ASPECTS OF THE ECOLOGY OF FISHES ASSOCIATED WITH SALT MARSHES AND ADJACENT HABITATS IN A TEMPERATE SOUTH AFRICAN ESTUARY

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ABSTRACT

There is a paucity of published information on fish utilization of salt marshes outside North America. This dissertation represents the first intensive examination of the ichthyofauna associated with salt marshes in southern Africa and examines the species composition, diversity, size structure, distribution and estuarine dependence of fishes that utilize salt marshes in the Kariega Estuary. The research was concentrated on Taylor's salt marsh, with comparative studies being conducted on other salt marshes and habitats within the marine dominated Kariega Estuary. The possible importance of salt marshes as feeding and refuge areas for fishes was examined, as was the role of salt marshes in the food web of the estuary.

The fishes frequenting salt marshes in the Kariega Estuary were predominantly the juveniles of marine species, with Mugilidae being the dominant family. The ichthyofauna was distributed primarily in the intertidal creeks with very few specimens captured on the vegetated *Spartina maritima* and *Sarcocornia perennis* flats. The different reaches of the intertidal creek were characterised by distinct fish assemblages.

The fish assemblages associated with the intertidal salt marsh creeks were significantly different from those found in the eelgrass beds, the other dominant intertidal habitat in the Kariega Estuary. The eelgrass beds were dominated by estuarine fish species and had a higher density and standing stock of fishes when compared to the salt marsh creeks. The diversity of fishes in the two habitats was however similar. The intertidal salt marsh creek ichthyofauna also differed significantly from that found in the main estuary channel. The creek ichthyofauna was dominated by 0+ juveniles while the main channel had many subadult and adult fishes. The channel habitat also had numerous large piscivorous fishes which were absent from the salt marsh creeks. The low number of piscivorous fishes, together with limited fish predation from other sources, may be the reason why salt marshes provide a refuge for juvenile fishes that frequent these habitats.

Unlike previous studies on North American, Australian and European salt marshes, the dominant fish species that frequented Taylor's marsh were not recorded feeding extensively on the marsh, and those that did had a limited distribution. The role of fishes in the transfer of energy off the Kariega salt marshes is therefore likely to be minimal.

A stable carbon isotope study on the dominant primary producers and consumers within the Kariega Estuary revealed that detritus originating from the high lying salt marsh plants *Sarcocornia perennis* and *Chenolea diffusa* was not utilized by fishes in the Kariega Estuary. Preliminary results indicated that the cord grass *Spartina maritima* may be an important energy source to the fishes in the Kariega Estuary, but further research is needed to confirm this.

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Chapter 1

General introduction

1.1 RATIONALE

A number of studies have been conducted on the fish composition and community structure in the different habitats of South African estuaries. The main channel habitat has been the focus of numerous gill net studies (Marais 1983a, Plumstead et al. 1985, 1989a,b) which investigated the utilization of South African estuaries by fishes. Ichthyoplankton in the main channels and mouths of a number of estuaries have also been examined in an attempt to elucidate the recruitment processes and factors which influence the abundance of larvae in estuaries (Melville-Smith & Baird 1980, Melville-Smith et al. 1981, Whitfield 1989a, Harris & Cyrus 1995). Eelgrass beds have also received attention with studies assessing the fish species associated with Zostera capensis in the Swartkops Estuary (Beckley 1983), the differences in the fish assemblages in eelgrass beds and adjacent bare areas (Hanekom & Baird 1984) and the longitudinal distribution of fish communities found in eelgrass beds (Ter Morshuizen & Whitfield 1994). The distribution of fishes in the different reaches of South African estuaries has also been studied in a wide range of estuarine types, e.g. in the littoral reaches of an estuarine coastal lake (Whitfield 1993) and in the upper reaches of a freshwater dominated system (Ter Morshuizen et al. 1996). While there is extensive ichthyological information from a variety of habitats, nothing is known about the fishes that utilize salt marshes, even though they form an important intertidal habitat in temperate South African estuaries. Salt marshes in this region occur in estuaries and protected embayments along the south eastern, southern and western coasts of the subcontinent (Adams & Bate in press). Their distribution along the east coast decreases markedly north of the Kei River where the more subtropical climate favours the development of mangroves (O'Callaghan 1994). Salt marshes in South Africa cover approximately 17 000 ha with more than 75% of this area being confined to the following systems: Langebaan, Knysna, Swartkops, Berg and Olifants (O'Callaghan 1994).

Ichthyofaunal research on Australian and European tidal marshes and creeks is also in its infancy with only a few studies having been undertaken (Australia - Morton *et al.* 1987, 1988, Connolly in press, Connolly *et al.* in press; **Europe** - Kelley & Reay 1988, Drake & Arias 1991a,b, Cattrijsse *et al.* 1994, Mathieson *et al.* in press a,b). In contrast, extensive research on the ichthyofauna associated with North American salt marshes has been undertaken, with the initial research dating back to the first half of this century. Since the 1970s there have been numerous investigations covering the composition and abundance of fishes in a range of tidal fresh and salt marsh habitats (Subrahmanyam & Drake 1975, Cain & Dean 1976, Bozeman & Dean 1980, Smith *et al.* 1984, Chamberlain & Barnhart 1993, Knieb 1997a). The research has not only been descriptive, but many of the factors that influence the utilization of tidal freshwater marshes, salt marsh creeks and salt marsh flats have been investigated (Rountree & Able 1993, Baltz *et al.* 1993, Knieb & Wagner 1994, Rozas 1995, Knieb 1997b). Building on the knowledge base described above, studies have also been undertaken to determine how these habitats can be managed, to assess mitigation efforts and to ascertain the most appropriate methods for restoring damaged areas (Moy & Levin 1991, Rulifson 1991, Rozas 1992a, Herke *et al.* 1992, Hoese & Konikoff 1995). Research has now reached the phase where concepts that have been expressed repeatedly in the literature, but in many cases are unsubstantiated, are being questioned and tested, e.g. that the shallow water habitats of salt marshes act as refuges from predators (Rountree & Able 1997).

This thesis is the first ichthyofaunal investigation of salt marshes in southern Africa and commences with a characterization of the fish assemblages that frequent this habitat. In particular, this dissertation will examine the species composition, estuarine dependence and size structure of the fishes that frequent salt marshes and their associated habitats in the Kariega Estuary. In addition, the salt marsh fish assemblage will be compared to those of other intertidal and subtidal habitats, thus providing a wider perspective regarding the relative importance of various habitats to the Kariega Estuary ichthyofauna. The results of this study will provide the basis for further ichthyofaunal research in the salt marshes of southern Africa.

An area of salt marsh research that has received considerable attention is the transfer of energy and nutrients between marshes and adjacent estuarine systems. The tidal 'outwelling' of a marsh's primary production appears to be system specific with some systems showing considerable export while others show little exchange of either energy or nutrients (Nixon 1980, Odum 1980, Dame *et al.* 1986, Taylor & Allanson 1995). Very few of these flux studies considered the role that nekton may play in the energy transfer between habitats but rather concentrated on the tidal fluxes of material and nutrients (Deegan 1993, Knieb 1997b). The above omission is surprising since ichthyofaunal salt marsh research has shown that many fish species move into salt marshes and their intertidal creeks, feed and then return to the subtidal estuarine environment, thus resulting in a possible nett export of energy from these systems (Valiela *et al.* 1977, Weinstein *et al.* 1980, Talbot & Able 1984, Allen *et al.* 1995, Knieb 1997b). Research in South Africa has shown that there is little tidal export of organic material from salt marshes in the Kariega and Swartkops estuaries (Baird & Winter 1992, Taylor & Allanson 1995) but no studies have been undertaken on the fishes that frequent these marshes and the role they may play in exporting energy from these systems.

Intrinsic to the argument regarding the importance of any nett export of primary production off salt marshes is whether the vascular detritus produced by marsh vegetation is utilized by invertebrates and fishes. However a debate has raged over the importance of vascular plant detritus, in particular *Spartina*, to food webs in estuaries (Haines 1977, Haines & Montague 1979, Peterson *et al.* 1980, Sherr 1982, Couch 1989, Currin *et al.* 1995). Preliminary isotope research in the Kariega Estuary indicated that the dominant intertidal vegetation (*Zostera capensis* and *Spartina maritima*) was not an important energy source to some of the invertebrate fauna studied (de Villiers 1990).

This thesis aims to provide an insight into the role that South African salt marshes play as refuge and feeding areas to the fishes that frequent them. The capacity that fishes might have in exporting energy and nutrients off salt marshes in the Kariega Estuary will be investigated, and an isotope study on the dominant primary producers and nekton in the Kariega Estuary will examine the possible role that the salt marsh plants have in the food web of the system.

1.2 THESIS STRUCTURE

The structure of this thesis is such that, while all chapters are linked to one another, each will stand alone (i.e. deal with a different topic). Each chapter will have its own introduction to the questions being asked, the materials and methods used in answering the questions, the results and discussion. Where different chapters have used the same materials and methods, reference will be made to their initial description.

Chapter 1 - General introduction: This chapter provides the rationale for the study, the thesis structure, and a general description of the Kariega Estuary, with an emphasis on Taylor's salt marsh which was the site for the majority of the research.

Chapter 2 - The fishes associated with Taylor's intertidal salt marsh creek: This chapter aims to determine the abundance and diversity of fishes found in a South African intertidal salt marsh creek, examine the ichthyofaunal community structure, determine any seasonal changes in the fish assemblage and compare the standing stock and density of fishes found in Taylor's creek with reported values for other estuarine habitats. This chapter was published in the Transactions of the Royal Society of Southern Africa (Paterson & Whitfield 1996).

Chapter 3 - The distribution of fishes within Taylor's salt marsh system: Chapter 2 examined the fishes that were associated with the intertidal creek that drains Taylor's salt marsh but did not document the distribution of fishes in the different habitats found within the marsh. In order to understand fish utilization of a salt marsh, an insight into the distribution patterns of fishes within the entire system is required. This chapter examines the distribution of fishes in the various habitats which make up Taylor's salt marsh e.g. intertidal creek, *Spartina maritima* flats, *Sarcocornia perennis* flats and high marsh pools. The fish assemblages associated with the lower, middle and upper reaches of the intertidal creek were also compared.

Chapter 4 - Ichthyofauna associated with Taylor's intertidal salt marsh creek and eelgrass beds: In order to appreciate the role that salt marshes play in the overall ecology of the ichthyofauna in the Kariega Estuary, it was necessary to compare the fish assemblages associated with this habitat to others within the system. Eelgrass beds form the other major intertidal habitat in the middle reaches of the Kariega Estuary and it has been shown that eelgrass beds in estuaries act as nursery areas for many estuarine and marine fish species. The aim of this chapter is to compare the density, standing stock and composition of fish assemblages found in Taylor's intertidal salt marsh creek with those found in the adjacent eelgrass beds, thus highlighting any habitat preferences exhibited by the different fish species. This chapter has been accepted for publication in Environmental Biology of Fishes (Paterson & Whitfield in press). Chapter 5 - Spatial variation in the fish assemblages associated with three intertidal salt marsh creeks and their adjacent eelgrass beds: While Chapters 2 and 4 established the similarities and differences between the fish assemblages associated with Taylor's intertidal salt marsh creek and adjacent eelgrass beds, the work was limited on a spatial scale to only one marsh system. This chapter aims to establish whether the conclusions reached in this earlier work are also valid for other intertidal creeks and eelgrass beds within the Kariega Estuary.

Chapter 6 - A comparison between the fishes associated with the benthic and epipelagic channel habitats and those found in Taylor's intertidal salt marsh creek: As in Chapter 4, there is a need to place the ichthyofauna that utilize salt marshes and their intertidal creeks into context within the wider Kariega Estuary fish assemblage. Rather than comparing two intertidal habitats, as in Chapter 4, this chapter compares the fishes found in Taylor's intertidal salt marsh creek with those associated with subtidal benthic and epipelagic habitats found in the main channel of the Kariega Estuary.

Chapter 7 - The role of the Kariega salt marshes as feeding and refuge areas for fish: The previous chapters deal with characterizing the fishes that utilize salt marshes and their different habitats or with comparing these results to other habitats within the Kariega Estuary. This chapter aims to provide some insight into why fishes utilize salt marshes and the role that salt marshes and their intertidal creeks play as refuge and/or feeding areas.

Chapter 8 - A stable carbon isotope study of the food web in the Kariega Estuary, with particular emphasis on the fishes: Following on from the feeding aspect of Chapter 7 this section aims, with the use of stable isotopes, to ascertain the extent to which the dominant salt marsh plants are utilized as an energy source by the nekton in the Kariega Estuary. This chapter was published in Estuarine, Coastal and Shelf Science (Paterson & Whitfield 1997).

Chapter 9 - Concluding discussion: The final chapter compares the characteristics (e.g. diversity, distribution, feeding, predation) of the ichthyofauna associated with the Kariega Estuary salt marshes to tidal marsh systems elsewhere in the world. A conceptual model on the availability and utilization by fishes of the primary producers in the Kariega Estuary is developed and

discussed. Lastly, the direction that future ichthyological research on South African salt marshes should take is addressed.

1.3 STUDY SITES

KARIEGA ESTUARY

The Kariega Estuary is situated on the east coast of South Africa (33° 41'S, 26° 42'E), adjacent to the town Kenton-on-Sea and is approximately 18 km long (Figure 1.1). The channel in the upper reaches is narrow (40 - 60 m) and usually flanked by steep slopes while in the lower reaches the estuary widens (100 m) and is bordered by sandflats and salt marshes (Grange 1992). The estuary is relatively shallow with an average midstream depth of between 2.5 and 3.5 metres. The Kariega Estuary is a mature Ria-type estuary which was formed by the drowning of a river valley following a rise in sea level (Reddering & Rust 1990). Using Whitfield's (1992) classification of South African estuaries, the Kariega Estuary can be categorized as a permanently open system.

As estuaries are the meeting points between the marine and riverine environments, the physical characteristics of these two water bodies play a significant role in the structuring of these systems. The Kariega Estuary is a marine dominated system (Plate 1.1) with very little riverine influence. The system has been known to be hypersaline in the upper reaches and apart from episodic freshwater inputs (which require the overflow of Settlers Dam), river inflow is negligible for extended periods (Hodgson 1987, Allanson & Read 1995, Grange *et al.* in press). This low freshwater input into the system is due to the Eastern Cape being relatively arid, which is exacerbated by a very poor rainfall to runoff conversion (Whitfield & Bruton 1989). In addition, the catchment of the Kariega Estuary is small (686 km²) and highly regulated by three dams and numerous farm weirs. In contrast, the marine environment has a major influence on the estuary which is demonstrated by the 106:1 ratio of tidal prism volume to river volume (Grange *et al.* in press). The mean spring tidal range along the Eastern Cape coast is 1.6 m and the Kariega Estuary may therefore be classified as being microtidal. Even without a strong freshwater input, scouring by tidal currents is sufficient to maintain a permanent connection with the sea.



