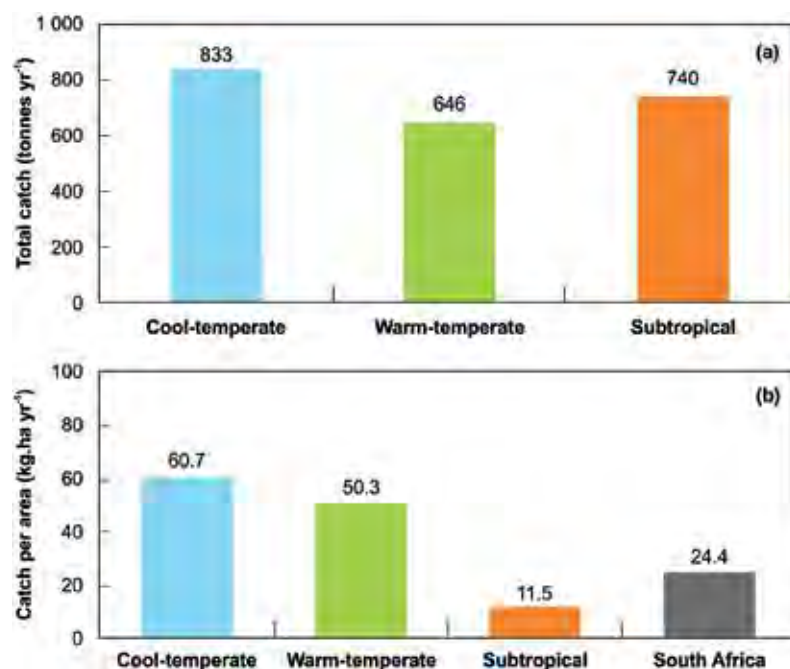
A better understanding of estuarine dependency, habitat use patterns and connectivity to the marine environment is required for the effective management of species that contribute to both estuarine and coastal stocks, e.g. it has been established that during their estuarine dependent phase, juvenile spotted grunter *P. commersonnii* exhibit specific habitat requirements and occupy small home ranges (Childs et al. 2008b), while juvenile dusky kob *A. japonicus* make extensive longitudinal movements within their estuarine nurseries and are extremely vulnerable to capture during this phase (Cowley et al. 2008).

Fishing effort (anglers per km of shoreline) within estuaries is far more intense compared to coastal areas, with the result that most of the fish yield is taken from estuarine habitats, especially in the lower and middle reaches. Furthermore, a large proportion of the landed catch comprises undersized fish, ranging from 90% on the west coast to 50% and 60% on the south and east coasts, respectively (Cowley et al. 2004). The collapse of the southern African *A. japonicus* stock, with a current spawner biomass-per-recruit ratio of approximately 2%, was ascribed to recruitment

overfishing during its juvenile estuarine-dependent phase (Griffiths 1997). Consequently, the management of estuarine fisheries in South Africa needs to be reviewed, with particular emphasis placed on compliance, fishing effort and the role of estuaries in terms of their contribution to coastal fisheries.

A good example of what is happening in many estuaries near urban areas is provided by the detailed analysis of fishery data from the Sundays Estuary (Cowley et al. 2013). These authors found that annual effort was 63 785 angler-hours and yielded an annual fish catch of 16 214 individuals (8 t). They also determined that 43% of the catch (3.4 t) was made up of *Argyrosomus japonicus* and 24% of the catch (1.9 t) comprised *Pomadasys commersonnii*. Based on the above empirical data, the authors concluded that the Sundays estuarine fishery was not sustainable due to the high proportion of juveniles in anglers catches and the targeting of vulnerable species such as *A. japonicus*. However, considerable progress has been achieved by SAIAB scientists working closely with angling competition organizers in this system to convert to catch-and-release events.

An assessment of the fishing pressures on South African estuaries indicated that about 1% of



**Figure 261.** Total annual estuarine fish catch in tonnes (a) and kilograms per hectare (b) in the three biogeographic regions (after van Niekerk & Turpie 2012).



estuaries are under excessive fishing pressure (van Niekerk et al. 2013). Most of this is confined to the cool-temperate region where excessive fishing pressure occurs in over 9% of estuaries as opposed to 1% or less in the other biogeographical regions. In addition, a large number of South African estuaries are under severe fishing pressure, ranging from 13% of those in the subtropical and warm-temperate regions to 3% in the cool-temperate region, with 4% of estuaries under moderate pressure. Only 14% of estuaries are not under some fishing pressure due to national, provincial or municipal protection status. Fishing effort, total catch and catch-per-unit-area have also been assessed (van Niekerk et al. 2013) and indications are that although total catch appeared to be equally distributed among the three biogeographic regions, the cool-temperate region was under severe threat of over-exploitation on a catch-per-unit-area basis ( $60 \text{ kg ha yr}^{-1}$ , Figure 261).

Besides the threat of overfishing, changes in freshwater flow and the associated loss or reduction in quality of estuarine habitat is likely to have serious consequences for fisheries targeting estuary-associated species (Clark 2006). A notable change has already been witnessed in the east coast prawn trawl fishery, which historically yielded approximately 70 tonnes per annum. Reduced environmental flows and revised management actions regarding estuary mouth manipulations have impacted on this small, yet locally important fishery (Forbes & Forbes 2013).

Numerous estuarine biota are harvested for bait, including sand prawn *Kraussillichirus kraussi*, mud prawn *Upogebia africana*, pencil bait *Solen capensis* and *S. cylindraceus*, blood worm *Arenicola loveni*, swimming prawns *Penaeus* spp. and small fish (mainly juvenile mugilids). Harvest levels of certain bait species are fairly significant, e.g. Cowley et al. (2004) estimated that the annual harvest of mud prawns from the Kowie Estuary was 260 648 individuals, while the annual yield of fish was estimated to be 16 240 individuals (1.013 tons). Despite a general lack of truly quantitative assessments, most of the harvested bait species are considered fairly resilient to high levels of exploitation (Wynberg & Branch 1991, Hodgson et al. 2000).

### Changing status of ubiquitous fish species

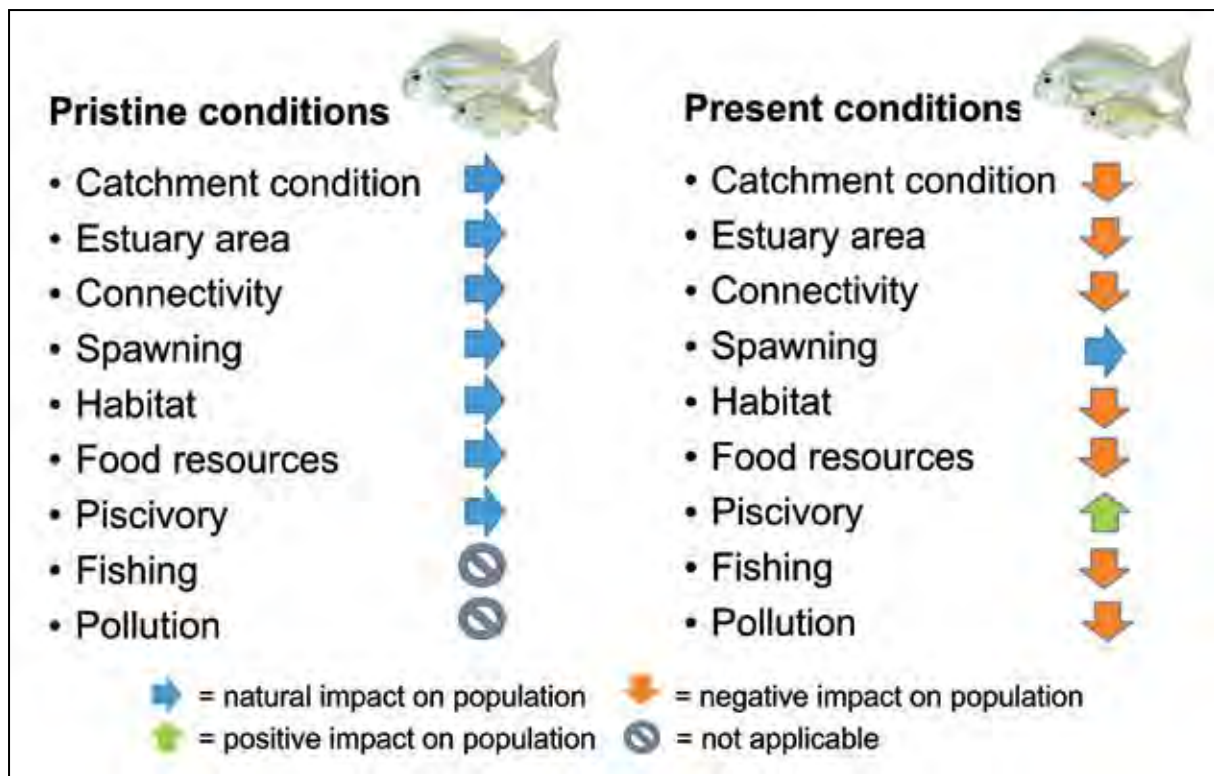
There is a general assumption that ubiquitous fish species are not under threat and therefore do not require the same degree of conservation attention as rare, endangered or highly endemic taxa. This assumption is incorrect and there are numerous examples of previously abundant and widespread species that are now commercially extinct, or showing little sign of recovery, arising from previous over-exploitation and degradation of the environment.

Currently *Rhabdosargus holubi* stocks appear to be healthy but there are numerous negative pressures being applied to these populations, all of which are associated with human impacts. Indeed, of the seven identified features associated with pristine populations of *R. holubi*, only a single aspect (spawning) is much the same as it was in the natural state (Figure 262) and this is probably attributable to the fact that the exact spawning localities of *R. holubi* in the marine environment remain undiscovered by commercial and recreational fishermen (Whitfield et al. 2018).

One attribute (natural predation) is probably lower than in the pristine state due to the depletion of piscivorous fishes by fishermen and the disturbance of piscivorous bird populations associated with human habitation around many estuaries. However, two attributes (pollution and fishing) were non-existent in the pristine state and these alone must have a significant negative impact on current stocks of this species.

Quantitative evidence from the Mhlanga Estuary suggests that the proportion of *R. holubi* in the fish population of that system declined with increased processed sewage inputs to the estuary between the 1970s and 1990s, and that the CPUE of the same species in the estuarine Swartvlei lake between the 1970s and 1980s collapsed in association with submerged macrophyte senescence. The apparent loss of *R. holubi* from the large Lake St Lucia during the first decade of this century (Cyrus et al. 2010a, 2011) also does not bode well for healthy populations of this species on the subcontinent.

The proven susceptibility of *R. holubi* to piscivory in the East and West Kleinemonde estuaries, and pollution events in KwaZulu-Natal



**Figure 262.** Comparative impacts between pristine and present condition factors on *Rhabdosargus holubi* populations in southern African estuaries (after Whitfield et al. 2018).

estuaries, have also been documented. Similarly, there is strong evidence that subsistence fishers in particular are targeting *R. holubi* as a protein food source in estuaries around the country. The Cape stumpnose is one of the most estuarine dependent of all the marine fish found in southern African estuaries, so the future of this species is closely tied to exploitation levels in these systems. Overall, present-day stocks of *R. holubi* are therefore likely to be much smaller than those in the pristine state, with urgent management measures needed to prevent current populations of this and other fish species from declining further (James et al. 2018).

### Fish conservation needs

Fish and fisheries management does not depend on the implementation of a single action but rather the co-ordination of a detailed plan, often in a multidisciplinary context (Colclough et al. 2002). Some examples of innovative means of contributing to fish conservation in a southern African context include the determination and implementation of the ecological freshwater

requirements of rivers and estuaries, the zoning of river catchments and estuaries for different uses, and the recognition that the maintenance of ecological processes is vital to aquatic ecosystem health. The compilation and implementation of estuary management plans for individual systems can also be regarded as innovative.

Apart from the designation of protected areas, the main direct means of conserving fish species include habitat conservation, controls over fishing methods, effort, efficiency and seasonality, construction of fish passes where weirs and dams impede the movement of fishes between estuaries and rivers, prevention of artificial manipulation of estuary mouths, pollution control, benign translocations and captive breeding (Bruton 1995). Of the above, the conservation of fish habitats is by far the most important since healthy aquatic environments invariably support healthy fish populations (Whitfield & Elliott 2002). However, for some targeted angling species, a healthy aquatic environment is insufficient to achieve overall fish conservation goals due to excessive offtake by the fishery.

### **Aquatic reserves**

The concept of marine protected areas (MPAs), particularly no-take zones is well established in South Africa and elsewhere (Bennett & Attwood 1993). Marine reserves are usually designed as a viable alternative to classical marine fisheries management techniques, or at least as an additional tool in the management of fishes (Buxton 1993). Reasons for this include (a) protection of the spawner stock, (b) providing a recruitment source for surrounding areas, (c) restocking of adjacent areas through adult emigration, (d) maintenance of natural population age structure, (e) conservation of biodiversity, undisturbed habitat and natural life support processes, (f) insurance against failure of other management techniques and (g) simplified law enforcement (Attwood et al. 1997). Most, if not all, of the above advantages apply equally to fishes in estuarine protected areas (EPAs), which would benefit enormously if planned in conjunction with MPAs.

In recent decades the benefits of marine reserves in replenishing depleted fish stocks and 'seeding' adjacent unprotected areas has become apparent (Bennett & Attwood 1991). For several decades estuaries have been recognized as nursery areas for a number of recreationally important fish species, yet these systems have not been targeted for protection or included as an integral component in the selection of marine reserves (Whitfield 1998). Clearly the dependence of many marine fishes on estuarine habitats as nursery areas necessitates the inclusion of these ecosystems in any marine reserve planning exercise.

Attwood et al. (1997) have pointed out that estuaries suffer from the unique problem of falling on the boundary of the jurisdiction of management authorities. These habitats are neither land nor sea and, being tidal with mostly marine species, they are usually excluded from river management initiatives. In practice the management of all these zones affect the estuary and, unless the estuary is specifically considered in management plans (Quick & Harding 1994), its requirements are generally ignored.

Within South Africa there are 37 functional estuaries where all (or major portions) of these systems are conserved by national, provincial or

municipal legislation (Figure 263). Few of the above conserved areas protect fish species from exploitation (Mann et al. 1998), which is surprising when it is considered that estuaries are important nursery areas for several important coastal angling species on the subcontinent. What is needed from a conservation perspective is an expansion of the existing EPA network, as well as the upgrading of selected 'estuarine reserves' where fishing is permitted, into 'estuarine sanctuaries' where no exploitation of biological resources is allowed (Figure 264).

In a recent analysis of the number of fish species receiving some form of conservation on the subcontinent, Solano-Fernández et al. (2012) found that 106 species, or 73% of the species recorded in the survey, obtained some benefit from existing marine and estuarine protected areas. At 20% similarity, the fish species from the individual estuary sites clustered into two major groups, with both groups having both full and partially protected systems (Figure 265). At 32% similarity, more estuarine fish community types were evident, all of which were represented in at least one EPA. However, the largest cluster without any representation in a protected area were 18 estuaries in the southern half of KwaZulu-Natal.

### **Legal and planning issues**

The conservation of estuary-associated fishes relies on the wise management of both the abiotic and biotic components of the ecosystems. Consequently the legal framework to ensure conservation of estuaries and their renewable resources needs to address activities that take place within catchments and within the boundaries of the estuary. Since 1994, environmental legislation, policy and institutional arrangements in South Africa have witnessed some major changes which, if fully implemented, will be very positive for environmental and fish conservation on the subcontinent. Estuaries are the recipients of whatever happens in the catchment, so good planning and management of catchment resources will positively influence estuarine ecology.

Water quality and quantity that are influenced by catchment activities are governed by the National Water Act of 1998, while the utilization



**Figure 263.** South African functional estuaries which have a formally recognized conservation or protected status. Those estuaries which have only a portion of the water area conserved are not shown.



**Figure 264.** The pristine Mendu Estuary, situated in the Dwesa Nature Reserve, currently offers protection to fish occurring within this system (Photo: Alan Whitfield).



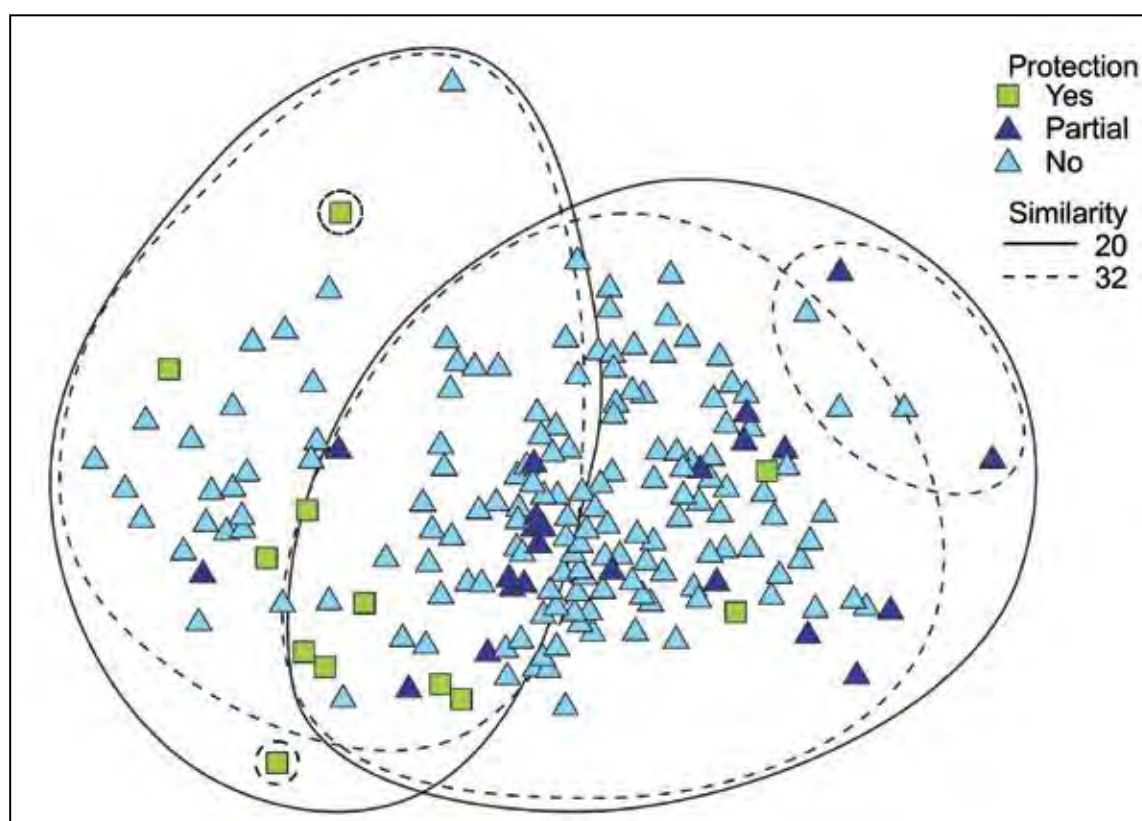
of living resources and aspects of estuarine ecology are regulated by the Marine Living Resources Act of 1998. Most development and infrastructure initiatives now fall under the management jurisdiction of the Department Environment & Natural Resources and the Department of Water & Sanitation, and are governed by diverse legislation. This includes the National Environmental Management: Protected Areas Act of 2003, National Environmental Management: Biodiversity Act of 2004 and the National Environmental Management: Integrated Coastal Management Act of 2008. In conjunction with the national guiding legislation, development activities also require approval from Municipal structures which now have much greater powers with regard to local estuarine environmental management.

Besides the plethora of new environmental legislation, the country has also become a signatory to a wide range of international treaties and conventions. The challenge, however, is to make best use of all this enabling legislation to safeguard

estuaries and their biota. It has been recommended that estuarine conservation planning needs to adopt a holistic approach by placing emphasis on the current health of each estuary as well as existing and future socio-economic pressures. Additionally, the requirements of neighbouring riverine, marine and terrestrial environments, and the potential impacts of climate changes need to be integrated into an adaptive strategy. Currently the opportunity to realize this need exists through the National Spatial Biodiversity Assessment Plan and the call for Integrated Development Plans via the National Environmental Management: Integrated Coastal Management Act. However, the key to a successful estuarine fish conservation strategy is the ability of government to implement the above plans.

### Reducing fishing pressure

In 2000, the Minister of Environmental Affairs announced a crisis in the South African hook and line fishery, resulting in the reduction of daily bag



**Figure 265.** A multi-dimensional scaling plot showing Bray-Curtis similarities in species composition from standardized seine net surveys in South African estuaries. Solid ellipses indicate the highest level of similarity for which each group has at least one MPA (after Solano-Fernández et al. 2012).





**Figure 266.** Catch-and-release fishing is being embraced by a new generation of young anglers (Photo: Paul Cowley).



**Figure 267.** Estuaries that fall within marine or estuarine protected areas need to have the support of local communities in order to be successful as fish sanctuaries (Photo: Alan Whitfield).

limits for many species and fishing effort in the offshore boat-based commercial fishery. However, the effectiveness of such management interventions had little bearing on the conservation of the inshore estuary-associated species. Effort and participation in estuarine fisheries continues to increase (Baird et al. 1996, Everett & Fennessy 2007), which has been exacerbated in recent years by a shift in effort from the coastal zone to estuaries following the ban of off-road vehicles on South African beaches in 2001.