Figure 1.1 Map of the Kariega Estuary indicating the system's position on the South African coastline as well as the three salt marshes covered in this study.

With a strong marine influence and negligible freshwater input, the salinity is normally uniformly marine (35) along the entire estuary. The system has a low turbidity (< 10 NTU) and is well mixed with almost no salinity or thermal stratification of the water column at any stage of the tidal cycle (Grange & Allanson 1995). As a consequence of the low riverine input into the Kariega Estuary and the resulting poor nutrient status of the system (Allanson & Read 1995, Grange & Allanson 1995), the phytoplankton stocks are low and the water column can be regarded as being oligotrophic. The low turbidity and marine dominance of the system has however resulted in eelgrass beds (*Zostera capensis*) occurring along the entire length of the estuary. This decrease in phytoplankton standing stocks and an increased dominance of aquatic macrophytes is a characteristic of Eastern Cape estuaries which have had long-term reductions in freshwater inputs (Adams & Talbot 1992). *Z. capensis* occurs mostly as a littoral band just above and below the low-water spring tide level and the mean width of the beds varies from 5.2 m in the lower reaches to 3.3 m in the upper reaches (Ter Morshuizen & Whitfield 1994).



Plate 1.1 Aerial photograph of the lower reaches of the Kariega Estuary showing the open connection with the sea and the clarity of the water which is indicative of the strong marine influence on the system.

KARIEGA SALT MARSHES

Salt marshes in the Kariega Estuary occupy approximately 24% of the surface area of the estuary (Taylor 1987), with salt marsh vegetation occurring as a narrow intertidal band along the entire length of the estuary. Distinct salt marsh embayments are generally found in the middle reaches of the estuary where alluvial sediments have been deposited between hillocks juxtapositioned against the estuary channel (Taylor 1987). The three salt marshes which were studied, Taylor's (Plate 1.2), Grant's (Plate 1.3) and Galpin's (Plate 1.4), are all found in the middle to lower reaches of the estuary (Figure 1.1). Only Taylor's salt marsh is described in this introductory chapter and descriptions of the other two marshes can be found in the comparative salt marsh section (Chapter 5).

Taylor's salt marsh (Figure 1.1) is a small intertidal marsh located 5 km from the estuary mouth and is situated between 0.5 and 1.8 metres above mean sea level (Taylor 1987). The marsh system has well differentiated marsh and tidal creek regions (Plate 1.2) and is dominated in the lower reaches by a single branched unvegetated intertidal creek (2608 m²). At spring high tide the creek is 25 m wide and approximately 1.2 m deep at its junction with the estuary, and drains the whole marsh at low tide (Taylor 1987). During neap high tides estuarine water is usually confined to the tidal creek but at higher tides the elevated, more extensive salt marsh flats may be inundated (Taylor 1987). In general the tidal water is confined to the creek during almost half of all high tides and the level of marsh inundation varies according to the interactions between the semi-lunar tidal cycles and changes in daily mean sea level (Taylor 1987, Taylor & Allanson 1995). Even when tides reach the average maximum tide elevation (1.0 m above MSL) only very small areas of the vegetated marsh flats are inundated (Taylor & Allanson 1995). This low level of inundation means that the vegetated marsh flats are exposed during most high tides and for the entire period between high tides (Taylor & Allanson 1995). When low elevation neap high tides coincide with depressed daily mean sea levels, tidal water fails to enter the intertidal creek (Taylor & Allanson 1995). The upper marsh is characterized by a number of high marsh pools that are flooded only during exceptionally high spring tides. Thirteen macrophyte species have been recorded on the salt marsh with the dominant species being the high marsh plants Sarcocornia perennis and Chenolea diffusa (Taylor 1987). The common salt marsh grass Spartina maritima is only found in the lower reaches of the marsh (Taylor 1987).



Plate 1.2 Aerial photograph of Taylor's salt marsh indicating the intertidal creek (C) and salt marsh flats (F).



Plate 1.3 Aerial photograph of Grant's salt marsh indicating the intertidal creek (C) and salt marsh flats (F).



Plate 1.4 Aerial photograph of Galpin's intertidal salt marsh creek (C), adjacent eelgrass beds (E) and bay (B).

Chapter 2

The fishes associated with Taylor's intertidal salt marsh creek

2.1 INTRODUCTION

Research into the functioning of salt marshes in South African estuaries has been limited to a few studies (Day 1967, Pierce 1983, Taylor 1992, Baird & Winter 1992, Heymans & Baird 1995, Taylor & Allanson 1995) with a paucity of information being available on the faunal utilization of these habitats. South African ichthyofaunal research in the intertidal regions of estuaries has concentrated on the nursery role of submerged aquatic vegetation, in particular the eelgrass *Zostera capensis* (Beckley 1983, Hanekom & Baird 1984, Whitfield *et al.* 1989, Ter Morshuizen & Whitfield 1994). No published information (except papers already published from this thesis) pertaining to fish utilization of South African salt marshes or their intertidal creeks is currently available.

International research on ichthyofaunal utilization of salt marsh systems has occurred at two levels, namely the individual species and community level. Numerous studies at the species level have been published, encompassing facets such as reproduction, feeding, growth and trophic interactions (Lotrich 1975, Knieb & Stiven 1978, Byrne 1978, Reis & Dean 1981, Weisberg *et al.* 1981, Currin *et al.* 1984, Weinstein *et al.* 1984, Lipcius & Subrahmanyam 1986, Allen *et al.* 1995). Research at the community level has ranged from general surveys (Cain & Dean 1976, Shenker & Dean 1979, Bozeman & Dean 1980, Hackney & de la Cruz 1981, Smith *et al.* 1984, Chamberlain & Barnhart 1993) to specific studies examining microhabitat, diel, tidal, freshwater and marsh structural influences on the ichthyofauna utilizing tidal salt and freshwater marsh systems (Baltz *et al.* 1993, Knieb & Wagner 1994, Rogers *et al.* 1984, Rountree & Able 1993, Rozas & Odum 1987a,b). A number of studies have also examined the role of salt marshes in estuaries in comparison to other vegetated and unvegetated intertidal habitats (Thayer *et al.* 1978, Weinstein & Brooks 1983, Sogard & Able 1991). Collectively this research has shown that salt marshes and their intertidal creeks are important nursery areas for certain marine and estuarine fishes, thus contributing significantly to the functioning of estuaries.

This chapter endeavours to provide the first baseline information on the fishes that utilize a South African intertidal salt marsh creek. The specific aims of this chapter are:

- (1) To determine the abundance and diversity of fishes found in an intertidal salt marsh creek.
- (2) To examine the community structure of the ichthyofauna.

- (3) To determine any temporal changes in the fish assemblage.
- (4) To compare the standing stock and density of fishes found in the intertidal salt marsh creek with reported values for other estuarine habitats.

2.2 MATERIALS AND METHODS

FIELD SAMPLING

Different salt marsh creek studies have utilized an array of gear types, ranging from the traditional active techniques e.g. seine netting (Weinstein 1979, Subrahmanyam & Coultas 1980) to the more passive approaches e.g. block netting (Shenker & Dean 1979) or even a combination of the two (Rountree & Able 1993). The unsuitability, due to varying topography and high water clarity, of Taylor's intertidal salt marsh creek (also referred to as Taylor's creek) to sub-sampling techniques such as seine netting, lift traps and drop samplers resulted in a block net method being used. This technique, which negates the need for sub-sampling as all the fish are sampled, avoids problems faced by other procedures such as size and species selectivity, net avoidance and variable towing speeds. Taylor's creek (Figure 2.1) is ideally suited to block netting as it has only one opening and drains fully at low tide. A 30 m long, 2.5 m deep block net (2.5 mm stretch mesh) with a weighted bottom line and a floating top line was pulled quickly across the opening of the intertidal creek at the height of the flood tide. Once across the mouth of the intertidal creek, the bottom line was pegged securely into the mud substratum so as to prevent the tide from lifting the net off the bottom while the creek drained. Wooden poles were then driven into the mud just behind the block net and the headline was suspended over these poles, raising the net to a minimum of 50 cm above the water surface. This prevented fish from jumping over the net, as recorded by Cain and Dean (1976). As the intertidal creek drained over the ebb tide, the fishes moved down towards the block net and were netted with the aid of small seine and hand nets. Many of the larger and more easily identifiable fish species were counted and measured (SL) on site and released unharmed into the estuary.



Figure 2.1 Map of Taylor's intertidal salt marsh creek (including *Spartina maritima* beds) indicating water chemistry sampling sites and position of fixed marker.

Selected physical and chemical parameters were recorded on the high tide at five fixed stations (Figure 2.1). Water temperature (°C) was measured *in situ* while water samples were taken so that salinity and turbidity (NTU) could be measured in the laboratory using an optical salinometer (Reichert 10419) and turbidimeter (Hach Model 2100A). Tide height (cm) was measured against a fixed marker in the creek (Figure 2.1) from which the average channel depth was calculated.

SAMPLING PERIODICITY

Two samples were taken per season in Taylor's intertidal salt marsh creek from winter 1992 to autumn 1994. As other studies (Shenker & Dean 1979, Reis & Dean 1981, Rountree & Able 1993) have reported diel variations in the fish utilization of marshes, one sample was taken at dawn and the other at dusk, one month apart. Sampling occurred over the same tidal phase in order to standardise as many physico-chemical parameters as possible. Large extractive samples have been shown to have a great effect on the local fish community structure associated with salt marshes, particularly on the more resident species which generally have small, relatively fixed populations and exchange between adjacent areas may be minimal (Cain & Dean 1976). The sampling interval would have ameliorated any change in community structure and maintained the integrity of future samples. Since the greatest inundation occurred during the spring tide cycle, which has its high tides in the late afternoon and early morning, a dawn-dusk sampling regime was adopted.

SAMPLE ANALYSIS

In the laboratory all the fishes were counted and identified to species level where possible. Mullet < 20 mm (SL) were recorded as Mugilidae. Standard lengths (SL) were measured to the nearest mm for all species. Sub-sampling for length data was employed when there were more than 100 individuals of a given species (Table 2.1). The total preserved wet mass of each species was measured to the nearest 0.1 g by weighing all the representatives of that species. The mass of any released individuals was calculated using the species length/weight relationship given in Harrison and Whitfield (1995). All the fishes were fixed in 10% formalin and preserved in 60% propyl alcohol.

Table 2.1 Abundance, size and life-history stages of the twenty-five most commonly caught taxain Taylor's intertidal salt marsh creek (July 1992 - May 1994).

Taxa Number	captured	Number measured	Average length (mm)	Standard deviation	Min/Max (mm)	Life stages present
Mugilidae (< 20 mm SL)	20462	2806	14.5	5.4	4-20	Juveniles
Liza dumerilii	15180	3439	43.5	31.8	20-232	Juveniles
Gilchristella aestuaria	7990	1147	29.4	4.3	7-47	Juveniles/Adults
Mugil cephalus	7567	3011	23.1	4.5	20-64	Juveniles
Diplodus sargus capensis	3639	455	12.5	9.4	4-51	Juveniles
Atherina breviceps	2323	1090	35.1	9.4	10-65	Juveniles/Adults
Psammogobius knysnaensis	2057	1310	25.7	7.4	10-73	Juveniles/Adults
Rhabdosargus holubi	1402	1319	23.4	19.3	7-161	Juveniles
Liza tricuspidens	840	611	33.1	8.2	20-122	Juveniles
Rhabdosargus globiceps	461	117	11.7	1.2	8-16	Juveniles
Pomadasys commersonnii	386	272	48.5	53.9	18-196	Juveniles
Glossogobius callidus	348	348	27.9	7.0	10-63	Juveniles/Adults
Terapon jarbua	345	342	21.7	7.6	6-45	Juveniles
Myxus capensis	148	139	26.7	28.0	20-265	Juveniles
Caffrogobius natalensis	125	125	39.8	15.2	7-93	Juveniles/Adults
Pomadasys olivaceum	64	64	59.5	13.2	23-94	Juveniles
Monodactylus falciformis	62	62	21.3	5.2	9-36	Juveniles
Caffrogobius gilchristi	60	60	38.2	18.4	12-93	Juveniles/Adults
Liza richardsonii	51	51	169.4	89.7	25-305	Juveniles/Adults
Solea bleekeri	49	49	27.6	10.8	15-65	Juveniles
Sarpa salpa	42	42	13.5	3.1	9-22	Juveniles
Caffrogobius nudiceps	27	27	38.2	10.7	27-80	Juveniles/Adults
Lithognathus lithognathus	25	25	23.3	8.4	10-32	Juveniles
Oreochromis mossambicus	16	16	26	6.1	18-41	Juveniles
Crenimugil crenilabis	12	12	28.1	6.4	20-38	Juveniles

Biomass, density, abundance and standing stock: The total composition, both by number and by mass, was calculated for each species for every sampling occasion. Fish density and standing stock were calculated by dividing the total mass and number respectively by the area of the salt marsh creek. The ichthyofauna caught in this study were regarded as being from the creek since very few fishes were found to venture over the vegetated salt marsh flats and the period of tidal inundation of these salt marsh flats was short (Chapter 3). Spearman Rank correlation tests were calculated for the total number and mass of fishes in the salt marsh creek, as well as for the fifteen numerically dominant species, against all the abiotic variables measured.

Ichthyofaunal composition: The dominant ichthyofauna utilizing the salt marsh creek was determined as follows. All samples were pooled and the total abundance, mass and percentage frequency of occurrence of each species were ranked. The sum of these three values was then ranked to establish which taxa were the most dominant. The estuarine association categories assigned to each species (Table 2.2) conform to those of Whitfield (1994b) and the percentage, both in terms of abundance and biomass, that each estuarine association category made to the total ichthyofauna was calculated. The size at which the different fish species were found to be utilizing the salt marsh creek was determined by the construction of length frequency histograms for selected species.

Seasonality: In all seasonal analyses the dawn and dusk samples were pooled for each season. Total fish abundance and biomass as well as the abundance of certain species were calculated for each season. The Margalef's species richness index (D), Shannon-Wiener species diversity index (H') and Pielou's evenness index (J') were all calculated on a seasonal basis using confirmed species only (Washington 1984).