The bulk of southern Africa's major estuaries are over-subscribed by open access recreational and subsistence fishers that are regulated by a suite of daily bag and size limit restrictions. The effectiveness of these control measures are plagued by a lack of law enforcement and non-compliance by fishery participants (Cowley et al. 2004), as well as illegal gill-netting. Consequently, the sustainability of estuarine fish catches hinges on improved public awareness and fishery compliance, as well as more effective management structures to achieve improved law enforcement, monitoring, effort control and the eradication of illegal practices.

Despite only 22% of the total fish catch by anglers in the Sundays Estuary being retained, almost 50% of that retained catch was below the minimum legal size limit (Cowley et al. 2013). High proportions of undersized fish have also been recorded being retained in estuaries such as the Kowie (80%) and Keurbooms (67%) (Cowley et al. 2004, K. Smith unpublished data). In addition, the species with the highest proportion of retained undersized specimens are derived from collapsed stocks such as *Argyrosomus japonicus* and *Lithognathus lithognathus* (Cowley et al. 2013). It is also likely that the proportion of retained undersized fish is probably much higher than roving creel surveys suggest, primarily due to fishers having a fear of prosecution. The legal size limit for species such as *A. japonicus* is such that immature specimens are retained before having had an opportunity to breed.

The overall low angler success rate emphasizes the precarious status of estuarine fish stocks. This is exemplified by the finding of Cowley et al. (2013) that catches of the non-collapsed *Pomadasys commersonnii* in the Sundays Estuary never exceed

the bag limit of five fish per person per day. Thus the current bag limit legislation for this species provides no protection for *P. commersonnii* in the above estuary.

Fishing effort in estuaries is already very high and continues to increase (Mann 1993). Furthermore, improved logistical access to previously remote estuaries, and the technological advances in boating equipment and fishing tackle, all place additional pressure on targeted fish stocks. Fortunately the fact that only a low proportion of anglers are dependent on fishery resources for their livelihoods provides management authorities with a greater array of options, such as catch-and-release, full protection for fish in certain estuaries, and no-take zones in many estuaries, all of which will assist in the survival of estuary-associated marine fish species.

It may be also expected that members of the public, private sector and non-governmental organizations will play an increasing role in estuarine fisheries management through the implementation of Estuary Management Plans for individual systems. In addition, the protection of a representative sample of estuaries in order to achieve the overall estuarine conservation targets as determined by the estuaries section of the SANBI National Biodiversity Assessment of 2011 is strongly supported.

There are also some positive developments regarding the compliance behaviour of anglers. In Durban Bay and the Mgeni Estuary, for example, a large proportion (>63%) of the catch is released by anglers because these fish are under the legal size limit (Pradervand et al. 2003). Similarly, there is an increasing trend of catch and release being practiced at coastal angling competitions such as that in the Sundays Estuary.

The origins of this improved angling behaviour (Figure 266) can perhaps be traced back to the Oceanographic Research Institute's Cooperative Fish Tagging Project that was initiated in 1984, involved more than 5 000 anglers, and resulted in over 250 000 fish from 368 different species being tagged and released (Dunlop et al. 2013). Three of the most commonly tagged species include the estuary-associated taxa *Argyrosomus japonicus*, *Lichia amia* and *Pomadasys commersonnii*.

The importance of obtaining local community 'buy-in' to fish conservation efforts cannot be over-emphasized. The creation of fish sanctuaries in MPAs or EPAs comes at a cost to local anglers, but if the medium- and long-term benefits of such protection are clearly articulated, then widespread acceptance of the conservation measures is more likely to succeed. In addition, ecotourism benefits to the local community are but one of the positive spin-offs of creating MPAs and EPAs (Figure 267).

### Focusing on endemic species

Endemic fishes are those species that are confined to a particular region and are found nowhere else in the world. In southern Africa approximately 13% of the marine species are endemic to the sub-continent (Smith & Heemstra 1986), compared to a freshwater ichthyofaunal endemism of approximately 61% (Skelton 2001). As expected, estuaries lie between these two extremes, with approximately 25% of all estuary-associated taxa being endemic to southern African waters (Whitfield 1998). However, the percentage endemism in the region increases from <20% in subtropical estuaries to >60% in cool-temperate estuaries, mainly due to the more widespread global distribution of tropical taxa extending into the subtropics.

A small number of estuary-associated fish species are vulnerable or threatened with extinction, but a much larger number are under pressure from environmental degradation and over-exploitation. The degradation of estuaries on the subcontinent during the past century has contributed to the depletion of previously abundant species such as the sparid *Acanthopagrus vagus*. According to van der Elst (1978) the catch of *A. vagus* in the St Lucia Estuary fluctuated between two and 48 per 100 angling hours between 1956 and 1962, but declined to less than two per 100 angling hours between 1963 and 1977. The average individual mass of *A. vagus* landed by anglers over the same period declined from approximately 900 g to almost 700 g. Although this species is not listed as threatened, the message that these catch statistics are conveying indicates that previously abundant estuary-associated species are showing major declines in abundance and size.

*Lithognathus lithognathus* is an iconic angling species in both temperate estuaries and the sea around southern Africa. Despite the collapsed state of the stocks of this endemic fish (Bennett 1993), angling pressure continues unabated, with virtually all *L. lithognathus* retained by anglers in estuaries being below the minimum legal size limit of 60 cm (Cowley et al. 2013). Fortunately the commercial harvesting of adult white steenbras in False Bay has been discontinued, thus relieving some of the pressure on this species.

The recent history of the estuarine pipefish *Syngnathus watermayeri* is even more disconcerting than that described for the above angling species. *Syngnathus watermayeri* was previously restricted to six estuaries in the Eastern Cape Province (Whitfield 1995) but now appears to have disappeared from four of these systems. Although speculative, it would appear that changes in freshwater supplies to most of the above estuaries may have been primarily responsible for this disturbing event. Catchment mismanagement within the Kariega system, particularly the absence of environmental freshwater allocations from dams and other impoundments, resulted in this estuary becoming deprived of essential freshwater pulses. These pulses provide nutrients which facilitate phytoplankton development within the estuary and, together with particulate organic material brought down by the river, supported the zooplankton community on which pipefish depend for food (Whitfield 1995c). Marked reductions in zooplankton stocks, arising from depleted pelagic food resources, would have placed additional survival pressures on a species which was already rare and had a limited distribution.

The freshwater mullet *Pseudomyxus capensis* has also been adversely affected by anthropogenic influences. Obstructions across rivers in the form of weirs and dams prevent the upstream migration of this catadromous species. According to Bok (1984) *P. capensis* penetrate between 100 km and 200 km above the estuarine zones of some of the larger Eastern Cape systems, but the widespread construction of low weirs and dams on coastal rivers has reduced both the range and abundance of this species. In addition, excessive freshwater abstraction from rivers has reduced the size and



number of large, deep pools in coastal rivers. Since these pools are a prime habitat for freshwater mullet, for up to 3 years in the case of males and 5 years in females (Bruton et al. 1987), one can only conclude that the decline in the numbers of freshwater mullet is also associated with this negative influence.

The responses of the above three endemic fish species can all be regarded as indicators of environmental deterioration. In the case of the estuarine pipefish there is a need for urgent remedial action to save the species. Such moves would benefit not only *S. watermeyeri* but also other estuarine inhabitants. This action could take the form of an environmental freshwater allocation from impoundments on the Kariega and Bushmans rivers.

The implementation of an upstream environmental freshwater release policy would also benefit *P. capensis*, particularly if such a move coincided

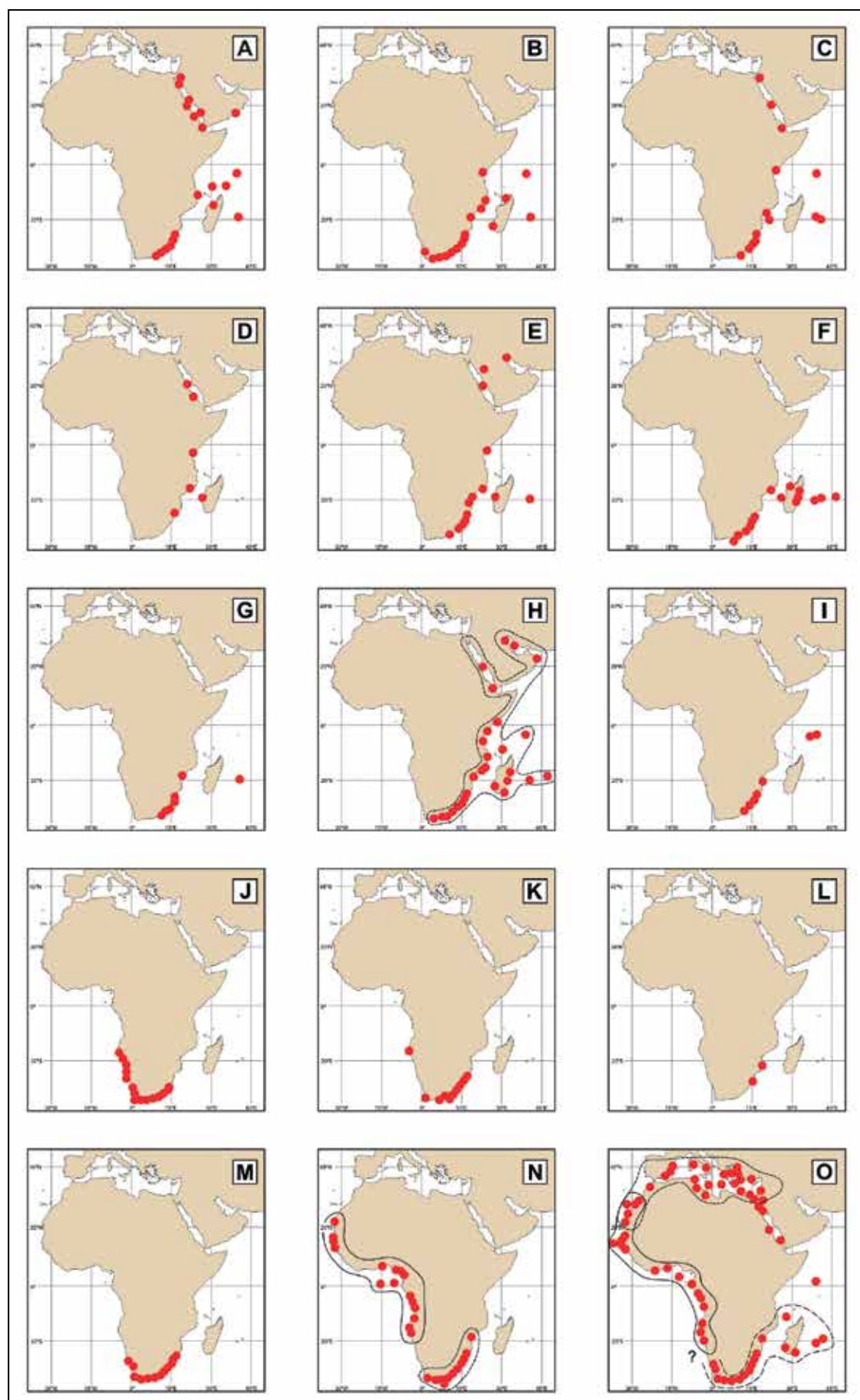
with the erection of fish ladders on dams and weirs where feasible (Figure 268). The case of *A. vagus* is more difficult to solve, since it involves catchment restoration and a reduction in angling pressure, both of which can be improved by appropriate legislation but in practice are difficult to enforce.

#### **Mugilid conservation priorities**

Southern Africa is richly endowed with a wide variety of grey mullet species, with more than half the described species (15) having strong links with either eastern or western Africa (Figure 269). However, there are several species that appear restricted to the southern half of the African continent, e.g. *Chelon richardsonii*, *Chelon tricuspidens* and *Pseudomyxus capensis*. In addition, the subcontinental populations of *Chelon dumerili*, *Mugil cephalus* and *Planiliza alata* appear to be separated from other populations of the same species elsewhere in Africa or the world (Durand



**Figure 268.** A fishway at the head of the Kowie Estuary has facilitated the facultative catadromous life cycle of the endemic freshwater mullet *Pseudomyxus capensis* (Photo: Alan Whitfield).





& Whitfield 2016) and may also be considered endemic. In this regard, the development of the Benguela Current and associated upwelling during the Pliocene-Pleistocene would have created a genetic isolation mechanism for the above species in much the same way as has been shown for the leervis *Lichia amia* (Henriques et al. 2012).

There is strong genetic and other evidence to suggest that a number of widely distributed mugilids have cryptic populations representing new species (Durand & Borsa 2015). This evidence is particularly strong for *Mugil cephalus* which, based on the distribution of evolutionary lineages, probably has at least three cryptic species present in coastal waters around the African continent alone, one of which is associated with the southern African and Madagascar region (Durand et al. 2012).

In addition to the above mugilid endemics, an undescribed species of *Chelon* from northern KwaZulu-Natal and southern Mozambique exists (Durand & Whitfield 2016) and, based on existing evidence, appears to be restricted to southern Africa. All the above actual and potential endemic taxa deserve priority conservation attention, since loss of any of these stocks from the subcontinent would have serious consequences for local and global mugilid diversity, as well as the ecology of estuaries in the region.

### Using fishes as conservation indicators

The concepts of 'indicator', 'keystone', 'umbrella' and 'flagship' species are useful in setting priorities for conservation action (Bruton 1995). Indicator species are those taxa that are sensitive to environmental changes and whose occurrence and abundance can be used to assess environmental quality. For example, the zoobenthic predator *Lithognathus lithognathus*, detritivorous *Chelon richardsonii*, planktivorous *Gilchristella aestuaria* and piscivorous *Lichia amia* would provide a

useful suite of keystone species for most temperate southern African estuaries. A similar equivalent suite of keystone species for subtropical estuaries could include the zoobenthic *Pomadasys commersonnii*, detritivorous *Moolgarda cunnesius*, planktivorous *Gilchristella aestuaria* and piscivorous *Argyrosomus japonicus*.

In the case of Lake St Lucia, *Mugil cephalus* is an ideal keystone species since this taxon is heavily preyed upon by all the top predators, including fish eagles, white pelicans and Nile crocodiles. Indeed, the virtual absence of this previously dominant species from the system during a decade long drought is testimony to its usefulness as an indicator species.

An umbrella species is important as its protection serves to conserve a multitude of lesser known co-existing taxa in the same habitat, both vertebrate and invertebrate (Bruton 1995). For example, the omnivorous *Rhabdosargus holubi* would be a useful umbrella species in all types of estuaries on the subcontinent. Because this species is ubiquitous, it would be easier and more appropriate to monitor population trends for *R. holubi* than rare or collapsed taxa.

Flagship species have particular public appeal and other features that render them suitable for communicating conservation concern. In this context the major angling fish species *Argyrosomus japonicus*, *Lithognathus lithognathus* (Figure 270) and *Pomadasys commersonnii* could all act as flagship species in southern African estuaries.

More recently, declining marine catches of *Rhabdosargus sarba* in northern KwaZulu-Natal was hypothesized to indicate prolonged mouth closure and loss of the St Lucia estuarine system as a nursery area (Mann & Pradervand 2007), thus confirming the possible value of this species as an indicator of environmental degradation and recovery of estuaries within the northern KwaZulu-Natal region.

**Figure 269 (opposite).** African distributional range of mugilid species found in southern African coastal and estuarine waters (modified from Durand & Whitfield 2016). Each dot corresponds to a record in the GBIF databank plus some fish barcoded by Durand et al. (2012). (A) *Crenimugil crenilabis*, (B) *Crenimugil buechanani* (C), *Crenimugil seheli*, (D) *Ellochelon vaigiensis* (E) *Moolgarda* sp. B, (F) *Osteomugil robustus* (G) *Planiliza alata* (H) *Planiliza macrolepis*, (I) *Chelon melinopterus*, (J) *Chelon richardsonii*, (K) *Chelon tricuspidens*, (L) *Liza subviridis*, (M) *Pseudomyxus capensis*, (N) *Chelon dumerili*, (O) *Mugil cephalus*.



**Figure 270.** The white steenbras *Lithognathus lithognathus*, an endemic sparid in southern African temperate estuaries, would be an ideal candidate to act as both a keystone and flagship species (Photo: Alan Whitfield).

### Promulgating enabling legislation

In recent years there has been a move towards promulgating legislation that addresses ecological quality or integrity, e.g. the Water Framework Directive in Europe and the National Water Act in South Africa. Such legislation seeks to define ecosystem quality in an integrative way by using both biotic and abiotic elements that allows for an assessment of the ecological status of the system (Borja et al. 2008). Methodologies and tools to support this approach have been developed in certain countries, including South Africa (Adams et al. 2002).

In addition to the above Ecosystem Based Management (EBM) approach, an effective fish conservation programme should also include appropriate legislation that addresses species specific issues, e.g. the USA Endangered Species Act (Angermeier & Williams 1994). Many countries, including South Africa, only have lists of threatened and extinct fishes, which do not have any legal standing. Conservation legislation or lists of

threatened species are ineffective if enforcement and restoration programmes are not implemented. Conservation actions need to be based on a sound knowledge of the biology and ecology of threatened species, their communities and their habitats. This view is reinforced by Skelton (1987) who stated “Research is an essential component of any conservation exercise. Conservation authorities need to know what species are threatened, why they are threatened, and what the priority requirements are for the effective conservation of those species”.

Cyrus (1991b) proposed that an assessment of the relative importance of all South African estuaries to the survival of fishes dependent on them should be conducted. The most important fish species should be singled out and a policy adopted that will, in the long-term, ensure the survival of these taxa. In the process, other fish species are also likely to benefit. Similar sentiments have been expressed by Skelton (1983) who suggested that apart from establishing data bases for fishes,

nature conservation authorities need to formulate and publish conservation policies with regard to both ichthyofauna and the aquatic environment.

### Concluding comments

Fish conservation needs to be approached from a different perspective to the conservation of terrestrial animals, mainly because of the high mobility of fishes and the continuous nature of many aquatic habitats. With few exceptions, fish species associated with southern African estuaries are highly mobile and have wide distributions, often encompassing both the marine and estuarine environments (Figure 271). Fish cannot be confined to specific protected estuaries by the erection of barriers, but this does not mean that estuarine reserves would have little or no value. On the contrary, well conserved estuaries (Figure 272) would facilitate the rapid recolonization of adjacent systems if the latter areas were depleted of fish stocks through catchment mismanagement or pollution (Whitfield 1997).

Moyle & Sato (1991) have proposed useful guidelines for the design of aquatic reserves. Conservation of the aquatic biota requires the protection not only of aquatic habitats but of the surrounding land habitats as well. However, the linear nature of most estuaries, and their high degree of linkage with freshwater and marine ecosystems, makes estuarine habitats highly vulnerable to external perturbations. Estuarine reserves therefore need the protection of upstream areas and adjacent coast if their full potential is to be realized.

The role of connectivity in sustaining estuarine fish populations has been emphasized by numerous independent global studies in recent decades. This applies not only to the gross negative impact of physical structures such as dams and weirs in preventing the movement of fish within and between river catchments and estuaries, it also applies to the loss of particular habitats in estuaries and the marine environment that fish use as nurseries in a sequential manner. Removal of obsolete physical structures that degrade aquatic ecosystems, and the restoration of lost habitats within estuaries, should become a priority strategy for coastal environmental management authorities.

Although it is generally recognized that the path to effective species conservation is through sound ecosystem conservation, threatened species sometimes demand urgent individual attention if they are to survive at all. In other words, each threatened species has its own set of circumstances which calls for different solutions (Whitfield 1997). Even if there is little or no room for a strategy aimed at the species level in southern Africa, the species themselves can be very useful indicators as to what are threatened ecosystems. Where such species have iconic value for anglers or the broader society, these taxa can be used to highlight the plight of both the wider ichthyofaunal community and provide motivation for the correct conservation and environmental management steps to be implemented.

There are approximately 280 functional estuaries (from a fish perspective) along southern Africa's coastline and each system requires careful management and protection if it is to be maintained as a vital national resource. A wide range of government authorities and interest groups form opinions and make decisions which have major impacts on these systems. Only with access to the best possible scientific information (Figure 273) can these decisions result in the wise management of estuarine resources (Slinger & Breen 1995).

The future health of estuaries on the subcontinent depends on sound resource management and on the improved implementation of conservation measures in partnership with decision-makers, managers, scientists and users. The goal proposed by Begg (1984b) of "implementing a comprehensive nation-wide policy to conserve estuaries and lagoons throughout the country no matter how large or small" is still relevant and needs to be pursued with vigour.