2.3 RESULTS

PHYSICO-CHEMICAL PARAMETERS

The innundation of Taylor's intertidal salt marsh creek varied between six and nine hours. The water temperature averaged 18.2°C (SD=3.6°C) and ranged from 14°C to 25.5°C. (Figure 2.2). There was a significant seasonal difference in water temperatures (ANOVA df=7, F=18.25, P<0.001) but no significant difference in water temperatures between sites (ANOVA df=4,

Table 2.2	The fi	ve categories	of fishes in	southern	African	estuaries	(modified	from	Whitfield
1994b).									

Group	Categories	Description of categories
Estuarine	1	Estuarine species which breed in southern African estuaries. Further subdivided into:
		1a. Resident species which have not been recorded spawning in the marine or freshwater environment.
		1b. Resident species which also have marine or freshwater breeding populations.
Euryhaline	2	Euryhaline marine species which usually breed at sea with juveniles
Marine		showing varying degrees of dependence on southern African estuaries. Further subdivided into:
		2a. Juveniles dependent on estuaries as nursery areas.
		2b. Juveniles occur mainly in estuaries but are also found at sea.
		2c. Juveniles occur in estuaries but are usually more abundant at sea.
Marine	3	Marine species which occur in estuaries in small numbers but are not dependent on these systems.
stragglers		
Freshwater	4	Euryhaline freshwater species whose penetration into estuaries is determined primarily by salinity tolerance. Includes some species which may breed in both freshwater and estuarine systems.
Catadromous	5	Catadromous species which utilize estuaries as transit routes between the marine and freshwater environments but may also occupy estuaries.
		Further subdivided into: 5a. Obligate catadromous species which require a freshwater phase in their development.
		5b. Facultative catadromous species which do not require a freshwater phase in their development.

F=0.09, P=0.99). Water temperatures showed a clear seasonal trend with highest temperatures in summer and lowest in winter (Figure 2.2). The channel water depth varied between 37 cm and 64 cm (Mean=51.6, SD=7.6) (Figure 2.2). Salinity averaged 34.7 (SD=0.8) and ranged between 32 and 35. Salinity differed significantly seasonally (ANOVA df=7, F=3.53, P<0.005) but not significantly between sites (ANOVA df=4, F=0.28, P=0.89). Although statistically significant differences in salinity occurred between seasons, only November 1992 and May 1994 showed any marked changes and no seasonal trends were visible (Figure 2.3). Turbidity ranged between 5.6 and 16.8 NTU (Mean=10.2, SD=4.3). Significant differences were found in turbidity between seasons (ANOVA df=7, F=6.62, P<0.001) but not between sites (ANOVA df=4, F=0.70, P=0.59). There were no seasonal trends in turbidity.

TOTAL BIOMASS, DENSITY, ABUNDANCE AND STANDING STOCK

A total of 63 726 individuals were collected between July 1992 and May 1994 with a total biomass of 101.3 kg. The average number of fishes found in the salt marsh creek was 3 982 (SD=2067) ranging from 494 to 7 080 individuals. Fish density ranged from 1.8 - 27.1 individuals $10m^{-2}$ with an average of $15.1 \ 10m^{-2}$ (SD=8.0). There was no significant correlation between total ichthyofaunal or individual species abundance and water temperature, depth, salinity or turbidity.

The average ichthyofaunal biomass in the salt marsh creek was 6.3 kg (SD=6.5) and ranged from 1.1 kg to 22.6 kg. There were modest positive correlations (Fowler & Cohen 1993) between total biomass and water temperature (r_s =0.54, P=0.03) as well as total biomass and depth (r_s =0.45, P=0.08). There was no correlation between total or individual species biomass and either turbidity or salinity. The ichthyofaunal standing stock in the salt marsh creek ranged between 4 g 10m⁻² and 86 g 10m⁻² with an average of 24 g 10m⁻² (SD=25).

ICHTHYOFAUNAL COMPOSITION

The ichthyofaunal community found in the salt marsh creek consisted of 24 families and 41 confirmed species. Using Whitfield's (1994b) estuary association categorization (Table 2.2), the ichthyofaunal assemblage was dominated in both numbers (52%) and biomass (87%) by



Figure 2.2 Temporal patterns of water temperature and mean channel depth in Taylor's intertidal salt marsh creek. No significant differences in water temperature were found between the water chemistry sampling sites during each sampling occasion.



Figure 2.3 Temporal patterns of turbidity and salinity in Taylor's intertidal salt marsh creek. No significant differences in water salinity or turbidity were found between the water chemistry sampling sites during each sampling occasion.

euryhaline marine species (Figure 2.4). Estuarine species were also well represented but were more important in terms of numbers (30%) than mass (5%). Facultative catadromous species comprised 17% of the numbers and 7% of the biomass. Both euryhaline freshwater species and marine stragglers were poorly represented and contributed <1% of the total numbers or mass (Figure 2.4). A similar pattern of marine and estuarine fish dominance was also observed in the number of species in each group, with the euryhaline marine species being the most dominant (Figure 2.4). Of the remaining three groups, the marine stragglers were the best represented with 15% of the total species found in the salt marsh creek. Very few freshwater and catadromous species were found to frequent the salt marsh creek.

The overwhelming majority of fishes captured were juveniles (Table 2.1). Those species with mature individuals were predominantly fishes known to breed in estuaries, e.g. *Gilchristella aestuaria* and *Psammogobius knysnaensis* (Figure 2.5). The only non-estuarine fish with adult populations was *Liza richardsonii*.

The five species ranked highest overall were, in order of dominance, *L. dumerilii, Mugil cephalus, Rhabdosargus holubi, G. aestuaria* and *Atherina breviceps* (Table 2.3). The top seven species ranked numerically (Table 2.1) contributed 93% of the total numbers of confirmed species. The dominant species *L. dumerilii* constituted 68% of the total mass and 24% of the total numbers. Mugilidae (< 20 mm SL) were a very important group as they comprised 32% of the total number of fishes sampled but only 1.5% of the total mass.

Taxa	Group	Number fish (n)	er of)	Mass of	fish (g)	Freque	ncy of ence	Overall rank
		Total	Rank	Total	Rank	%	Rank	
Liza dumerilii	2b	15180	2	69489.1	1	100	1	1
Mugilidae (< 20 mm)	-	20462	1	1592.5	7	100	1	2
Mugil cephalus	5b	7567	4	6126.5	3	87.5	7	3
Rhabdosargus holubi	2a	1402	8	3819.2	5	100	1	3
Gilchristella aestuaria	la	7990	3	2405.1	6	87.5	7	5
Atherina breviceps	1Ь	2323	6	1499.1	8	93.8	4	6
Pomadasys commersonnii	2a	386	11	4165.3	4	93.8	4	7

Table 2.3 Summary statistics for all fish species and taxa sampled in Taylor's intertidal salt marsh creek for the period July 1992 - May 1994 (Group=Estuarine association group, Table 2.2).

Table 2.3 continued		(1		1		1	
Psammogobius knysnaensis	la	2057	7	659.8	10	87.5	7	8
Diplodus sargus capensis	2c	3639	5	185.9	14	68.8	11	9
Liza tricuspidens	2b	840	9	784.0	9	62.5	13	10
Glossogobius callidus	16	348	12	151.9	16	93.8	4	11
Caffrogobius natalensis	16	125	15	249.2	13	87.5	7	12
Liza richardsonii	2c	51	19	8553.7	2	56.3	15	13
Myxus capensis	56	148	14	656.7	11	62.5	13	14
Terapon jarbua	2a	345	13	156.8	15	68.8	11	15
Pomadasys olivaceum	3	64	16	395.4	12	50	17	16
Caffrogobius gilchristi	lЬ	60	18	133.0	17	43.8	18	17
Rhabdosargus glabiceps	2c	461	10	18.9	22	25	22	18
Solea bleekeri	2b	49	20	26.0	20	56.3	15	19
Monodactylus falciformis	2a	62	17	25.5	21	43.8	18	20
Caffrogobius nudiceps	16	27	22	37.5	19	43.8	18	21
Diplodus cervinus	3	7	26	96.9	18	18.8	24	22
Oreochromis mossambicus	4	16	24	13.2	23	18.8	24	23
Lithognathus lithognathus	2a	25	23	9.1	24	18.8	24	23
Sarpa salpa	2c	42	21	1.7	34	38	21	25
Crenimugil crenilabis	2c	12	25	3.3	30	18.8	24	26
Clinus superciliosus	1b	6	27	2.1	32	18.8	24	27
Lichia amia	2a	3	29	5.0	26	12.5	29	28
Elaps machnata	2a	5	28	0.6	38	25	22	29
Syngnathus acus	1Ь	3	29	2.6	31	12.5	29	30
Ophisurus serpens	2c	2	31	3.4	29	12.5	29	30
Periophthalmus sobrinus	la	1	35	8.3	25	6.3	34	32
Gobiopsis pinto	3	1	35	4.9	27	6.3	34	33
Pomatomus saltatrix	2c	1	35	4.1	28	6.3	34	34
Iso natalensis	3	2	31	0.7	35	6.3	34	35
Ambassis gymnocephalus	16	ι	35	2.0	33	6.3	34	36
Omobranchus woodi	la	2	31	0.1	45	12.5	29	37
Arothron hispidus	3	1	35	0.7	36	6.3	34	37
Saurida gracilis	3	1	35	0.7	36	6.3	34	37
Unidentified	-	2	31	<0.1	46	12.5	29	40
Sphyraenidae		1	35	0.6	39	6.3	34	41
Monodactylus argenteus	2a	1	35	0.6	40	6.3	34	42
Lactoria fornasini	3	1	35	0.4	41	6.3	34	43
Heteromycteris capensis	Zb	1	35	0.4	42	6.3	34	44
Eel larvae		1	35	0.3	43	6.3	34	45
Tetraodontidae	-	1	35	0.3	44	6.3	34	46
Abudefduf sp.	-	1	35	<0.1	46	6.3	34	47



Figure 2.4 Percentage contributions made by different estuarine associated fish groups (after Whitfield 1994b) to the ichthyofaunal community sampled in Taylor's intertidal salt marsh creek.



Figure 2.5 Length frequency distributions for two estuarine (G. aestuaria and P. knysnaensis) and two marine (L. dumerilii and R. holubi) fish species caught in Taylor's intertidal salt marsh creek (n=number of fish measured).

The three most dominant families were the Mugilidae, Sparidae and Clupeidae. The Mugilidae (six species) were by far the most well represented family and comprised 70% of the total number and 86% of the total mass of ichthyofauna. The Sparidae were also well represented with six species, but only contributed 9% and 4% to the total number and mass respectively. *G. aestuaria* was the only clupeid and contributed 13% to the total number but only 2% of the total mass.

SEASONALITY

The average number of fishes found in Taylor's creek varied greatly between years, with twice as many fishes being caught in the first year (42 163) in comparison to the second (21 563). In year one, the variation in numbers between dawn and dusk samples was high but no trends were discernible. The average number was nonetheless relatively constant throughout the year (Figure 2.6). Year two showed a more seasonal pattern, with higher utilization of the salt marsh creek in the warmer months (Figure 2.6). The low numbers in year two's winter assemblage can be attributed to a very poor recruitment of *Mugil cephalus* which were recorded in high numbers in the first year's winter sample.

The mass of fishes in the intertidal salt marsh creek differed greatly between years (Figure 2.7). Seventy two percent of the overall biomass was caught in year one with only 28% being caught in year two. This dissimilarity was primarily due to schools of larger mullet only utilizing the salt marsh creek in the spring and summer of year one. There was no discernible seasonal trend in the mass of fishes found during year two (Figure 2.7).

The diversity indices (Figure 2.8) showed distinct interannual differences and seasonal trends in the diversity and species richness of the ichthyofaunal community. Both the Margalef (D) and Shannon-Wiener (H') indices were far higher in year one than year two. In year one the Margalef index, which is indicative of species richness, was higher in spring, summer and autumn than in winter. In year two, the same pattern was not demonstrated and a marked decrease in species richness was found in summer. This decrease was probably due to a cold marine upwelling event in February 1994 which caused water temperatures in the salt marsh creek to decline to 17 °C.



Figure 2.6 The mean and range of fish numbers (n) caught in Taylor's intertidal salt marsh creek.



Figure 2.7 The mean and range of total fish biomass (g) caught in Taylor's intertidal salt marsh creek.

The diversity index of Shannon-Weiner showed a similar pattern to that of the Margalef index in year one, with the highest diversity being found in the summer and considerably lower diversities recorded in both winter seasons. The seasonal trend in the diversity of fishes in year two was not as prominent as in year one, but there was a slight increase in diversity in spring and summer (Figure 2.8). The Pielou evenness index showed a slight seasonal trend, with evenness being lowest in the winter months.



Seasons (1992-1994)

Figure 2.8 Seasonal cycles of the species richness (Margalef index), species diversity (Shannon Wiener index) and species evenness (Pielou index) of the ichthyofaunal community sampled from Taylor's intertidal salt marsh creek.
Although seasonal trends in total numbers of fishes were complicated by a high variability, several species and families showed distinct seasonal patterns in their abundance. The Mugilidae were by far the most important family and they dominated the ichthyofaunal assemblage in all seasons in both years except for spring 1992. Two species, the mugilid *Liza dumerilii* and sparid *Rhabdosargus holubi*, were ubiquitous whereas *Atherina breviceps*, *Pomadasys commersonnii* and *Glossogobius callidus* all had a frequency of occurrence of over 93% (Table 2.3). Though the natural variation displayed by fishes moving into the salt marsh creek is high, a number of species showed real seasonal trends in that they were repeated in both years (Figure 2.9). Most of the species which exhibited seasonal patterns showed an increase in numbers in the warmer months of spring, summer and autumn, followed by a sharp decrease in winter (e.g. *Liza tricuspidens, Glossogobius callidus, Caffrogobius natalensis, Pomadasys commersonnii* and *Psammogobius knysnaensis*). Summer peaks were exhibited by *L. tricuspidens, G. callidus* and *P. commersonnii*, whereas *P. knysnaensis* peaked in autumn. The only species to show a decrease in summer abundance and have higher numbers in winter and spring was *M. cephalus* (Figure 2.9).