The value of estuarine and marine protected areas for fishes cannot be over-emphasized, e.g. recent work by Bennett et al. (2017b) has shown that 60% of 351 dart tagged *Lithognathus lithognathus* were recaptured within 1 km of their tagging site and that 77% of these recaptures were within MPAs. This provides strong evidence to suggest that MPAs provide important protection for post-estuarine life stages of this overexploited species. Future research needs to be conducted on



**Figure 271.** The magnificent subtropical Msikaba Estuary, a deep system (35 m in places) that has a high proportion large marine piscivores, especially various carangid species (Photo: Alan Whitfield).



**Figure 272.** The temporarily open/closed Ku-Mpenzu Estuary in the Dwesa Nature Reserve. Small estuaries are vital in boosting fish stocks along the entire southern African coast (Photo: Alan Whitfield).



a wide variety of estuary-associated marine fish species to ensure that MPAs and EPAs perform a similar role, especially for threatened taxa.

Estuaries, like many other types of wetland worldwide, are under long-term threat of damage and destruction. A number of southern African fish species are dependent on estuaries for at least part of their life cycle and many of these taxa are endemic to the subcontinent. The viability of estuaries as nurseries is directly related to the large amount of suitable food that is both autochthonous and allochthonous in origin. Mismanagement of river catchments and estuaries leads to impoverished systems that are of little value to fish or people. Conversely the conservation of estuarine resources will lead to ecosystems that support healthy fish populations and allow appropriate levels of exploitation.

Humans have shared the African subcontinent with other animals, including fishes, for millennia.

Indeed, the fish species currently threatened with extinction by human activities were residents in the area long before *Homo sapiens* arrived on the scene. Unfortunately this fact has not helped the case for harmonious co-existence in the present situation. Until we change our attitudes towards manipulation of the natural environment and over-exploitation of fishes, all species and endemic taxa in particular will continue to decline in status from vulnerable to threatened to critically endangered.

As inhabitants of this region we have a responsibility for the maintenance of aquatic biodiversity and the survival of indigenous fishes in particular. Greater emphasis on catchment conservation, aquatic reserves and wise utilization of fish resources is urgently required. Actions today will ensure an improvement in the quality of life tomorrow, not only for people, but for all organisms inhabiting and depending on southern African estuaries for their existence.



**Figure 273.** The author about to release a juvenile *Lichia amia* captured during a fish research project in the East Kleinemonde Estuary (Photo: Jill Sheppard).





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## Glossary

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- Abdomen:** the underside of the body between the pectoral and pelvic fins.
- Abiotic:** non-living (characteristics).
- Adaptation:** a genetically determined characteristic that enhances the ability of an organism to cope with its environment.
- Aggregation:** a group of fish not necessarily all swimming in a co-ordinated manner, i.e. as opposed to a shoal.
- Algae:** simple aquatic plants without roots that may be single cells, strands of cells or simple leaf fronds.
- Alien species:** a species not naturally occurring in a defined area but introduced into that area from elsewhere.
- Allochthonous:** materials or organisms originating in another biotope.
- Amphipods:** bilaterally compressed crustaceans of the order Amphipoda.
- Anadromous:** descriptive of fish which migrate from the sea to spawn in freshwater.
- Anal fin:** ventral median fin behind the anus.
- Anomura:** decapod crustaceans including burrowing prawns.
- Anoxic:** devoid of oxygen.
- Anthropogenic:** caused by humans.
- Anus:** the termination of the alimentary canal, through which faeces are excreted.
- Anterior:** front or head region.
- Assemblage:** group of organisms sharing a particular environment by chance.
- Assimilation:** the transformation of absorbed nutrient substances into body substances.
- Autecology:** ecology of individual organisms and populations.
- Authochthonous:** materials or organisms arising in the biotope under consideration.
- Autotroph:** organism that uses carbon dioxide as its main or sole source of carbon.
- Avifauna:** bird life.
- Barbel:** a slender projection on the jaws or head, used mainly as an organ of taste and touch.
- Barrier overwash:** marine overtopping of the sand bar in the mouth region of estuaries.
- Bathymetry:** depth profile or bottom contours of a water body obtained by measurements from the surface.
- Benthic:** living on the bottom.
- Biodiversity:** the variety of plant and animal species in an area.
- Biogenic:** resulting from life processes of organisms.
- Biogeographical:** biological subdivision of the Earth's surface.
- Biomass:** the mass of living matter present.
- Biotic:** living (characteristics).
- Bivalves:** common name for a large class of molluscs that have a soft body enclosed in a calcareous two-part shell.
- Body length (BL):** the notochord length of fish larvae.
- Bony fishes:** or teleosts, i.e. fishes with a true bone skeleton.
- Brachyura:** true crabs
- Branchial:** pertaining to the gills.
- Buccal:** pertaining to the mouth or cheek.
- Canine:** a sharp-pointed conical tooth.
- Carnivorous:** flesh eating.
- Catadromous:** descriptive of fish which migrate from freshwater to the sea in order to breed.
- Caudal fin:** the unpaired fin at the tail of most fishes.
- Caudal peduncle:** the narrow region that attaches the caudal fin to the body.
- Cellulase:** enzyme that catalyses the hydrolysis of cellulose into glucose.
- Cephalopods:** a class of molluscs, the members of which have distinct heads, e.g. squid and octopus.
- Cestodes:** endoparasitic flatworms which lack an alimentary canal.
- Cohort:** group of individuals of the same age.
- Common name:** an informal vernacular name for an organism.
- Community:** populations of different organisms living together in a particular environment.
- Competition:** use or defense of a resource by one individual that reduces the availability of that resource to other individuals.
- Conspecific:** applied to individuals that belong to the same species.
- Cool-temperate region:** the area north of Cape Agulhas on the West Coast.
- Copepods:** a subclass of minute crustaceans which usually form part of the zooplankton.
- Crepuscular:** active around dusk and dawn.
- CPUE:** Catch per unit of fishing effort.
- Crustaceans:** a large group of mostly aquatic invertebrate animals such as shrimps and crabs.
- Cryptic:** protective coloration and/or behaviour that maximizes an organism's ability to conceal itself.
- Demersal:** living near the bottom.
- Denticles:** small tooth-like processes (e.g. scales of certain elasmobranchs) composed of dentine.
- Dentition:** the characteristic arrangement of teeth.

- Detritivorous:** feeding primarily on detritus.
- Detritus:** particles of decaying plant and animal material, and associated micro-organisms.
- Devonian:** a period that began 410 million years ago and lasted approximately 65 million years.
- Diadromous:** migrating between the sea and fresh-water.
- Diatoms:** unicellular algae with walls impregnated with silica.
- Diel:** during a 24 hour period.
- Digestion:** chemical breakdown of food into a form that can be assimilated by the organism.
- Disc:** the fused head and fin region of some depressed fishes, e.g. skates and rays.
- Disc width:** the width or 'wingspan' of rays.
- Dispersal:** movement of organisms away from the place of birth or from centres of population density.
- Diurnal:** pertaining to daylight hours.
- Diversity index:** an index used to characterize the diversity of species in a community or area.
- Dorsal:** pertaining to the uppermost surface.
- Dorsal fin:** a fin located on the back between the head and caudal fin.
- Dygynous:** fish species that have females maturing directly from juveniles and also from previously mature males in the population.
- East Coast:** the coastline between East London in the south and Mozambique in the north.
- Ecology:** study of the relationships between living organisms and their environment.
- Ecoregion:** a region of relative ecological similarity.
- Ecosystem:** a natural system of interacting organisms and their environment.
- Elasmobranchs:** cartilaginous fishes, including all modern sharks and rays.
- Embryo:** the developing organism either within the egg envelope or hatched, and which is dependent on egg yolk for nourishment.
- Endemic:** organisms that are limited to a particular geographic region.
- Environment:** surroundings of an organism, including the plants and animals with which it interacts.
- Epifauna:** animals found on the surface of any substratum.
- Epilimnion:** the surface layer of a lake.
- Epiphyte:** non-parasitic plants which live on the surface of other plants.
- Episodic floods:** irregular large river floods.
- Equinox:** time or date at which the sun crosses the equator and day and night are equal.
- Estuarine fish species:** fishes which breed in estuaries and spend most or all of their life-cycle within the estuarine environment.
- Estuary:** that part of a river system closest to the sea where salinities fluctuate considerably.
- Euhaline:** salinities between 30 and 39.9.
- Euryhaline:** the ability of an organism to tolerate a wide range of salinities.
- Eurytopic:** an organism that tolerates a wide variation in one or more environmental factors.
- Eustatic:** applied to worldwide changes in sea-level caused by tectonic movements or by the growth or decay of glaciers.
- Eutrophic:** waters with an excellent supply of nutrients and hence high organic production.
- Eutrophication:** enrichment of water bodies, primarily caused by sewage and runoff from fertilized agricultural land.
- Extant:** applied to a taxon, some of whose members are living at the present time.
- Extinct:** applied to a taxon, no member of which is living at the present time.
- Fauna:** the assemblage of animals in a particular area.
- Fecundity:** reproductive potential.
- Filamentous:** thin and thread-like.
- Food chain:** a continuum of organisms in which each is the food of one or more subsequent members of the chain.
- Food web:** a system of inter-relating food chains.
- Foraminifera:** microscopic animals with calcareous exoskeletons.
- Fork length (FL):** the length of a fish measured from the tip of the snout to the tip of the mid-caudal rays.
- Freshwater fish species:** fishes which breed in inland waters and spend most or all of their life cycle in freshwater environments.
- Fry:** a lay term for early juvenile fish.
- Gastropods:** molluscs with a ventral muscular disc adapted for creeping.
- Genital papilla:** a projection behind the anus that carries the external opening of the reproductive system.
- Genus:** a taxonomic category that includes one or more species descended from a single common ancestor.
- Geomorphology:** study of the physical features of the earth's surface and their relation to its geological structures.
- Gestation period:** length of time from conception to birth in a viviparous animal.
- Gill arch:** the bony arch to which the gill membranes and rakers are attached.
- Gill chamber:** the space behind the gill arches for the gills.
- Gill net:** a vertically hung net left in the water, usually

- overnight, into which fish swim and become enmeshed.
- Gill rakers:** projections along the edge of each gill arch that filter food from water passing through the gill chamber.
- Gills:** the breathing organs of fishes consisting of vascularised filaments attached to the gill arches.
- Glass eel:** transparent larval stage of anguillid eels.
- Gonads:** the internal reproductive organs (either testes or ovaries).
- Gravid:** female with eggs or pregnant uterus.
- Gregarious:** descriptive of behaviour that, in fish, leads to the formation of aggregations or shoals.
- Habitat:** the specific environment of an organism.
- Halocline:** a layer of water exhibiting a steep salinity gradient.
- Herbivorous:** feeding on plants.
- Hermaphrodite:** an organism possessing both male and female reproductive organs.
- Heterotroph:** organism that uses organic compounds as its main or sole source of carbon.
- Holocene:** period that covers the last 10 000 years.
- Hybrid:** the offspring produced by parents each of a different species.
- Hydrography:** scientific study of water bodies.
- Hyperhaline:** water that has a salt concentration greater than euhaline, i.e. 40 and above.
- Hypersaline:** water that has a salt concentration greater than the normal seawater average of 35.
- Hypertonic:** fluid with a higher concentration of dissolved salt than another fluid.
- Hypolimnion:** the deep layer of a lake removed from surface influences.
- Hypotonic:** fluid with a lower concentration of dissolved salt than another fluid.
- Ichthyofauna:** the assemblage of fishes in a particular area.
- Ichthyology:** the scientific study of fishes.
- Ichthyonekton:** fish larvae and juveniles which are motile.
- Ichthyoplankton:** larval fishes that are part of the plankton.
- Indo-Pacific:** embracing the Indian and, usually, the western Pacific oceans.
- Incisors:** front, cutting teeth.
- Intermittent estuary:** an estuary which is open to the sea for only a brief period each year.
- Interspecific:** referring to interactions between individuals of different species.
- Intertidal:** between the high-tide and low-tide levels on the shore.
- Intraspecific:** referring to interactions between individuals of the same species.
- Invertebrates:** any animal which lacks a vertebral column or backbone.
- Isopods:** dorsoventrally flattened crustaceans.
- Isotopes:** elements that occupy the same place in the periodic table but have a different atomic weight.
- Juvenile:** young organism essentially similar to the adult form.
- Larva:** a developing organism after hatching from the egg, which has begun to feed itself and is not solely dependent on egg yolk for nourishment.
- Lateral line:** a series of sensory tubercles forming a raised line along either side of the body of some fishes.
- Lepidophagous:** feeding on fish scales.
- Leptocephalus:** the transparent, leaf-like larva of eels and tarpons.
- Littoral:** at or near the shore of a water body.
- Longitudinal salinity gradient:** the difference in mean salinity between the tidal head and mouth region of an estuary.
- Lower reaches:** the lower longitudinal third of an estuary.
- Macrophytes:** large plants.
- Macrotidal:** applied to coastal areas or estuaries in which the tidal range is in excess of 4 metres.
- Macrurans:** decapod crustaceans such as swimming prawns and shrimps.
- Marine fish species:** fishes which breed at sea and spend most or all of their life-cycle in the marine environment.
- Marine stragglers:** marine fish species which rarely enter estuaries.
- Meiofauna:** microscopic or semi-microscopic animals that inhabit sediments (often interstitial).
- Melanophore:** cell containing black pigment.
- Meromixis:** water bodies (usually lakes) that undergo only partial circulation down to a depth determined by density stratification.
- Mesentery:** a fold of the peritoneum that connects the intestine with the abdominal wall.
- Mesohaline:** salinities between 5 and 17.9.
- Mesotrophic:** waters with a moderate supply of nutrients and hence a moderate organic production.
- Microalgae:** unicellular plants.
- Microphytobenthos:** benthic microalgae.
- Microtidal:** applied to coastal areas or estuaries in which the tidal range is less than 2 metres.
- Middle reaches:** the middle longitudinal third of an estuary.
- Migration:** coordinated movement of animals from one place to another.
- Molar:** tooth with a smooth, flattened or rounded surface for grinding.

- Molluscs:** invertebrates mostly distinguished by the presence of a hard, calcareous external shell.
- Morphology:** the study of shape or form.
- Morphometry:** physical dimensions such as shape, depth, width, length, etc.
- Mucus:** a viscous or slimy fluid secreted by the skin of many fishes.
- Mutualism:** interaction of species populations that benefit both populations.
- Mysids:** small, shrimp-like crustaceans.
- Neap tide:** smallest tidal range experienced due to the sun's gravitational forces acting against those of the moon.
- Nekton:** animals that are highly mobile within the water column.
- Nematode:** small cylindrical worm with tapered ends.
- Neritic:** inhabiting the sea above the continental shelf.
- Niche:** the place or position that an organism occupies in its environment.
- Nocturnal:** pertaining to the night hours.
- Nuchal:** body region behind the head.
- Nutrient:** any substance required by organisms for normal growth and maintenance.
- Oesophagus:** part of the alimentary canal between the pharynx and stomach.
- Olfactory:** concerned with the sense of smell.
- Oligohaline:** salinities between 0.5 and 4.9.
- Oligotrophic:** waters with a limited supply of nutrients and hence a reduced organic production.
- Omnivorous:** feeding on a wide variety of foods including both plant and animal material.
- Operculum:** the principal bone in the gill cover of a fish.
- Opportunistic species:** a species that takes advantage of temporary or local conditions.
- Organic matter:** carbon compounds derived from plants and animals.
- Osmoregulation:** the control of osmotic processes (water/salt balance) within an organism.
- Osteichthyes:** class of bony fish.
- Ostracods:** minute crustaceans, often living in a paired shell.
- Otolith:** a calcium carbonate structure in the inner ear of bony fishes.
- Oviparous:** producing eggs that are fertilised, develop and hatch after being laid.
- Ovoviviparous:** reproduction in which the eggs are fertilised internally and the embryos develop within maternal body and are expelled at hatching.
- Parasite:** an organism living on or in another and being nourished by it.
- Pectoral fin:** paired fins located closely behind the head.
- Pelagic:** organisms living in open water, especially near the surface.
- Pelvic fin:** a paired fin located on the ventral side of the body, below and behind the pectoral fin, and in front of the anal fin.
- Periphyton:** Biotic material found on, or attached to, the submerged parts of aquatic plants.
- Pharynx:** the throat or hind region of the mouth, surrounded by the gill arches.
- Phytoplankton:** microscopic plants drifting in the plankton.
- Piscivorous:** feeding primarily on fish.
- Placenta:** an organ in the uterus through which nutrient is passed to the embryo.
- Planktivorous:** feeding primarily on plankton.
- Plankton:** mainly microscopic floating organisms that drift more or less passively within the water column.
- Polyhaline:** salinities between 18 and 29.9.
- Postflexion larva:** developmental stage from formation of the caudal fin to attainment of full external meristic complements (fin rays and scales).
- Predator:** an animal that feeds on other animals.
- Preflexion larva:** developmental stage beginning at hatching and ending with commencement of upward flexion of the notochord.
- Preopercle:** the cheek bone lying in front of the gill cover (or operculum) and behind the eye.
- Prey:** animals that are the food of predators.
- Primary production:** the production of organic matter from inorganic materials by autotrophic organisms.
- Protandrous:** an individual that is initially male, then becomes female.
- Protogynous:** an individual that is initially female and later becomes male.
- Protrusible:** capable of being extended and retracted.
- Pyloric caecum:** blind sac developed from the alimentary canal at the junction of the stomach and intestine.
- Ray:** a cartilaginous and jointed fin support.
- Relative abundance:** the proportional representation of a species in a sample or a community.
- Resource:** a substance or object required by an organism for normal maintenance, growth and reproduction.
- Ripe running:** term used to describe fish about to spawn.
- Rostrum:** the forward projection or extension of the snout of a fish.
- Scientific name:** a species' official name consisting of two words, the first for the genus name and the second a species name.
- Scutes:** enlarged dermal plates or scales.



- Sea level:** level continuous with that of the sea, half-way between high and low tide.
- Sea surface temperature (SST):** temperature of surface waters in the sea, usually measured and mapped by satellite.
- Seine net:** a net, hanging from floats and having a central bag and equal-sized wings that can be pulled through the water and onto the shore.
- Semi-diurnal tides:** tides with two high and two low waters during a tidal day (24 hours and 50 minutes).
- Sensory:** capable of perceiving external stimuli.
- Serrate:** notched or saw-like.
- Seston:** particulate matter in the water column.
- Shoal:** a group of fish, with most members swimming in the same direction.
- Snout:** the front end of the head, the head section before the eyes.
- Soft ray:** a flexible, segmented fin ray.
- South Coast:** the coastline of South Africa between East London in the east and False Bay in the west.
- Species:** a particular kind of organism; the fundamental taxonomic unit.
- Species diversity:** the variety (usually number of taxa) of species in a community or area (see also Diversity index).
- Species richness (R):** a diversity index which relates the number of species present in a community or area to the total number of individuals sampled.
- Spent:** describes reproductive condition after spawning has been completed.
- Spine:** pointed bony fin support.
- Spiracle:** a small respiratory opening behind the eye and first gill slit of most sharks and rays.
- Spring tide:** maximum tidal amplitude during the new and full moon periods.
- Standard length (SL):** the length of a fish from the tip of the snout to the base of the tail.
- Standing stock:** the biomass present in a body of water at a particular time.
- Stenohaline:** species which cannot tolerate a wide range of salinities during their life histories.
- Stenotopic:** an organism with a narrow tolerance range.
- Stratification:** a word used to describe a layered water body.
- Substratum:** a bottom surface of a habitat.
- Subterminal mouth:** a mouth located on the underside of the head, behind the snout.
- Subtidal:** below the lowest level on the shore reached by the tides.
- Subtropical region:** the area between the Mbhashe Estuary and Maputo Bay.
- Supratidal:** above the level on the shore reached by the tides.
- Surf zone:** the area of beach where the waves break.
- Suspensoids:** fine particles of an insoluble substance uniformly dispersed throughout the water column.
- Swim bladder:** a gas-filled sac situated below the backbone of many bony fishes.
- Sympatry:** the occurrence of species together in the same area.
- Synecology:** the study of whole plant and animal communities.
- Synonym:** one of two or more different names applied to the same taxon.
- Tactile:** pertaining to the sense of touch.
- Taxon:** any taxonomic unit (e.g. family, genus, species).
- Teleosts:** see bony fishes.
- Thermocline:** a relatively narrow layer of water with a steep temperature gradient across it.
- Tidal delta:** delta formed in the estuary mouth region due to deposition of riverine and marine sediments.
- Tidal prism:** the difference between the volume of water (in an estuary) at high tide and that at low tide.
- Total length (TL):** the overall length of a fish measured in a straight line from the tip of the snout to the tip of the tail.
- Trawl net:** a net which is pulled by a boat.
- Tricuspid:** teeth with three points.
- Trophic group:** a group of consumers that feed at a similar trophic level.
- Turbid:** descriptive of water which is muddy or murky due to the presence of suspended particles.
- Upper reaches:** the upper longitudinal third of an estuary.
- Upwelling:** a process whereby deeper, cold waters, rise to the surface as a result of the combined effects of wind, ocean currents and the Earth's rotation.
- Ventral:** on or near the lower surface of the body.
- Villiform:** fine bristles.
- Viviparous:** bearing live young after the development of an embryo within the maternal organism.
- Vlei:** a marsh or shallow water body with emergent vegetation.
- Warm-temperate region:** the area between the Mbhashe Estuary and Cape Agulhas.
- Water column:** the body of water between the bottom and surface.
- West Coast:** the Atlantic coastline from Cape Agulhas northwards into Namibia.
- Wetland:** an ecosystem which is periodically flooded.
- Zoea:** pelagic larval stage of certain crustaceans.
- Zoobenthos:** bottom-dwelling animals.
- Zooplankton:** minute animals drifting in the water column.