2.4 DISCUSSION

TOTAL BIOMASS, DENSITY, ABUNDANCE AND STANDING STOCK

Taylor's intertidal salt marsh creek is frequented by a wide variety of fishes. However, this utilization in terms of density and standing stock is difficult to evaluate, both locally and internationally, in comparison to other salt marsh systems and estuarine habitats. The reasons for this are that there is a paucity of information on salt marshes in southern Africa, many international salt marsh studies are not sufficiently quantitative (Cain & Dean 1976, Shenker & Dean 1979, Bozeman & Dean 1980) and some investigations give values for only the dominant species and not the total ichthyofauna (Rogers *et al.* 1984, Rozas & Reed 1993). Despite these limitations, the density of fishes in Taylor's creek falls within the range of values reported for other estuarine habitats (Table 2.4). The density of fishes in salt marsh creeks from different systems varies greatly, from 8.3 individuals $10m^{-2}$ (Rountree & Able 1993) to 520 individuals $10m^{-2}$ (Sogard & Able 1991), with Taylor's creek (15 individuals $10m^{-2}$) having a relatively low fish density in comparison to other salt marsh channel habitats. This low density may be a function



Figure 2.9 The mean and range (numbers) of selected species sampled in Taylor's intertidal salt marsh creek.

of an impoverished overall estuarine ichthyofauna since the Kariega Estuary is a freshwater deprived system (Allanson & Read 1995). Research into the freshwater requirements of estuaries in the Eastern Cape has shown that estuaries with a strong axial salinity gradient and high freshwater input have better recruitment of euryhaline marine species and far higher fish densities than freshwater deprived systems (Whitfield 1994c, Whitfield *et al.* 1994). Salt marsh creeks have been shown in comparative studies to support higher densities but lower diversity of fishes in comparison to other estuarine habitats (Weinstein & Brooks 1983, Sogard & Able 1991). Ter Morshuizen and Whitfield (1994) reported mean spring fish densities of between 109 individuals $10m^{-2}$ and 173 individuals $10m^{-2}$ for eelgrass beds in the Kariega Estuary. These densities are higher than those found in the intertidal salt marsh creek, which ranged between 6.4 individuals $10m^{-2}$ and 23 individuals $10m^{-2}$ in the spring months.

The standing stocks of fishes found in Taylor's creek are comparable with most other estuarine habitats except for mangroves, which tend to have far higher standing stocks (Table 2.5). Mangrove habitats are known to function as both nursery and feeding areas for adult fishes (Morton 1990), whereas Taylor's creek was dominated almost entirely by juvenile fishes with schools of subadult mullet being sporadic visitors.

ICHTHYOFAUNAL COMPOSITION

An analysis of the estuarine association categories of the fish species recorded in Taylor's creek (Figure 2.4) shows that their relative percentages are very similar to those of South African estuaries as a whole (Whitfield 1994a, Whitfield 1994b). Consequently, Taylor's creek appears to be utilized by the entire cross-section of estuarine associated fish species. Numerically and gravimetrically the euryhaline marine category of fishes were the most dominant. This group of species is known to exhibit many eurytopic traits, e.g. mobility, a broad habitat tolerance range and large adult body size (Whitfield 1994d), which facilitates utilization of estuaries where environmental stress is pronounced and periods of stability are relatively short (Whitfield 1994d). Salt marshes and other intertidal habitats within this environment have marked daily fluctuations in many abiotic characteristics, hence the dominance of the ichthyofaunal community by eurytopic species is to be expected. In comparison, the estuarine group of species are generally more stenotopic in character, having a narrow habitat tolerance range, limited distribution, relatively

Sampling region	Physical environment	Sampling method	Density (no.10m ⁻²)	Reference
Galveston Bay LISA	Salt marsh creek	Drop trap	170 - 1530	Minello et al (1004)
Little Egg Harbour-Great Bay, USA	Salt marsh creek	Throw trap	520	Sogard & Able (1991)
Alligator Creek, Australia	Intertidal mangrove creek	Seine net	313	Robertson & Duke (1990)
Kariega Estuary, South Africa	Eelgrass	Fry seine	129	Ter Morshuizen & Whitfield (1994)
Little Egg Harbour-Great Bay, USA	Eelgrass	Throw trap	90	Sogard & Able (1991)
Everglades National Park, USA	Mangrove	Block net	80	Thayer et al. (1987)
Little Egg Harbour-Great Bay, USA	Salt marsh creek	Weir	8 - 69	Rountree & Able (1993)
Terrebonne-Timbalier Estuary, USA	Intertidal marsh	Lift net	53	Rozas (1992b)
Little Egg Harbour-Great Bay, USA	Macroalgae	Throw trap	50	Sogard & Able (1991)
St Johns River, USA	Salt marsh creek	Seine net	45	Carr & Giesel (1975)
Humboldt Bay, USA	Mitigation salt marsh	Drop trap	17	Chamberlain & Barnhart (1993)
Kariega Estuary, South Africa	Intertidal salt marsh creek	Block net	15	This study
Botany Bay, Australia	Mangrove creek	Block net	9	Bell et al. (1984)
Galveston Island, USA	Salt marsh creek and pans	Drop trap	9	Zimmerman & Minello (1984)
Peel-Harvey Estuary, Australia	Estuarine shallows	Seine net	0.2 -5	Loneragan et al. (1986)
Moreton Bay, Australia	Mangrove	Block net	3	Morton (1990)
Everglades National Park, USA	Seagrass	Trawl net	2	Thayer et al. (1987)
Moreton Bay, Australia	Estuary	Seine net	2	Morton (1990)
Humboldt Bay, USA	Mitigation salt marsh	Seine net	1	Chamberlain & Barnhart (1993)

 Table 2.4 A comparison of the fish density in Taylor's intertidal salt marsh creek with published

 values for other estuarine habitats.

Sampling region	Physical environment	Sampling method	Standing stock (g 10m ⁻²)	Reference
Embley Estuary,	Intertidal mudflats	Stake net	706	Blaber et al. (1989)
Australia	next to mangroves			
Alligator Creek,	Intertidal mangrove	Seine net	290	Robertson & Duke
Australia	creek			(1990)
Moreton Bay,	Mangrove	Block net	253	Morton (1990)
Australia				
Embley Estuary,	Open water	Gill net	71 - 161	Blaber et al. (1989)
Australia				
Everglades National	Mangrove	Block net	150	Thayer et al. (1987)
Park, USA				
Swartvlei,	Estuarine lake	Lift and gill	124	Whitfield (1993)
South Africa		nets		
Embley Estuary,	Mangrove creek	Block net	82	Blaber et al. (1989)
Australia				
Botany Bay, Australia	Mangrove creek	Block net	64	Bell et al. (1984)
Embley Estuary,	Beaches	Seine net	50	Blaber et al. (1989)
Australia				
Peel-Harvey Estuary,	Estuarine shallows	Seine net	1 - 42	Loneragan
Australia				et al. (1986)
Moreton Bay,	Estuary	Seine net	29	Morton (1990)
Australia				
Kariega Estuary,	Intertidal salt marsh	Block net	24	This study
South Africa	creek			
Newport River	Salt marsh	Block net	19	Hettler (1989)
Estuary, USA				
Embley Estuary,	Seagrass	Beam trawl	5 - 18	Blaber et al. (1989)
Australia				
Everglades National	Seagrass	Trawl	8	Thayer et al. (1987)
Park, USA				

Table 2.5 A comparison of fish standing stock in Taylor's intertidal salt marsh creek with published values for other estuarine habitats.

sedentary lifestyle and small adult body size (Whitfield 1994d). Some estuarine species such as *Gilchristella aestuaria* and *Atherina breviceps* do, however, exhibit a number of typically eurytopic traits (Whitfield 1994d) and as these species dominated the estuarine fish component of the community, the overall salt marsh creek ichthyofauna could be described as eurytopic. The low number of stenotopic species (e.g. *Clinus superciliosus* and *Syngnathus acus*) found in the intertidal salt marsh creek is most likely a function of the highly dynamic nature of the intertidal salt marsh compared to adjacent estuarine habitats.

The overwhelming gravimetric dominance of the marine component of the ichthyofauna is mainly an effect of the small body size of species within the estuarine group. The low proportion of freshwater species found utilizing Taylor's creek is indicative of the marine conditions prevalent in the Kariega Estuary. During this study the upper reaches of the estuary were hypersaline (>35) for much of the time which would restrict the penetration of freshwater species into the estuary.

Studies on salt marshes and their creeks have shown that migrant marine fishes may form an important component of the ichthyofauna (Cain & Dean 1976, Weinstein 1979, Bozeman & Dean 1980, Rountree & Able 1993). Transient species recruiting from the sea and residing in salt marshes during their early life stages have been shown to form a conspicuous seasonal component of the marsh fauna and play an important role in the organization of marsh communities (Weinstein *et al.* 1980). Similarly, marine migrant fish species dominated the ichthyofaunal community associated with Taylor's creek (Figure 2.4).

The majority of tidal marsh studies have shown that the ichthyofauna is dominated by only a few species (Cain & Dean 1976, Bozeman & Dean 1980, Weinstein *et al.* 1980, Weinstein & Brooks 1983, Smith *et al.* 1984). Taylor's creek was no exception, with the seven most numerically abundant species contributing >90% to the total ichthyofauna. The dominant species found in Taylor's creek (Table 2.3) were very similar to the dominant species found in the neighbouring Kowie and Great Fish estuaries (Whitfield *et al.* 1994). The species richness values (D) for Taylor's creek were comparable to those of Ter Morshuizen and Whitfield's (1994) eelgrass study, but slightly lower than the values reported for seine netting in the Kowie and Great Fish estuaries (Whitfield *et al.* 1994).

One of the most striking characteristics of the ichthyofauna associated with Taylor's creek was the overwhelming dominance of the community by fishes in their early life-history stages. Very few of the species which were found in the salt marsh creek had adult components and the vast majority of the fishes were 0+ juveniles. Other studies have also shown the importance of salt marshes and their constituent intertidal habitats as nursery areas for fishes (Cain & Dean 1976, Weinstein 1979, Stout 1984, Hettler 1989, Rozas 1992a, Knieb 1997a,b, Mathieson *et al.* in press a,b). Two major factors affecting habitat selection in fishes are foraging profitability and predator avoidance (McIvor & Odum 1988) and these two factors are examined in Chapter 7. The findings of this chapter do however indicate that very few of the common piscivorous fishes caught in the main estuary channel (Chapter 6) were recorded in Taylor's creek and this may be a factor as to why juvenile fishes utilize this habitat.

SEASONALITY

Interannual variation in total numbers, total mass, species richness and diversity of the fishes found in Taylor's creek was high. This variability may be attributed to the dominance of the ichthyofauna by marine migrants which show variability in both the timing of spawning and magnitude of recruitment into estuaries. This variability in the timing of spawning and consequent recruitment into estuaries is a function of the extended spawning seasons characteristic of many of the marine migrants (Wallace 1975). The fluctuations in the numbers of larvae available for recruitment into the estuary may be a function of spawning success, ocean currents, upwellings, larval mortality and freshwater olfactory cues. It would appear that the interannual variation cannot be attributed to specific abiotic factors in the salt marsh creek, such as water temperature, turbidity, salinity and channel depth, as these parameters varied little between years.

Previous salt marsh studies have all shown a degree of seasonality in their nektonic communities. Rountree and Able (1992) reported that although the timing of peak abundance can exhibit spatial and annual variation in a particular study, strong seasonal patterns are typical. Most studies show a peak in abundance and/or diversity in the spring, summer or autumn months with a decrease in winter (Subrahmanyam & Coultas 1980, Hettler 1989, Rountree & Able 1992, Rozas & Reed 1993). Cain and Dean (1976) reported that season had a highly significant effect on all indices and the number of species, but had no effect on the number of individuals caught. Taylor's creek exhibited an increase in fish diversity in the warmer months but the abundance of fishes was highly variable between years, with the first showing no seasonal difference while the second exhibited a marked variation. Many of the dominant marine migrant species (e.g. *Liza tricuspidens*, *Pomadasys commersonnii* and *Mugil cephalus*) entered the salt marsh creek during periods corresponding to their peak recruitment periods into estuaries (Whitfield 1990, Whitfield & Kok 1992). Overall, Taylor's creek appears to be occupied throughout the year with some species displaying distinct periods of utilization.

Due to the extended spawning periods of many South African marine migrants, cohort analysis is difficult and trends in ontogenetic habitat use may consequently be masked. The size classes of *M. cephalus* in the salt marsh creek did, however, indicate that after recruitment into the estuary the fry utilized the salt marsh creek nursery area extensively, but as they grew their occupation of the salt marsh creek habitat decreased and individuals of >65 mm were not recorded. Ontogenetic shifts in habitat use within salt marshes, and between salt marshes and the estuary, have been documented (Weinstein & Brooks 1983, Baltz *et al.* 1993).

In conclusion Taylor's intertidal salt marsh creek, when inundated, supports an ichthyofaunal community which is dominated by 0+ juvenile fishes and hence forms another nursery habitat which is available to the ichthyofauna found within the Kariega Estuary. The abundance and standing stock of fishes found in Taylor's creek falls within the range recorded for other estuarine habitats. However, further comparative research on other nursery areas in the Kariega Estuary is needed (Chapters 4 - 6) to establish the overall importance of salt marshes and their intertidal creeks to the estuary's ichthyofauna. The fish community was dominated by only a few species with the major group being marine migrants. The occupation of the creek was variable but some seasonal trends were apparent at the species level. Both the function of food and refuge in nursery habitat selection need to be examined (Chapters 7 - 8) in order to fully comprehend the role that salt marshes and their creeks play in the Kariega Estuary.

Chapter 3

The distribution of fishes within Taylor's salt marsh system

3.1 INTRODUCTION

Estuaries are highly variable and dynamic environments in which physico-chemical parameters such as temperature, salinity, turbidity, oxygen concentration and depth are variable on a temporal and spatial scale. Fishes found in estuaries have different life-history strategies and dependencies on these systems (Whitfield 1994b), with marine fishes using estuaries as nursery areas also showing species specific temporal variations in their recruitment patterns (Whitfield & Kok 1992). Notwithstanding this variability in the physical attributes of the estuarine environment and the cyclical nature of estuarine-associated fish immigration and emigration, distinctive ichthyofaunal communities are associated with the different habitats (Weinstein & Brooks 1983, Sogard & Able 1991, Connolly 1994a, Chapter 4) and reaches (Ter Morshuizen *et al.* 1996) within estuaries.

Salt marshes comprise a number of different physiographic features (e.g. creeks, high marsh pools and vegetated marsh flats), with some of these features exhibiting a tidal zonation in vegetation type (Long & Mason 1983). The different habitats within salt marshes all have a range of physical characteristics or forces acting on them due to their varying elevations, vegetation, distance from creek and hydroperiod. Most North American tidal marsh ichthyofaunal research has been conducted on tidal creeks (Cain & Dean 1976, Bozeman & Dean 1980, Smith *et al.* 1984, Chamberlain & Barnhart 1993) and marsh flats (Knieb 1984, Hettler 1989, Rozas 1992b, Rozas & Reed 1993, Knieb & Wagner 1994, Minello & Webb 1997, Knieb 1997a,b). Limited research has been undertaken on the fishes associated with high marsh areas and salt marsh pools (Talbot & Able 1984, Gosselink 1984, Stout 1984, Smith & Able 1994).