# General Index

(*italicised* numeral = occurrence within caption)

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## Appendix

A list of the fish family, species and common names, as well as the international estuarine functional guild classification (after Potter et al. 2015), as applied to fishes occurring in southern African estuaries. Scientific nomenclature after Eschmeyer et al. (2018).

Fish guild key: SE = solely estuarine species, E&M = estuarine and marine species, E&F = estuarine and freshwater species, MEO = marine estuarine-opportunist species, MED = marine estuarine-dependent species, MS = marine stragglers, FEO = freshwater estuarine-opportunist species, FS = freshwater stragglers, CA = catadromous species (after Potter et al. 2015).

Fish family	Scientific name	Common name	Fish guild
Ambassidae	<i>Ambassis ambassis</i>	Longspine glassy	E&M
Ambassidae	<i>Ambassis dussumieri</i>	Bald glassy	E&M
Ambassidae	<i>Ambassis natalensis</i>	Slender glassy	E&M
Anguillidae	<i>Anguilla bengalensis</i>	African mottled eel	CA
Anguillidae	<i>Anguilla bicolor</i>	Shortfin eel	CA
Anguillidae	<i>Anguilla marmorata</i>	Giant mottled eel	CA
Anguillidae	<i>Anguilla mossambica</i>	Longfin eel	CA
Antennariidae	<i>Antennarius striatus</i>	Striped angler	MS
Ariidae	<i>Galeichthys feliceps</i>	White seacatfish	MEO
Atherinidae	<i>Atherina breviceps</i>	Cape silverside	E&M
Atherinidae	<i>Atherinomorus duodecimalis</i>	Tropical silverside	MS
Atherinidae	<i>Atherinomorus lacunosus</i>	Hardyhead silverside	MS
Belonidae	<i>Strongylura leiura</i>	Yellowfin needlefish	MEO
Blenniidae	<i>Omobranchus woodi</i>	Kappie blenny	E&M
Blenniidae	<i>Parablennius pilicornis</i>	Ringneck blenny	MS
Bothidae	<i>Bothus pantherinus</i>	Leopard flounder	MS
Carangidae	<i>Caranx heberi</i>	Blacktip kingfish	MS
Carangidae	<i>Caranx ignobilis</i>	Giant kingfish	MEO
Carangidae	<i>Caranx melampygus</i>	Bluefin kingfish	MEO
Carangidae	<i>Caranx papuensis</i>	Brassy kingfish	MEO
Carangidae	<i>Caranx sexfasciatus</i>	Bigeye kingfish	MEO
Carangidae	<i>Lichia amia</i>	Garrick/Leervis	MED
Carangidae	<i>Scomberoides commersonnianus</i>	Talang queenfish	MS
Carangidae	<i>Scomberoides lysan</i>	Doublespotted queenfish	MEO
Carangidae	<i>Scomberoides tol</i>	Needlescaled queenfish	MEO
Carangidae	<i>Trachinotus africanus</i>	Southern pompano	MS
Carangidae	<i>Trachurus delagoa</i>	African maasbanker	MS
Carcharhinidae	<i>Carcharhinus leucas</i>	Zambezi shark	MEO
Chanidae	<i>Chanos chanos</i>	Milkfish	MEO
Cichlidae	<i>Coptodon rendalli</i>	Redbreast tilapia	FEO

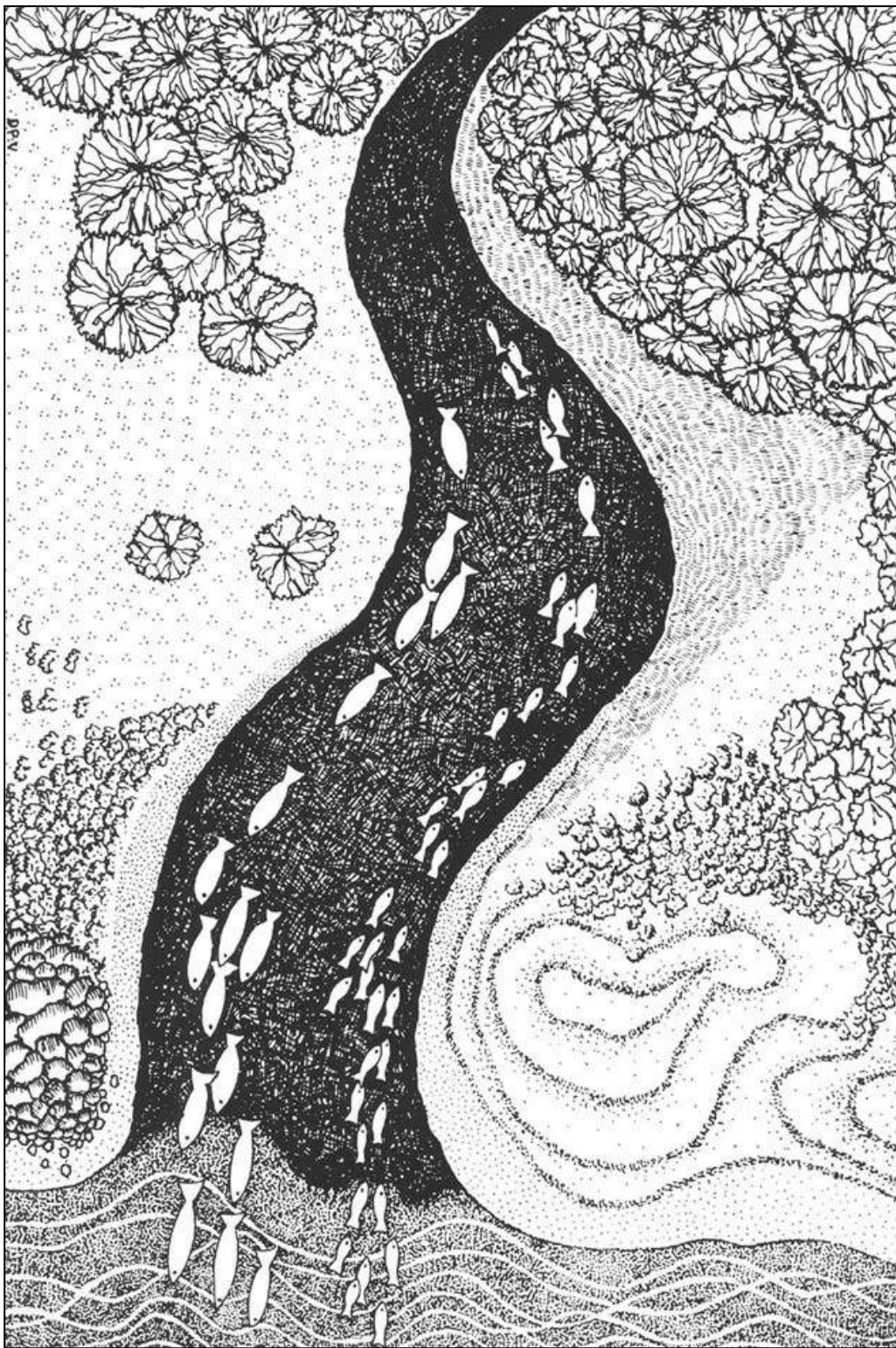


Fish family (cont.)	Scientific name (cont.)	Common name (cont.)	Fish guild (cont.)
Cichlidae	<i>Oreochromis mossambicus</i>	Mozambique tilapia	FEO
Cichlidae	<i>Pseudocrenilabrus philander</i>	Southern mouthbrooder	FEO
Cichlidae	<i>Tilapia sparrmanii</i>	Banded tilapia	FS
Clariidae	<i>Clarias gariepinus</i>	Sharptooth catfish	FEO
Clinidae	<i>Clinus spatulatus</i>	Estuary klipfish	SE
Clinidae	<i>Clinus superciliosus</i>	Super klipfish	E&M
Clupeidae	<i>Etrumeus whiteheadi</i>	Redeye roundherring	MS
Clupeidae	<i>Gilchristella aestuaria</i>	Estuarine roundherring	SE
Clupeidae	<i>Herklotsichthys quadrimaculatus</i>	Blueline herring	MS
Clupeidae	<i>Hilsa kelee</i>	Kelee shad	MEO
Clupeidae	<i>Sardinops ocellatus</i>	South African pilchard	MS
Dasyatidae	<i>Dasyatis chrysonota</i>	Blue stingray	MS
Dasyatidae	<i>Gymnura natalensis</i>	Backwater butterflyray	MS
Dasyatidae	<i>Himantura leoparda</i>	Honeycomb stingray	MEO
Drepanidae	<i>Drepane longimana</i>	Concertina fish	MS
Eleotridae	<i>Butis butis</i>	Duckbill sleeper	SE
Eleotridae	<i>Eleotris fusca</i>	Dusky sleeper	SE
Eleotridae	<i>Eleotris mauritiana</i>	Widehead sleeper	SE
Eleotridae	<i>Eleotris melanosoma</i>	Broadhead sleeper	SE
Eleotridae	<i>Hypseleotris cyprinoides</i>	Golden sleeper	E&F
Elopidae	<i>Elops machnata</i>	Ladyfish	MED
Engraulidae	<i>Engraulis capensis</i>	Cape anchovy	MS
Engraulidae	<i>Stolephorus holodon</i>	Thorny anchovy	MEO
Engraulidae	<i>Thryssa setirostris</i>	Longjaw glassnose	MEO
Engraulidae	<i>Thryssa vitrirostris</i>	Orangemouth glassnose	MEO
Fistulariidae	<i>Fistularia commersonii</i>	Smooth flutemouth	MS
Galaxiidae	<i>Galaxias zebratus</i>	Cape galaxias	FS
Gerreidae	<i>Gerres filamentosus</i>	Longspine pursemouth	MEO
Gerreidae	<i>Gerres longirostris</i>	Strongspine pursemouth	MEO
Gerreidae	<i>Gerres methueni</i>	Evenfin pursemouth	MEO
Gerreidae	<i>Gerres oblongus</i>	Oblong pursemouth	MS
Gerreidae	<i>Gerres oyena</i>	Slenderspine pursemouth	MEO
Gobiidae	<i>Awaous aeneofuscus</i>	Freshwater goby	FEO
Gobiidae	<i>Caffrogobius gilchristi</i>	Prison goby	E&M
Gobiidae	<i>Caffrogobius natalensis</i>	Baldy	E&M
Gobiidae	<i>Caffrogobius nudiceps</i>	Barehead goby	E&M
Gobiidae	<i>Croilia mossambica</i>	Naked goby	SE
Gobiidae	<i>Favonigobius melanobranchus</i>	Blackthroat goby	E&F
Gobiidae	<i>Favonigobius reichei</i>	Spotted sandgoby	E&F
Gobiidae	<i>Glossogobius callidus</i>	River goby	E&F
Gobiidae	<i>Glossogobius giuris</i>	Tank goby	FEO

Fish family (cont.)	Scientific name (cont.)	Common name (cont.)	Fish guild (cont.)
Gobiidae	<i>Oligolepis acutipennis</i>	Sharptail goby	SE
Gobiidae	<i>Oxyurichthys keiensis</i>	Speartail goby	SE
Gobiidae	<i>Oxyurichthys ophthalmonema</i>	Eyeblink goby	SE
Gobiidae	<i>Pandaka silvana</i>	Dwarf goby	SE
Gobiidae	<i>Paratrypauchen microcephalus</i>	Comb goby	E&M
Gobiidae	<i>Periophthalmus argentilineatus</i>	Bigfin mudskipper	SE
Gobiidae	<i>Psammogobius biocellatus</i>	Sleepy goby	SE
Gobiidae	<i>Psammogobius knysnaensis</i>	Speckled sandgoby	E&M
Gobiidae	<i>Redigobius bikolanus</i>	Bigmouth goby	SE
Gobiidae	<i>Redigobius dewaali</i>	Checked goby	E&F
Gobiidae	<i>Silhouettea sibayi</i>	Barebreast goby	E&F
Gobiidae	<i>Stenogobius polyzona</i>	Chinestripe goby	E&F
Gobiidae	<i>Taenioides esquivel</i>	Bulldog eelgoby	E&M
Gobiidae	<i>Trypauchenopsis intermedia</i>	Bearded eelgoby	E&M
Gobiidae	<i>Yongeichthys nebulosus</i>	Shadow goby	E&M
Haemulidae	<i>Plectorhinchus gibbosus</i>	Harry hotlips	MS
Haemulidae	<i>Pomadasys commersonnii</i>	Spotted grunter	MED
Haemulidae	<i>Pomadasys kaakan</i>	Javelin grunter	MEO
Haemulidae	<i>Pomadasys multimaculatus</i>	Cock grunter	MEO
Haemulidae	<i>Pomadasys olivaceus</i>	Piggy	MEO
Hemiramphidae	<i>Hemiramphus far</i>	Spotted halfbeak	MEO
Hemiramphidae	<i>Hyporhamphus capensis</i>	Cape halfbeak	SE
Kuhliidae	<i>Kuhlia mugil</i>	Barred flagtail	MS
Kuhliidae	<i>Kuhlia rupestris</i>	Rock flagtail	MEO
Leiognathidae	<i>Leiognathus equula</i>	Slimy	MEO
Lethrinidae	<i>Lethrinus nebulosus</i>	Blue emperor	MS
Lobotidae	<i>Lobotes surinamensis</i>	Tripletail	MEO
Lutjanidae	<i>Lutjanus argentimaculatus</i>	Mangrove snapper	MEO
Lutjanidae	<i>Lutjanus fulviflamma</i>	Dory snapper	MEO
Megalopidae	<i>Megalops cyprinoides</i>	Oxeye tarpon	MED
Monacanthidae	<i>Stephanolepis auratus</i>	Porky	MS
Monodactylidae	<i>Monodactylus argenteus</i>	Round moony	MEO
Monodactylidae	<i>Monodactylus falciformis</i>	Oval moony	MED
Mugilidae	<i>Chelon dumerili</i>	Grooved mullet	MED
Mugilidae	<i>Chelon melinopterus</i>	Giantscale mullet	MEO
Mugilidae	<i>Chelon richardsonii</i>	Southern mullet	MEO
Mugilidae	<i>Chelon tricuspidens</i>	Striped mullet	MEO
Mugilidae	<i>Crenimugil buehneri</i>	Bluetail mullet	MEO
Mugilidae	<i>Crenimugil crenilabis</i>	Fringelip mullet	MS
Mugilidae	<i>Crenimugil sebeli</i>	Bluespot mullet	MEO
Mugilidae	<i>Moolgarda cunnesius</i>	Longarm mullet	MED

Fish family (cont.)	Scientific name (cont.)	Common name (cont.)	Fish guild (cont.)
Mugilidae	<i>Mugil cephalus</i>	Flathead mullet	MED
Mugilidae	<i>Osteomugil robustus</i>	Robust mullet	MED
Mugilidae	<i>Planiliza alata</i>	Diamond mullet	MED
Mugilidae	<i>Planiliza macrolepis</i>	Largescale mullet	MED
Mugilidae	<i>Planiliza subviridis</i>	Greenback mullet	MEO
Mugilidae	<i>Pseudomyxus capensis</i>	Freshwater mullet	MED
Muraenesocidae	<i>Muraenesox bagio</i>	Pike conger	MEO
Muraenidae	<i>Strophidon sathete</i>	Slender giant moray	MEO
Myliobatidae	<i>Myliobatis aquila</i>	Eagleray	MEO
Ophichthidae	<i>Ophisurus serpens</i>	Sand snake-eel	MEO
Ophichthidae	<i>Pisodonophis boro</i>	Estuary snake-eel	MEO
Paralichthyidae	<i>Pseudorhombus arsius</i>	Large-tooth flounder	MS
Platycephalidae	<i>Platycephalus indicus</i>	Bartail flathead	MEO
Polynemidae	<i>Polydactylus plebius</i>	Striped threadfin	MS
Polynemidae	<i>Polydactylus sextarius</i>	Sixfinger threadfin	MS
Pomatomidae	<i>Pomatomus saltatrix</i>	Elf /Shad	MEO
Pristidae	<i>Pristis zijsron</i>	Green sawfish	MEO
Rhinobatidae	<i>Acroteriobatus annulatus</i>	Lesser guitarfish	MS
Sciaenidae	<i>Argyrosomus japonicus</i>	Dusky kob	MED
Sciaenidae	<i>Johnius dorsalis</i>	Small kob	MEO
Sciaenidae	<i>Otolithes ruber</i>	Snapper kob	MEO
Scorpaenidae	<i>Pterois miles</i>	Devil firefish	MS
Serranidae	<i>Epinephelus andersoni</i>	Catface rockcod	MS
Serranidae	<i>Epinephelus malabaricus</i>	Malabar rockcod	MS
Serranidae	<i>Epinephelus marginatus</i>	Yellowbelly rockcod	MS
Siganidae	<i>Siganus sutor</i>	Whitespotted rabbitfish	MS
Sillaginidae	<i>Sillago sihama</i>	Silver sillago	MEO
Soleidae	<i>Heteromycteris capensis</i>	Cape sole	MED
Soleidae	<i>Solea turbynei</i>	Blackhand sole	MED
Sparidae	<i>Acanthopagrus vagus</i>	Estuarine bream	MED
Sparidae	<i>Crenidens crenidens</i>	Karanteen	MS
Sparidae	<i>Diplodus capensis</i>	Blacktail	MEO
Sparidae	<i>Diplodus hottentotus</i>	Zebra	MEO
Sparidae	<i>Lithognathus lithognathus</i>	White steenbras	MED
Sparidae	<i>Lithognathus mormyrus</i>	Sand steenbras	MEO
Sparidae	<i>Rhabdosargus globiceps</i>	White stumpnose	MEO
Sparidae	<i>Rhabdosargus holubi</i>	Cape stumpnose	MED
Sparidae	<i>Rhabdosargus sarba</i>	Tropical stumpnose	MEO
Sparidae	<i>Rhabdosargus thorpei</i>	Bigeye stumpnose	MEO
Sparidae	<i>Sarpa salpa</i>	Strepie	MEO
Sparidae	<i>Sparodon durbanensis</i>	White musselcracker	MEO

Fish family (cont.)	Scientific name (cont.)	Common name (cont.)	Fish guild (cont.)
Sparidae	<i>Spondyllosoma emarginatum</i>	Steentjie	MEO
Sphyracidae	<i>Sphyracna barracuda</i>	Great barracuda	MEO
Sphyracidae	<i>Sphyracna jello</i>	Pickhandle barracuda	MEO
Syngnathidae	<i>Hippichthys heptagonus</i>	Belly pipefish	E&M
Syngnathidae	<i>Hippichthys spicifer</i>	Bellybarred pipefish	E&M
Syngnathidae	<i>Hippocampus capensis</i>	Knysna seahorse	SE
Syngnathidae	<i>Microphis brachyurus</i>	Short-tail pipefish	E&F
Syngnathidae	<i>Microphis fluviatilis</i>	Freshwater pipefish	E&F
Syngnathidae	<i>Syngnathus temmincki</i>	Longsnout pipefish	E&M
Syngnathidae	<i>Syngnathus watermeyer</i>	Estuarine pipefish	SE
Terapontidae	<i>Pelates quadrilineatus</i>	Trumpeter	MEO
Terapontidae	<i>Terapon jarbua</i>	Thornfish	MED
Tetraodontidae	<i>Arothron hispidus</i>	Whitespotted pufferfish	MEO
Tetraodontidae	<i>Arothron immaculatus</i>	Blackedged pufferfish	MEO
Tetraodontidae	<i>Geneion honckenii</i>	Evileye pufferfish	MEO
Tetraodontidae	<i>Leiodon laticeps</i>	Bluespotted pufferfish	MS
Torpedinidae	<i>Torpedo fuscomaculata</i>	Blackspotted electric ray	MEO
Torpedinidae	<i>Torpedo sinuspersici</i>	Marbled electric ray	MEO
Trichiuridae	<i>Trichiurus lepturus</i>	Cutlass fish	MS



Drifting over an undulating meadow of green  
Ears filled by a myriad of sounds from far and near  
Parachutes of bubbles rising to meet the summer sky  
and shards of light dancing over the rippled sand  
This is the home of silver shoals, folding and unfolding secrets  
for all who want to share their world





The conservation and wise utilization of estuaries is dependent upon a scientific understanding of the biology and ecology of resident and migrant fishes. This monograph brings together a wealth of information on the teleosts of southern African estuaries, highlighting the importance and value of these systems to both the ichthyofauna and people of this region.