The exact criteria which influence fish habitat choice are unclear but are most likely a combination of the need for food and refuge. Research has shown that the distribution of fishes in tidal salt and freshwater marsh habitats is related to a number of physical factors such as stream order (Rozas & Odum 1987a, Hettler 1989); distance from creek (Minello *et al.* 1994, Peterson & Turner 1994); submerged aquatic vegetation (Rozas & Odum 1987b); elevation, depth and hydroperiod (Knieb & Wagner 1994, Rozas 1995); point of entry (Rozas *et al.* 1988) and creek bank topography (McIvor & Odum 1988), many of which affect the food availability or refuge function of the habitat, or both.

Understanding the distribution of fishes within a number of habitats in a single salt marsh system is demanding due to the myriad of interacting variables associated with biota comparisons on a wide spatial scale. In contrast to the large salt marsh systems in the USA, Taylor's salt marsh in the Kariega Estuary is small and thus has the advantage that many of the different physiographic features of the salt marsh are in close proximity to one another. This reduction in spatial scale affords the opportunity to examine fish distribution in all the different habitats at the same time. Temporal scale matching is of particular importance since the abundance of tidal salt marsh fauna has been shown to be highly variable (Varnell *et al.* 1995). Research on the ichthyofauna associated with Taylor's salt marsh (Chapter 2) indicated that the salt marsh system was of importance to both marine and estuarine fish species. This study was, however, conducted using a block net which caught all the fishes that were in the salt marsh system over the slack high tide. Although giving an accurate indication of the fishes utilizing the system, it does not provide much information on the distribution of fishes in the different habitats within the salt marsh.

In order to understand the importance of the different salt marsh habitats to fishes, a thorough understanding of the species distribution patterns and life-history stages found within the various habitats is required. Knowledge of fish distribution within salt marshes is a prerequisite when trying to assess the magnitude of energy transfers attributable to those species that frequent these systems (Chapters 7 & 8). Information on which marsh habitats are utilized by fishes is also imperative in the assessment and implementation of marsh mitigation and reconstruction efforts.

This chapter endeavours to examine:

- 1) Fish distribution throughout Taylor's intertidal salt marsh creek.
- Fish distribution within the different habitats within Taylor's salt marsh, viz. creek, Spartina maritima flats, Sarcocornia perennis flats, and high marsh pools.

3.2 MATERIALS AND METHODS

This chapter is divided into two main sections, the first covering the distribution of fishes within Taylor's intertidal salt marsh creek (also referred to as Taylor's creek) and the second dealing with the distribution of fishes between the dominant habitats found on Taylor's salt marsh.

SECTION 1 - THE ICHTHYOFAUNAL DISTRIBUTION WITHIN TAYLOR'S INTERTIDAL

SALT MARSH CREEK.

Sampling regime: Samples were collected monthly in the different reaches of Taylor's creek from January to April 1995, over the dawn full moon spring tide. The standardisation of sampling time was to ensure that the creek had similar levels of inundation on all sampling occasions, as the level of inundation and hydroperiod have been shown to be very important factors in regulating the manner in which nekton utilize intertidal marsh habitats (Rakocinski *et al.* 1992, Rozas 1995). Due to an absolute sampling method being employed in this study, involving the removal of large numbers (proportional to the size of the estuary) of fishes from the system, a monthly sampling interval was necessary to ameliorate any localised depletion in fish numbers (see Materials & Methods, Chapter 2).

Field sampling: The field sampling technique was identical to that discussed in Chapter 2 (Paterson & Whitfield 1996), except that three block nets were used in separating the lower, middle and upper reaches of the creek (Figure 3.1) instead of just one at the creek mouth. At slack high tide the block nets (see Chapter 2 for net design and measurements) were simultaneously deployed across the creek at three points (Figure 3.1). Once in position, the weighted bottom line was securely pegged into the mud substratum and the top of the net was raised above the water surface with the aid of wooden poles. As the tide receded the fishes were collected at each net.

Block nets were used in this study as they had been field tested and found to be effective in previous work on the Kariega Estuary salt marsh systems (Chapter 2). When comparing different reaches of a creek, block netting allows for all reaches to be simultaneously isolated from one another. This technique avoids cross contamination of samples in one reach while working on another.



Figure 3.1 Map of Taylor's salt marsh indicating the positions of the three block nets (-----) dividing the lower, middle and upper reaches of the intertidal creek.

Sample analysis: All the fishes were fixed in 10% formalin and preserved in 60% propyl alcohol. In the laboratory the fishes were counted and identified to species level where possible (mullet less than 20 mm SL were recorded as Mugilidae). Standard lengths were measured to the nearest mm for all species. Sub-sampling for length data was employed when there were more than 100 individuals of a given species. The total preserved wet mass of each species was measured to the nearest 0.1 g by weighing all the representatives of that species. *Physico-chemical sampling*: During each sampling occasion three water samples were collected at fixed stations in the lower, middle and upper reaches of the creek. Temperature (°C) was measured in the field using a hand held thermometer, while turbidity (NTU) and salinity were measured in the laboratory using a turbidimeter and salinometer respectively. The depth of water at selected stations down the centre of the creek channel was recorded to the nearest centimetre immediately after the block nets were deployed.

Data analysis: The density (number per 10 m^2) and standing stock (grams per 10 m^2) of fishes in each of the three creek reaches were calculated by dividing the number or mass of fishes caught in each of the reaches by the reach's surface area. To test for significant differences in the density and standing stock of fish in the different reaches, for the total ichthyofauna as well as the dominant species, a two-way ANOVA (time & reach) for single observations was used (Fowler & Cohen 1993). This technique is suitable for experimental designs with only single observations (absolute samples in this study). All the data was $log_{10}(x+0.5)$ transformed following Cochran's C test for heteroscedacity. A Tukey range test using a 95% confidence limit was conducted *a posteriori* if significant differences were found in the ANOVA.

Length frequency histograms were calculated for the four numerically dominant fish species recorded in the creek viz. Gilchristella aestuaria, Psammogobius knysnaensis, Liza dumerilii and Rhabdosargus holubi.

A two-way ANOVA (time & reach) was calculated to test for significant differences between temperature, salinity, turbidity and depth between the different reaches and sampling periods. Prior to calculation of the ANOVA, a Cochran's C test was undertaken to test for heteroscedacity. A Tukey range test using a 95% confidence limit was conducted *a posteriori* if significant differences were found in the ANOVA.

Ordination and classification: The ichthyofaunal density data collected in the three reaches of Taylor's creek were root-root transformed. An association matrix was produced using the Bray-Curtis similarity measure, from which classification and ordination procedures were conducted. The similarity matrix was classified using hierarchical agglomerative clustering with group average

linking, while the ordination used multidimensional scaling (MDS) techniques (Clarke & Warwick 1994).

The environmental variables temperature, salinity, turbidity and depth were superimposed on an ordination produced by the creek fish community data. In Taylor's creek the depth and the distance from the creek mouth are inversely related and therefore only depth was considered since these variables would be difficult to disentangle (Clarke & Warwick 1994). This method was first proposed by Field *et al.* (1982) and allows for a simple examination of which environmental parameters may be important in influencing the biotic groupings produced by multidimensional scaling techniques.

SECTION 2 - THE ICHTHYOFAUNAL DISTRIBUTION WITHIN THE DOMINANT HABITATS OF TAYLOR'S SALT MARSH.

Sampling regime: The sampling programme to investigate the distribution of fishes in the different salt marsh habitats viz. creek, Sarcocornia perennis flats, Spartina maritima flats and high marsh pools, was divided into two sections. The first study (2a) examined the distribution of fishes in all the above habitats from January 1993 to May 1994. This study was undertaken together with a general ichthyofaunal investigation of Taylor's salt marsh (Chapter 2) and the sampling protocol and rationale behind it is covered in Chapter 2. A total of 12 sampling periods were covered, in which each habitat in the salt marsh was sampled over the same slack high tide. The second study (2b) was initiated in 1995 to look specifically at the Spartina maritima flats as this habitat had not been adequately sampled during the first study. A winter, summer sampling protocol was implemented for this investigation, with four consecutive full moon spring high tides being sampled in May, June, November and December 1995.

Section 2a: Distribution of fishes in the creek, *Spartina maritima* flats, *Sarcocornia perennis* flats and high marsh pools.

Field sampling: As with other estuarine studies which have examined the distribution of fishes in different habitats (Blaber *et al.* 1989, Chong *et al.* 1990), this study used a range of gear types. The methods selected were the most effective and therefore the most likely to produce realistic estimates of fish abundance and standing stock in each habitat.

On the slack high tide a block net was deployed across the mouth of Taylor's creek (Figure 3.1). The weighted bottom line was then pegged into the mud substratum and the top rope suspended a minimum of 50 cm above the water surface with the use of wooden poles. As the tide receded the fishes were collected at the net and at low tide any remaining pools in the creek were seined (for further information see Materials & Methods, Chapter 2).

Immediately after the block net was deployed, the Sarcocornia perennis flats and high marsh pools were sampled using a 5 m long, 2.5 m deep, 2.5 mm stretch mesh seine net. Depending on the level of inundation, between four and six sites were seined in the Sarcocornia perennis flats and between two and three sites were netted in the high marsh pools. Preliminary visual transects conducted in the Sarcocornia perennis flats, Spartina maritima flats and high marsh pools indicated that the fishes were scarce, patchily distributed and small in size. Seine nets were therefore used as they covered the large area needed to procure adequate samples. While enclosure techniques such as Rozas's (1992b) bottomless lift trap have been successfully used in vegetated marsh habitats, it was recommended that where fishes are patchily distributed and a larger sampling area is required, one should utilize other more appropriate techniques (Rozas 1992b). Seine netting, as with all techniques, has certain limitations. In particular this method is known to under sample some benthic species (Weinstein & Davis 1980, Connolly 1994b) and pose difficulties when trying to accurately work out the sample area (Rozas & Minello 1997). Seine netting has proved to be a suitable technique in selected tidal creeks (Weinstein & Davis 1980), especially where the sample surface is flat, as in the high marsh pools and Sarcocornia perennis flats. In order to counteract as much gear bias as possible, the seine net was made from the same netting as the block net and was fitted with a heavy bottom line. Visual observations while seining indicated that the bottom line was flush with the mud substratum and no larger fishes were observed avoiding the net. In addition to the seine netting a 0.7 m² circular throw trap was used in both the Sarcocornia perennis and Spartina maritima habitats with 10 samples being taken in each habitat. This technique did not however catch any fishes and after 140 samples it was discontinued.

Sample analysis: The analysis of the ichthyofaunal samples follows that of the fish distribution study within the creek (Section 1 - Materials & Methods).

Data analysis: The density (number per 10 m^2) and standing stock (grams per 10 m^2) of fishes in the high marsh pools, *Sarcocornia perennis* flats and *Spartina maritima* flats were calculated by dividing the area sampled by the number and mass of fishes caught respectively. The density and standing stock of fishes in the creek was back-calculated by dividing the total number or mass of fishes caught in the block net minus the estimated number of fishes over the inundated flats by the total area of the intertidal creek. The non-parametric Wilcoxon test (samples paired on a seasonal basis) was used to see if there was a significant difference in both the density and standing stock of fishes found in the creek and high marsh pools, as well as the creek and *Sarcocornia perennis* flats (Fowler & Cohen 1993).

Section 2b: Distribution of fishes in the Spartina maritima flats.

Field sampling: The unsuitability of seining methods necessitated the use of a modified block netting method in the Spartina maritima habitat. Two suitable sample areas (56 m² and 28 m²) were identified within the Spartina maritima beds and stout wooden poles were driven into the mud substratum to demarcate these areas. Both sample areas stretched from the edge of the creek up the entire tidal profile. At low tide a bin containing a block net (identical to that used in the creek block netting - Section 1) was placed at the bottom of the sample area and ropes attached to the net were then laid along the edge of the poles demarcating the sample area. At slack high tide both ends of the net were simultaneously pulled out of the bin and along the poles, thus enclosing the sample area. The weighted bottom ropes of the net were securely pegged into the mud substratum and the float line was hung over the tops of the poles. As the tide receded the fishes moved out of the vegetated areas and into the lower sections of the net, where they were collected using small aquarium nets.

Sample analysis: The analysis of the ichthyofaunal samples follows that of the fish distribution study within the creek (Section 1 - Materials & Methods).

Data analysis: The density (number per 10 m^2) and standing stock (grams per 10 m^2) of fishes were calculated for the *Spartina maritima* flats.

3.3 RESULTS

SECTION 1 - THE ICHTHYOFAUNAL DISTRIBUTION WITHIN TAYLOR'S INTERTIDAL SALT MARSH CREEK.

Physico-chemical parameters: The temperature, salinity and turbidity (Table 3.1) of the water in the creek was not significantly different between reaches but was significantly different (p<0.01) between each sampling period (Table 3.2). The mean water temperature in the creek ranged between 14.2 and 19.8 °C while the mean turbidity ranged between 20 and 25 NTU. The salinity of the water was full sea water (35) except for the February sample when it dropped to approximately 33 (Table 3.1).

Table 3.1 Physico-chemical water parameters for the three reaches of Taylor's intertidal salt marsh creek during the period January to April 1994.

		Lower	reach	Middle	e reach	Upper	reach
		Mean	SD	Mean	SD	Mean	SD
January	Temperature (°C)	14.2	0.28	14.2	0.28	14.3	0.28
	Salinity	35.0	0.00	35.0	0.00	35.0	0.00
	Turbidity (NTU)	22.3	0.51	22.0	2.64	23.0	1.00
	Depth (cm)	71.1	4.30	61.8	1.93	50.8	4.07
February	Temperature (°C)	19.5	0.50	19.8	0.28	19.8	0.28
	Salinity	31.6	0.57	33.3	0.57	33.3	0.57
	Turbidity (NTU)	21.3	2.08	20.0	2.00	20.0	3.60
	Depth (cm)	60.1	4.30	50.8	1.93	39.8	4.07
March	Temperature (°C)	15.8	0.28	15.6	0.28	15.8	0.57
	Salinity	35.0	0.00	35.0	0.00	35.0	0.00
	Turbidity (NTU)	19.0	3.60	20.0	2.00	19.6	2.51
	Depth (cm)	57.1	4.30	47.8	1.93	36.8	4.07
April	Temperature (°C)	15.1	0.05	15.8	0.76	15.0	0.00
	Salinity	35.0	0.00	35.0	0.00	35.0	0.00
	Turbidity (NTU)	23.0	2.00	24.6	4.04	24.3	4.16
	Depth (cm)	57.1	4.30	47.8	1.93	36.8	4.07

The depth of water within the creek was significantly different between the different reaches (p<0.001) and between the sampling periods (p<0.001). A Tukey multiple range analysis indicated that all three reaches had significantly different water depths, with the lower reach being the deepest and the upper reach the shallowest (Table 3.2).

Table 3.2 Results of ANOVA and Tukey range tests for temperature, salinity, turbidity and depth in the three reaches of Taylor's intertidal salt marsh creek, for the period January to April 1994. In the time range analysis 1=January, 2=February, 3=March and 4=April. In the reach range analysis 1=lower reach, 2=middle reach and 3=upper reach. In both range analyses *= significant difference at the 95% confidence level.

	Time	Reach	Interactions	Range analysis	Range analysis
	(Df =3)	(Df =2)	(time x reach)	Time	Reach
Temperature (°C)	p < 0.0001	p = 0.4028	p = 0.2691	1 - 2*; 1 - 3*;	
	F = 344.88	F = 0.98	F = 1.36	1 - 4*; 2 - 3*;	
				2 - 4*; 3 - 4	
Salinity	p < 0.0001	p = 0.7198	p = 0.9126	1 - 2*; 1 - 3;	
	F = 65.33	F = 0.33	F = 0.33	1 - 4; 2 - 3*;	
				2 - 4*; 3 - 4	
Turbidity (NTU)	p = 0.0096	p = 0.9534	p = 0.9611	1 - 2; 1 - 3;	
	F = 4.76	F = 0.09	F = 0.23	1 - 4; 2 - 3;	
				2 - 4; 3 - 4*	
Depth (cm)	p < 0.0001	p < 0.0001	p = 1.0000	1 - 2*; 1 - 3*;	1 - 2*; 1 - 3*;
	F = 102.37	F = 318.55	F = 0.00	1 - 4*; 2 - 3*;	2 - 3*
				2 - 4*; 3 - 4	

Density and standing stock: A total of 32 984 individuals were caught in Taylor's creek during this study. The density of fishes did not differ significantly (Table 3.3) between reaches (p=0.233) or between sampling periods (p=0.440). The highest density was recorded in the middle reaches (47.7 fishes per 10 m²) and the lowest in the upper reaches (23.6 fishes per 10 m²) (Table 3.4).

Of the dominant taxa the Mugilidae (< 20 mm), *Gilchristella aestuaria*, *Psammogobius knysnaensis* and *Rhabdosargus holubi* all showed significant differences in their densities between

the different sampling periods, with the January sample tending to be different from the other sample months (Table 3.3). The densities of *Liza dumerilii*, *G. aestuaria* and *R. holubi* all showed significant differences (Table 3.3) between the different reaches.

There was a clear relationship between fish density and intertidal habitat affinities (See Chapter 4). Those fish species which were found to be common in the adjacent eelgrass beds (Chapter 4) all had their highest densities in the lower and middle reaches of the creek (Table 3.4). Some of these eelgrass-associated species (e.g. *C. natalensis* and *C. nudiceps*) were not recorded in the upper reaches of the creek (Table 3.4). In contrast, creek-associated species (Chapter 4) either had a uniform distribution or their highest densities in the middle or upper reaches of the creek (Table 3.4).

The total mass of fishes caught in Taylor's creek during the study was 37 719 g. The total standing stock of fishes was not significantly different between sampling periods (p=0.054) but did differ significantly between reaches (p=0.005) (Table 3.3). The fish standing stock was an order of magnitude higher in the middle reaches (119.8 g per 10 m²) than in the lower (13.5 g per 10m²) and upper reaches (4.9 g per 10 m²) of the creek (Table 3.5). Amongst the dominant fish species, *Liza dumerilii* and *Rhabdosargus holubi* both showed a significant difference in their standing stocks in the different creek reaches (Table 3.3), with the upper reaches having a significantly lower standing stocks of Mugilidae (<20 mm), *G. aestuaria* and *P. knysnaensis* all showed a significant difference over time (Table 3.3). The eelgrass-associated fish species (Table 3.5) had their highest standing stocks in the lower to middle reaches, while the standing stocks of the creek-associated species were highest in the middle or upper reaches of the creek (Table 3.5).

Composition: The overall numerical composition of the ichthyofauna caught in Taylor's creek during this study was very similar to that caught in previous years (Chapter 2). The dominant taxa were the Mugilidae (< 20 mm)(52.9%), *L. dumerilii* (20%), *G. aestuaria* (10%), *P. knysnaensis* (10%), *R. holubi* (1.8%), *L. tricuspidens* (1.2%) and *M. cephalus* (1.0%).

Table 3.3 Results of ANOVA and Tukey range tests on the density and standing stock of the dominant fish taxa caught in the three reaches of Taylor's intertidal salt marsh creek, for the period January to April 1994. In the time range analysis 1=January, 2=February, 3=March and 4 =April. In the reach range analysis 1=lower reach, 2=middle reach and 3=upper reach. In both range analyses * = significant difference at the 95% confidence level.

	Time	Reach	Time range	Reach range
	(Df = 3)	(Df = 2)	analysis	analysis
DENSITY				
Total ichthyofauna	p=0.440	p = 0.233		
	F = 1.03	F = 1.87		
Mugilidae (< 20 mm)	p = 0.045	p = 0.670	1 - 2"; 1 - 3;	
,	F = 4.97	F = 0.43	1 - 4; 2 - 3;	
			2 - 4; 3 - 4	
Liza dumerilii	p = 0.544	p = 0.014		1 - 2; 1 - 3*;
	F = 4.58	F = 23.78		2 - 3'
Gilchristella aestuaria	p = 0.009	p = 0.040	1-2;1-3;	1 - 2; 1 - 3';
	F = 9.88	F = 5.15	1 - 4*; 2 - 3;	2 - 3
			2 - 4; 3 - 4	
Psammogobius knysnaensis	p = 0.018	p = 0.116	1 - 2; 1 - 3;	
	F = 7.52	F = 3.15	1 - 4'; 2 - 3;	
			2-4;3-4	
Rhabdosargus holubi	p = 0.024	p = 0.015		1 - 2; 1 - 3";
	F = 6.65	F = 9.16		2-3
STANDING STOCK				
Total ichthyofauna	p = 0.054	p = 0.005		1 - 2*; 1 - 3;
	F = 4.54	F = 34.59		2 - 3'
Liza dumerilii	p = 0.118	p < 0.001		1 - 2'; 1 - 3;
	F = 2.97	F = 29.52		2 - 3*
Rhabdosareus holubi	p = 0.192	p = 0.042		1 - 2; 1 - 3*;
0	F = 2.17	F = 5.62		2 - 3
Gilchristella aestuaria	p = 0.033	p = 0.060	1-2'; 1-3';	
	F = 5.77	F = 4.51	1 - 4; 2 - 3;	
			2 - 4; 3 - 4	
Psammogobius knysnaensis	p = 0.025	p = 0.040	1 - 2; 1 - 3;	
1.0000000000000000000000000000000000000	F = 6.59	F = 5.67	1 - 4"; 2 - 3;	
			2 - 4'; 3 - 4	
Mugil cephalus	p = 0.199	p = 0.146		
and the second se	F = 2.13	F = 2.68		
Mugilidae (< 20 mm)	p = 0.008	p = 0.605	1 - 2*; 1 - 3*;	
	F = 10.34	F = 0.54	1 - 4; 2 - 3;	
			2-4;3-4	

		Lower r	each			Middle r	reach			Upper re	each			
Taxa	Density No. 10m ⁻²	(±1SE)	R	Comp. (%)	Density No. 10m ⁻²	(± 1SE)	R	Comp. (%)	Density No. 10m ⁻²	(±1SE)	R	Comp. (%)	Dominant reach	Habitat association
Gilchristella aestuaria	9.91	(8.70)	2	28.5	6.10	(5.80)	3	12.8	0.25	(0.26)	4	1.0	Lower / Middle	Eelgrass
Rhabdosargus holubi	1.59	(0.69)	5	4.5	0.92	(0.47)	7	1.9	0.10	(0.08)	8	0.4	Lower / Middle	Eelgrass
Atherina breviceps	0.83	(0.40)	6	2.4	0.05	(0.03)	11	0.1	0.01	(0.007)	12	<0.1	Lower	Eelgrass
Glossogobius callidus	0.17	(0.05)	7	0.5	0.27	(0.12)	8	0.6	0.06	(0.04)	9	0.2	Middle / Lower	Eelgrass
Caffrogobius natalensis	0.06	(0.02)	12	0.2	0.04	(0.007)	12	<0.1					Lower / Middle	Eelgrass
Caffrogobius nudiceps	0.07	(0.02)	10	0.2	0.02	(0.008)	13	<0.1					Lower / Middle	Eelgrass
Pomadasys commersonnii	0.14	(0.06)	8	0.4	0.13	(0.05)	10	0.3	0.01	(0.006)	12	<0.1	Lower / Middle	Marsh creek
Mugilidae (< 20 mm)	17.13	(11.30)	1	49.2	15.47	(6.10)	2	32.4	17.20	(6.25)	1	73.1	Even	Marsh creek
Liza dumerilii	2.00	(0.80)	4	5.7	17.04	(3.47)	1	35.6	2.75	(0.89)	2	11.7	Middle	Marsh creek
Psammogobius knysnaensis	2.55	(0.54)	3	7.3	5.35	(2.15)	4	11.2	2.50	(1.30)	3	10.6	Middle	Marsh creek
Liza tricuspidens	0.11	(0.09)	9	0.3	1.01	(0.56)	5	2.1	0.18	(0.06)	6	0.8	Middle	Marsh creek
Mugil cephalus	0.02	(0.01)	13	<0.1	0.96	(0.77)	6	2.0	0.13	(0.10)	7	0.5	Middle / Upper	Marsh creek
Oreochromis mossambicus	0.07	(0.05)	10	0.2	0.25	(0.19)	9	0.5	0.23	(0.10)	5	0.9	Middle / Upper	
Elops machnata	<0.01	(0.005)	14	<0.1					0.04	(0.03)	10	0.2	Upper	
Monodactylus falciformis	<0.01	(0.005)	14	<0.1	<0.01	(0.002)	14	<0.1	0.03	(0.03)	11	0.1	Upper	
Total ichthyofauna	34.77	(10.58)			47.66	(4.40)			23.55	(6.33)				

Table 3.4 Density, rank and percentage composition of the 15 dominant taxa sampled in the three reaches of Taylor's creek for the period January to April 1994. Habitat associations were based on the densities of each species in the creek and adjacent eelgrass habitats (Chapter 4).

Other species: Caffrogobius gilchristi, Myxus capensis, Solea bleekeri, Lithagnathus lithognathus, Diplodus sargus, Clinus superciliosus, Heteromycteris capensis, Omobranchus woodi, Galeichthys feliceps, Terapon jarbua.

		Lower r	each			Middle	each			Upper r	each			
Taxa	Standing st g. 10m ⁻² (ock (± 1SE)	R	Comp. (%)	Standing g. 10m ⁻²	stock (± 1SE)	R	Comp. (%)	Standing s g. 10m ⁻²	tock (± 1SE)	R	Comp. %	Dominant reach	Habitat association
Gilchristella aestuaria	2.70	(2.07)	3	19.9	1.40	(1.29)	6	1.2	0.06	(0.04)	7	1.2	Lower / Middle	Eelgrass
Rhabdosargus holubi	3.06	(1.65)	2	22.6	1.62	(0.68)	4	1.4	0.02	(0.01)	9	0.4	Lower / Middle	Eelgrass
Atherina breviceps	0.55	(0.27)	5	4.1	0.04	(0.03)	13	<0.1	0.01	(0.004)	11	0.1	Lower	Eelgrass
Glossogobius callidus	0.12	(0.05)	11	0.9	0.10	(0.03)	12	0.1	0.01	(0.01)	10	0.2	Lower / Middle	Eelgrass
Caffrogobius natalensis	0.32	(0.17)	7	2.3	0.13	(0.04)	11	0.1					Lower / Middle	Eelgrass
Caffrogobius nudiceps	0.09	(0.05)	12	0.6	0.03	(0.01)	14	<0.1					Lower / Middle	Eelgrass
Caffrogobius gilchristi	0.15	(0.15)	9	1.1	0.01	(0.004)	15	<0.1					Lower	Eelgrass
Pomadasys commersonnii	0.18	(0.08)	8	1.3	0.16	(0.10)	10	0.1	0.02	(0.01)	8	0.4	Lower / Middle	Marsh creek
Mugilidae (< 20 mm)	2.21	(0.87)	4	16.3	1.45	(0.49)	5	1.2	1.34	(0.42)	2	27.2	Even	Marsh creek
Liza dumerilii	3.54	(1.41)	1	26.1	109.02	(51.25)	1	91.0	2.45	(0.76)	1	49.6	Middle	Marsh creek
Psammogobius knysnaensis	0.41	(0.07)	6	3.0	1.09	(0.37)	7	0.9	0.51	(0.25)	3	10.2	Middle	Marsh creek
Liza tricuspidens	0.13	(0.10)	10	0.9	0.79	(0.25)	8	0.7	0.18	(0.06)	5	3.7	Middle	Marsh creek
Mugil cephalus	0.01	(0.004)	14	0.1	1.91	(1.18)	2	1.6	0.25	(0.23)	4	5.0	Middle / Upper	Marsh creek
Oreochromis mossambicus	0.02	(0.01)	13	0.2	0.18	(0.11)	9	0.1	0.08	(0.04)	6	1.7	Middle	-
Galeichthys feliceps					1.83	(1.83)	3	1.5					Middle	-
Total ichthyofauna	13.53	(2.77)			119.76	(52.06)			4.94	(0.79)				

Table 3.5 Standing stock, rank and percentage composition of the 15 dominant taxa sampled in the three reaches of Taylor's creek for the period January to April 1994. Habitat associations were based on the densities of each species in the creek and adjacent eelgrass habitats (Chapter 4).

Other species: Lithognathus lithognathus, Solea bleekeri, Elops machnata, Myxus capensis, Clinus superciliosus, Diplodus sargus, Monodactylus falciformis, Heteromycteris capensis, Omobranchus woodi, Terapon jarbua.

In all three reaches the Mugilidae (< 20 mm) were ranked either first or second in order of importance. G. aestuaria contributed significantly to the ichthyofaunal density in the lower (29%) and middle reaches (13%) while L. dumerilii was important in the middle (36%) and upper reaches (12%). The lower reaches had the highest proportion of eelgrass-associated fishes (36%), with species such as G. aestuaria, R. holubi, A. breviceps, C. natalensis, and C. nudiceps being relatively common. The middle reaches were dominated by L. dumerilii, with other creek-associated species e.g. P. knysnaensis and L. tricuspidens also being important. Eelgrass-associated species (e.g. G. aestuaria and R. holubi) constituted 16% of the ichthyofauna of the middle reach and an insignificant proportion (2%) of the ichthyofauna in the upper reach, which was dominated almost entirely by mugilids.

The overall gravimetric composition of the ichthyofauna caught in Taylor's creek was similar to that recorded in previous years (Chapter 2). The fish biomass was dominated by *L. dumerilii* (84%), followed by *R. holubi* (2.6%), *G. aestuaria* (2.3%), *P. knysnaensis* (1.7%) and *M. cephalus* (1.7%). In all three reaches *L. dumerilii* was ranked by weight as the most important species, contributing over 90% of the fish standing stock in the middle reaches (Table 3.5). In the lower reaches, eelgrass-associated species (e.g. *G. aestuaria*, *R. holubi*, *A. breviceps*) contributed 52% towards the overall standing stock. In the middle and upper reaches the eelgrass-associated species comprised only 3% and 2% of the biomass respectively, with the standing stock of fishes being dominated by the mugilids.

The length frequency histograms (Figures 3.2 and 3.3) of the four numerically dominant species (viz. L. dumerilii, R. holubi, G. aestuaria and P. knysnaensis) indicate that there is considerable variation in the size of fishes utilizing the different reaches of the creek. The estuarine fish species (G. aestuaria and P. knysnaensis), which have a small adult body size, were found to have very similar average lengths and length distributions in each of the three reaches (Figure 3.2). In comparison, the marine species (L. dumerilii and R. holubi) showed marked differences in their average sizes in each of the reaches (Figure 3.3), with the upper reaches being frequented only by small individuals (< 40 mm).



Figure 3.2 Length (SL) frequencies (mm) of *Gilchristella aestuaria* and *Psammogobius* knysnaensis collected in the three reaches of Taylor's intertidal salt marsh creek for the period January to April 1994.



Figure 3.3 Length (SL) frequencies (mm) of *Liza dumerilii* and *Rhabdosargus holubi* collected in the three reaches of Taylor's intertidal salt marsh creek for the period January to April 1994.

Classification and ordination: The dendrogram (Figure 3.4) produced by hierarchical clustering indicated that at the 62% similarity level the January lower and middle reach samples formed a distinct group from the other samples. At the 69% similarity level, the dendrogram and MDS plot exhibit a clear dichotomy in the larger grouping, with the upper reach fish assemblages from each sampling occasion forming a discrete cluster (Figures 3.4 and 3.5).

The superimposition of average depths, salinities, temperatures and turbidities in the different reaches over the MDS plot indicated that average depth was the only likely causal agent influencing the communities associated with the different reaches in Taylor's creek (Figure 3.5).



Figure 3.4 Dendrogram showing classification of 12 fish assemblages from the three reaches of Taylor's intertidal salt marsh creek. The classification used fish density data collected from January to April 1994.



Figure 3.5 a) Multidimensional scaling ordination plot of 12 fish assemblages from the three reaches of Taylor's intertidal salt marsh creek. The plot used fish density data collected from January to April 1994. b) Matching depth data superimposed on each data point of plot 3.5a.

SECTION 2 - THE ICHTHYOFAUNAL DISTRIBUTION WITHIN THE DOMINANT HABITATS OF TAYLOR'S SALT MARSH.

Section 2a - Distribution of fishes in the creek, *Spartina maritima* flats, *Sarcocornia perennis* flats and high marsh pools.

Density and standing stock: The density and standing stock of fishes over the slack high tide was significantly different between the four dominant habitats sampled in Taylor's salt marsh. The Sarcocornia perennis flats had the lowest fish density (3.3 fishes per 10 m²) and standing stock (0.6 g per 10 m²) of all four habitats and these values were significantly lower than those recorded in the creek (Density: Wilcoxon T=0, p<0.001; Standing stock: Wilcoxon T=0, p<0.001). The high marsh pools had a higher fish density (18.3 fishes per 10 m²) than the intertidal creek (11.7 fishes per 10 m²) but this difference was not significant (Wilcoxon T=41, p >0.1). The standing stock of fishes in the high marsh pools (7.5 g per 10 m²) was significantly lower (Wilcoxon T=7, p<0.01) than that recorded in the creek (21.1 g per 10 m²).

Composition: There was a substantial difference in the diversity of fishes in the three habitats. Both the Sarcocornia perennis flats (6 species; 3 families) and the high marsh pools (11 species; 5 families) were utilized by comparatively fewer taxa in comparison to the intertidal creek habitat (39 species; 23 families). In terms of ichthyofaunal density and standing stock (Table 3.6) the Sarcocornia perennis flats were dominated almost entirely by mugilids which comprised > 99% of the total fish density and standing stock. The high marsh pools were also dominated by mugilids which comprised over 96% of the total density and 95% of the standing stock, with L. dumerilii being the dominant species. Although the creek was also dominated numerically and gravimetrically by mugilids, significant contributions by other taxa (e.g. G. aestuaria, A. breviceps, P. knysnaensis and R. holubi) were also recorded (Table 3.6).

Table 3.6 Density, standing stock and their associated ranks and percentage compositions of thefish sampled in the Sarcocornia perennis flats, high marsh pools and intertidal creek for the periodJanuary 1993 to May 1994. Group = Estuarine association group, Table 2.2.

Taxa	Group	Density	SE	R	%	S. stock	SE	R	%
		(No. 10 m ⁻²)	_			(g 10 m ⁻²)			
Sarcocornia flats									
Mugilidae (< 20 mm)	-	2.120	0.869	1	64.7	0.203	0.087	2	35.2
Liza dumerilii	2b	1.112	0.733	2	33.9	0.362	0.220	1	63.0
Myxus capensis	5b	0.021	0.014	3	0.7	0.004	0.003	3	0.7
Mugil cephalus	5b	0.013	0.013	4	0.4	0.003	0.002	4	0.4
Terapon jarbua	2a	0.005	0.003	5	0.1	<0.001	<0.001	7	<0.1
Liza tricuspidens	2b	0.005	0.002	6	0.1	0.002	0.001	5	0.4
Rhabdosargus holubi	2a	0.003	0.002	7	0.1	0.001	<0.001	6	0.2
Total ichthyofauna	-	3.279	1.330	-	100.0	0.576	0.291	-	100.0
High marsh pools									
Mugilidae (< 20 mm)		9.463	1.495	1	51.7	0.735	0.307	3	9.8
Liza dumerilii	2b	7.312	2.529	2	39.9	4.921	2.201	1	65.9
Mugil cephalus	5b	0.572	0.229	3	3.1	1.230	0.601	2	16.5
Psammogobius knysnaensis	la	0.404	0.262	4	2.2	0.318	0.189	4	4.2
Liza tricuspidens	2b	0.231	0.132	5	1.3	0.184	0.102	5	2.4
Rhabdosargus holubi	2a	0.130	0.117	6	0.7	0.035	0.025	6	0.5
Crenimugil crenilabis	2c	0.063	0.049	7	0.4	0.015	0.011	7	0.2
Terapon jarbua	2a	0.050	0.039	8	0.3	0.004	0.003	10	0.1
Myxus capensis	5b	0.034	0.025	9	0.2	0.012	0.009	9	0.2
Elops machnata	2a	0.018	0.012	10	0.1	0.001	0.001	12	<0.1
Liza richardsonii	2c	0.014	0.014	11	<0.1	0.014	0.013	8	0.2
Glossogobius callidus	ІЬ	0.005	0.004	12	<0.1	0.002	0.002	11	<0.1
Total ichthyofauna		18.296	6.70		100.0	7.471	2.947		100.0

Table 3.6 continued

Таха	Group	Density	SE	R	%	S. stock	SE	R	%
	_	(No. 10 m ⁻²)	_		_	(g 10 m ⁻²)			_
Intertidal creek									
Mugilidae (< 20 mm)	-	4.153	0.999	1	35.3	0.264	0.005	7	1.7
Liza dumerilii	2b	3.338	0.818	2	28.4	15.184	6.166	1	70.2
Gilchristella aestuaria	la	1.872	0.808	3	15.9	0.571	0.290	5	2.6
Atherina breviceps	16	0.644	0.200	4	5.4	0.392	0.122	6	1.8
Psammogobius knysnaensis	la	0.563	0.133	5	4.8	0.157	0.073	11	0.7
Liza tricuspidens	2b	0.265	0.102	6	2.3	0.221	0.080	8	1.0
Rhabdosargus holubi	2a	0.238	0.063	7	2.0	1.142	0.566	4	5.2
Mugil cephalus	5b	0.167	0.055	8	1.4	0.193	0.073	10	0.9
Pomadasys commersonnii	2a	0.120	0.059	9	1.0	1.310	0.445	3	6.0
Terapon jarbua	2a	0.109	0.050	10	0.9	0.050	0.030	14	0.2
Glossogobius callidus	lb	0.104	0.035	11	0.9	0.044	0.012	15	0.2
Caffrogobius natalensis	1b	0.037	0.008	12	0.3	0.076	0.002	13	0.3
Diplodus sargus	2c	0.022	0.009	13	0.2	0.031	0.015	16	0.1
Pomadasys olivaceum	3	0.017	0.006	14	0.1	0.105	0.033	12	0.5
Monodactylus falciformis	2a	0.016	0.014	15	0.1	0.007	0.006	18	<0.1
Total ichthyofauna		11.747	1.81	-		21.160	6.108	-	

Other intertidal creek species: Myxus capensis, Solea bleekeri, Liza richardsonii, Sarpa salpa, Oreochromis mossambicus, Rhabdosargus globiceps, Crenimugil crenilabis, Caffrogobius nudiceps, Caffrogobius gilchristi, Diplodus cervinus, Elops machnata, Clinus superciliosus, Syngnathus acus, Ambassis gymnocephalus, Periopthalmus sobrinus, Lichia amia, Arothron hispidus, Pomatomus saltatrix, Ophisurus serpens, Lithognathus lithognathus, Omobranchus woodi, Saurida gracilis, Gobiopsis pinto, Monodactylus argenteus, Heteromycteris capensis.

The life-history stages of the numerically dominant species caught in the high marsh pools and *Sarcocornia perennis* habitats were mainly 0+ juveniles (Table 3.7). The creek ichthyofauna was also dominated by 0+ juveniles but the adults of a number of estuarine and marine species (e.g. *G. aestuaria*, *A. breviceps*, *P. knysnaensis*, *G. callidus*, *C. natalensis*, *C. gilchristi*, *C. nudiceps* and *L. richardsonii*) were also recorded (Chapter 2). The mean standard lengths of many of the common species (e.g. *R. holubi*) were also greater in the creek habitat (\bar{x} =23.4 mm) than in either the *Sarcocornia perennis* or the high marsh pool habitats (\bar{x} =12.0 mm).

Table 3.7 Mean lengths, standard deviations, length ranges and dominant life-history stages of the dominant fish taxa caught in the *Sarcocornia perennis* flats and high marsh pools for the period January 1993 to May 1994.

Таха	Number	Measured	Mean length (mm)	SD	Range (mm)	Life-history stage
Sarcocornia perennis flats						
Mugilidae (< 20 mm)	660	428	11.3	3.3	6.0 - 19.9	Juveniles
Liza dumerilii	279	279	26.6	9.7	20.0 - 76.5	Juveniles
Myxus capensis	9	9	22.5	3.2	10.0 - 28.1	Juveniles
High marsh pools						
Mugilidae (<20 mm)	1968	718	13.3	3.3	6.4 - 19.9	Juveniles
Liza dumerilii	1392	887	26.5	7.7	20.0 - 93.0	Juveniles
Mugil cephalus	104	104	38.1	15.0	20.0 - 73.6	Juveniles
Psammogobius knysnaensis	65	65	32.6	6.2	20.0 - 45.2	Juveniles / Adults
Liza tricuspidens	50	50	32.5	5.2	21.8 - 40.3	Juveniles
Rhabdosargus holubi	27	27	12.0	3.8	9.5 - 30.0	Juveniles

Section 2b - Distribution of fishes in the Spartina maritima habitat.

Density and standing stock: During this study only 16 individuals were caught in the Spartina maritima. Average fish density was 0.31 fishes per 10 m^2 (Table 3.8), ranging between 0 and 1.05 fishes per 10 m^2 . Similarly, the average standing stock of fishes in the Spartina maritima habitat was very low (0.33 g per 10 m^2) and ranged between 0 and 2.9 g per 10 m^2 .

Composition: Six species from three families were sampled (Table 3.8) with the Mugilidae accounting for over 60% of the numbers caught. The Gobiidae were the most species rich family, with four species. The mugilids and the single R. holubi were all juvenile fishes while the gobies were adults (Table 3.8).

	Density (No. 10 m ⁻²)	SD	S. stock (g. 10 m ⁻²)	SD	Length range (mm)
Mugilidae (< 20 mm)	0.14	0.25	0.006	0.009	10 - 17
Psammogobius knysnaensis	0.04	0.10	0.001	0.005	25
Glossogobius callidus	0.03	0.10	0.038	0.132	34
Caffrogobius nudiceps	0.03	0.10	0.145	0.500	57
Caffrogobius natalensis	0.03	0.10	0.090	0.310	48
Myxus capensis	0.03	0.10	0.005	0.021	21 - 22
Rhabdosargus holubi	0.01	0.04	0.050	0.170	49
Total ichthyofauna	0.31		0.335		

Table 3.8 Density, standing stock and length ranges of fish taxa sampled on the *Spartina maritima* flats of Taylor's salt marsh in May, June, November and December 1995.

3.4 DISCUSSION

THE ICHTHYOFAUNAL DISTRIBUTION WITHIN TAYLOR'S INTERTIDAL SALT MARSH CREEK.

Taylor's creek is relatively short in length with minor differences in topography and channel form between the three reaches. While the structural differences between the reaches are subtle, similarity analyses consistently revealed that the fish communities differed between the reaches. The ichthyofaunal differences were also apparent at the species level, with individual species standing stocks and densities varying markedly between reaches. Although there were no significant differences in overall fish density between the three reaches, the upper section was found to have the lowest densities. In contrast, Weinstein (1979) found that young fishes and macro-invertebrates were concentrated in the upper reaches of tidal creeks in the Cape Fear River, North Carolina and it was hypothesised that marsh creeks 'fill up backwards' during recruitment. At the species level Haplin (1997) demonstrated that *Fundulus heteroclitus* was concentrated in the upper reaches of intertidal creeks in New England.

Factors influencing habitat choice or microhabitat use by fishes are difficult to identify. Most of these factors are interactive and the relative importance of one factor compared to another is often difficult to quantify. The habitat that a fish selects is presumably in response to factors which will optimise its nett energy gain, while avoiding predators and minimizing interactions with competitors (Baltz et al. 1993). These factors are in turn influenced by a variety of abiotic and biotic parameters such as water temperature, salinity, turbidity, depth, water currents, substratum characteristics and vegetation cover, to name but a few. In this study water temperature, salinity and turbidity were not found to differ significantly between reaches (Table 3.2) and are therefore unlikely to have been the causal agents for the different fish assemblages, individual species densities and standing stocks associated with the three reaches. However, the average depth in the three reaches did show significant differences. This, in combination with the simple but effective superimposition 'Field plots', demonstrates that water depth may be important in influencing the ichthyofaunal assemblages. The level of inundation, hydroperiod and surface elevation have all been highlighted as very important factors in regulating nekton utilization of salt marshes (Rozas & Reed 1993, Rozas 1995). Recent studies (Minello & Webb 1997) using multiple regression models to examine the relationships between nekton densities on the marsh surface and environmental factors also found that the most important factors were water depth and annual tidal flooding periods.

A spatial cline was exhibited in this study with the density and standing stock of fishes which were abundant in the adjacent eelgrass beds (e.g. *R. holubi* and *A. breviceps*) being concentrated in the lower and middle reaches of the intertidal creek, whereas the common creek species (e.g. *L. dumerilii* and *P. knysnaensis*) were concentrated predominantly in the middle, and/or upper reaches (Tables 3.4 and 3.5). One hypothesis which might explain why the eelgrass-associated species are restricted to the lower reaches of the creek is that these species are not adapted to the clear, unvegetated, shallow conditions associated with the upper reaches and therefore do not stray far from their preferred vegetated habitat into an environment where they may be susceptible to predation. In contrast, the dominant creek-associated species which were found in the upper reaches of the creek are either highly camouflaged (*P. knysnaensis*) or they school (mugilids) and are therefore able to make use of the unvegetated creek.

Tidal creeks are the launching points for nekton that use the marsh surface and thus they influence the ichthyofaunal composition of the marsh (Rozas & Odum 1987a). Studies have shown that in salt marshes and tidal freshwater marshes the nature of the creek (e.g. depth, presence or absence of vegetation and stream order) have an effect on the ichthyofauna utilizing the bordering salt marsh vegetation (Rozas & Odum 1987a,b, McIvor & Odum 1988, Hettler 1989). This study has shown that the separate reaches of a single salt marsh intertidal creek have different fish assemblages and are frequented by different sizes of marine fishes. What is of particular importance is that these differences were found in a creek which is relatively short, has minor topographical differences and small, albeit significant, depth changes.

THE ICHTHYOFAUNAL DISTRIBUTION WITHIN THE DOMINANT HABITATS OF TAYLOR'S SALT MARSH.

Considerable differences were found in the densities and standing stocks of fishes utilizing the different habitats within Taylor's salt marsh. In general, fish densities, standing stocks and diversity were far higher in the creek in comparison to other habitats, with the fishes seldom utilizing the higher lying intertidal vegetated areas. These differences were greatest between the creek and Spartina maritima flats, with the creek habitat being frequented by six times the numbers of species and an order of magnitude more fish. The relative importance of the vegetated salt marsh habitats is put into perspective when the distribution of fishes over the entire marsh is examined at the slack high tide and on average 91% of the numbers and 98% of the biomass of fishes are recorded in the creek. The fact that the Spartina maritima and Sarcocornia perennis habitats are in general only inundated over spring high tides, and then only for short periods, further illustrates the importance of the creek habitat to the ichthyofauna that frequent the salt marsh as a whole. In contrast to this study, research on North American vegetated tidal marsh flats, in particular Spartina alterniflora, have shown that this habitat is utilized by fishes (Zimmerman & Minello 1984, Stout 1984, Talbot & Able 1984, Hettler 1989, Rakocinski et al. 1992, Baltz et al. 1993, Rozas & Reed 1993, Knieb & Wagner 1994, Peterson & Turner 1994, Knieb 1997a,b). In general the interior of tidal marshes are used primarily by resident fishes while the marsh edge is used by resident and transient species (Peterson & Turner 1994, Knieb 1997b). Hettler (1989) reported that in the regularly flooded cord grass marshes of North Carolina approximately 50% of the species from adjacent estuarine areas were caught in the Spartina alterniflora beds within that system. Unlike many of the North American marsh systems the fish species caught in the vegetated reaches of Taylor's salt marsh were almost exclusively marine transient species. In addition, less than 20% of the fish species caught in Taylor's creek, let alone the adjacent estuarine channel, were caught in the vegetated salt marsh flats.

The vegetated salt marsh flats in many North American estuaries are frequented by juvenile fishes, probably due to the shallow and vegetated nature of the habitat, with these two attributes providing protection against predators as well as a food rich environment (Baltz *et al.* 1993). Field studies have demonstrated the importance of the flooded intertidal marsh surface as an energy source to *Fundulus heteroclitus* (Weisberg & Lotrich 1982). Knieb (1987) indicated that predation is a causal factor in habitat choice by young killifish, with juvenile fish remaining in the high intertidal habitats, thus avoiding concentrations of larger piscivorous fishes in the subtidal regions. Vegetated habitats in estuaries (e.g. eelgrass beds) have been shown to harbour higher densities of juvenile fishes in comparison to unvegetated areas. This has been attributed to a range of mechanisms including habitat complexity, increased food supplies and prey refugia (Orth 1992). Similarly, Rozas & Odum (1988) demonstrated that food availability is higher and predation pressure is lower in vegetated compared to unvegetated areas in tidal freshwater creeks.

The factors responsible for the minimal utilization of the vegetated areas of Taylor's salt marsh by fishes are probably linked primarily to the distribution of predators and hydroperiod within the salt marsh. None of the common piscivorous fishes found in Eastern Cape estuaries (e.g. *Lichia amia, Elops machnata* or *Argyrosomus japonicus*) were caught in Taylor's creek and the creek ichthyofauna was dominated by zooplanktivores and detritivores (Chapter 7). Consequently one of the incentives for small fishes to move into a shallow water vegetated refuge is absent and may even lead to higher mortalities due to the increased chance of stranding or avian predation. In comparison to *Spartina alterniflora*, which grows up to 1m in height and has broad blades, *Spartina maritima* provides far less cover for fishes as it is less dense and complex due to its shorter height and rolled blade formation (Goodman 1958). In addition, the Kariega Estuary also has large tracts of *Zostera capensis* which are extensively used by fishes (Chapter 4), thus fulfilling any vegetated habitat requirements by particular species. Hydroperiod is very important in the functioning of tidal marshes. It directly affects the nekton use of the marsh surface by controlling access to the habitat and may also indirectly affect habitat use through its influence on marsh vegetation and the prey of fishes (Rozas 1995). Regional differences in fish utilization of salt marshes along the American Gulf coast compared to those along the south east coast of North America are thought to be a function of hydroperiod, with the duration of flooding appearing to be more important than the predictability (Rozas 1995). The S. maritima and S. perennis habitats in Taylor's salt marsh are inundated for short periods of time only over the high spring tides (Taylor & Allanson 1995). This inundation period is considerably less than reported for many S. alterniflora marshes which may be inundated during 95% of flood tides (Eleuterius & Eleuterius 1979, Rozas & Reed 1993). The irregularity and shortness in duration of flooding of the vegetated marsh habitats in the Kariega Estuary, in comparison to many North American systems, is partly due to S. alterniflora extending further down the tidal profile than S. maritima and S. perennis (Goodman 1958, Eleuterius & Eleuterius 1979, Pierce 1979, McKee & Patrick 1988, O' Callaghan 1994). The overall possible benefits of fish frequenting the vegetated habitats in Taylor's salt marsh are probably outweighed by factors such as risk of stranding, increased bird predation and the lack of suitable food resources. Similarly, the low fish densities of fishes caught on the vegetated salt marsh flats in Australian (Connolly et al. in press) and European salt marshes (Cattrijsse et al. 1994, Knieb 1997b) are also thought to be due to the short periods of inundation.

While water depth and period of inundation may be important factors in the structuring of marsh nekton, North American high marshes, which are irregularly flooded, have also been shown to be used by marsh resident fishes (Stout 1984, Talbot & Able 1984). Killifish have also been shown to be unconstrained by shallow water and actively move with the tidal front from *S. alterniflora* marshes into higher *Distichlis spicata* marshes as they become accessible later in the tidal cycle (Rozas & Reed 1993). In contrast, there is no evidence that fishes actively seek out the vegetated surfaces in the Kariega salt marshes.

The densities of fishes found in the high marsh pools was greater than that found in the intertidal creek, whereas the standing stock was an order of magnitude less. The higher densities of fishes in the high marsh pools is difficult to explain but could be due to fishes concentrating in these
pools to avoid stranding once the tide recedes. The fishes in the high marsh pools were dominated by marine transient species, which is in contrast to most other studies in this type of habitat where the ichthyofaunal communities were dominated by marsh resident species (Knieb 1997b). This dominance by marine transient species in Taylor's high salt marsh pools is probably linked to these pools drying up at regular intervals and consequently being unable to sustain a fish community for any length of time.

Permanently resident marsh fishes are an important component of the ichthyofauna associated with salt marshes in North America (Peterson & Turner 1994, Knieb 1997a,b). Inspections of the Kariega salt marshes at low tide indicate that there is no obvious resident fish fauna. The reason for this is that there is very little standing water in the Kariega salt marshes to act as a refuge over the low tide period. Unlike many North American tidal marsh systems where shallow subtidal creeks are utilized as low tide refuges, the intertidal creeks found in the Kariega salt marshes drain fully. Furthermore, the Kariega vegetated salt marsh flats are at a higher elevation (Taylor 1987, O' Callaghan 1994) than some of the dominant vegetated flats (e.g. *S. maritima*) found in North American systems (McKee & Patrick 1988) and in contrast to these systems there is very little standing water in the vegetation at low tide. The short hydroperiod associated with the elevation of the Kariega marshes results in few aquatic microhabitats which can act as refuges over the low tide. Thus the ichthyofauna that utilize the salt marshes are marine transients or estuarine species which only move into the marsh and its intertidal creek over the high tide.

Of the five different classes of fish that utilize South African estuaries, only species from the estuarine group (Table 2.2) would have the potential to be permanent marsh residents. However, the life-history traits of the dominant estuarine species which were caught in Taylor's intertidal salt marsh, creek e.g. *G. aestuaria*, *P. knysnaensis*, *C. gilchristi*, *C. nudiceps* and *C. natalensis*, preclude them from spending their entire lives on a salt marsh. The gobies have a marine larval stage and *G. aestuaria* spawns in the water column in the upper reaches of estuaries (Whitfield 1998).

Peterson & Turner (1994) formulated a four tier system to categorise fishes in a Louisiana salt marsh. The four categories included interior marsh residents, interior marsh users, edge marsh

users and a marsh subtidal group. The vast majority of fishes which were caught in Taylor's salt marsh fit into the latter two categories, with no fish exhibiting the characteristics or distribution patterns that would classify them as interior marsh residents or interior marsh users. The above system is not applicable to the salt marshes studied in the Kariega Estuary. A system which places more emphasis on the transient fish fauna and the unvegetated, more regularly inundated intertidal creek would be better suited to marshes where little utilization is made of the vegetated habitats by fishes and there are few marsh residents. A preliminary classification system for the fishes that frequent salt marshes in the Kariega Estuary could be divided into the following categories:

(1) General creek species	Fish that are found along the entire length of the intertidal creek.
	a) Restricted to the intertidal creek (e.g. P. knysnaensis).
	b) Caught in the intertidal creek and occasionally over the vegetated salt marsh flats
	(e.g. Mugilidae < 20 mm, L. dumerilii).
(2) Lower creek species	Fish that are found predominantly in the lower reaches of the intertidal creek.
	a) Restricted to the intertidal creek (e.g. A. breviceps).
	b) Caught in the intertidal creek and occasionally over the vegetated salt marsh flats
	(e.g. R. holubi).
(3) Upper creek species	Fish that are found predominantly in the upper reaches of the intertidal creek.
	a) Restricted to the intertidal creek (e.g. E. machnata, M. falciformis).
	b) Caught in the intertidal creek and occasionally over the vegetated salt marsh flats
	(e.g. M. cephalus).

Chapter 4

Ichthyofauna associated with Taylor's intertidal salt marsh creek and the adjacent eelgrass beds

4.1 INTRODUCTION

Seagrasses and salt marshes act as nursery areas for fishes (Adams 1976a, Cain & Dean 1976, Shenker & Dean 1979, Bozeman & Dean 1980, Pollard 1984, Smith *et al.* 1984, Bell & Pollard 1989, Chamberlain & Barnhart 1993, Knieb 1997b). Most of these studies have, however, been restricted to a single habitat and very few have compared the ichthyofaunal utilization of different habitats within the same estuary. Comparative research between seagrass and unvegetated areas (Bell & Pollard 1989, Heck *et al.* 1989, Ferell & Bell 1991, Connolly 1994a, West & King 1996) has shown that, in general, seagrass habitats have a greater diversity and abundance of nekton than unvegetated sites. Research comparing the fish assemblages of seagrass and tidal creeks has demonstrated that eelgrass beds usually have a far higher diversity and richness of fishes than tidal creeks. In contrast, tidal creeks have higher overall densities of fishes than seagrass beds. However, these higher densities were attributed to very high numbers of only one or two species (Weinstein & Brooks 1983, Sogard & Able 1991).

Within southern Africa, estuarine ichthyological research has shown that Zostera capensis habitats are utilized extensively by juvenile fishes (Beckley 1983). Comparative ichthyofaunal studies have been limited to Zostera and non-Zostera habitat comparisons (Branch & Grindley 1979, Hanekom & Baird 1984, Whitfield 1988) and Zostera associated ichthyofaunal distributional studies within (Ter Morshuizen & Whitfield 1994) and between estuarine systems (Whitfield *et al.* 1989). Research on the fish utilization of salt marshes and their tidal creeks has been confined to Paterson & Whitfield (1996), which indicated that intertidal salt marsh creeks are, as with eelgrass beds, dominated by juvenile marine and estuarine fishes.

In order to ascertain the relative importance of salt marsh creeks as an intertidal habitat for fishes in the Kariega Estuary it is necessary to establish whether this habitat is utilized by a distinct ichthyofaunal assemblage in comparison to the other dominant intertidal habitat in the estuary *viz*. eelgrass. In particular this chapter aims to ascertain whether:

- Taylor's intertidal salt marsh creek and adjacent eelgrass beds have distinct fish compositions.
- Taylor's intertidal salt marsh creek supports a similar density, biomass and diversity of fishes as the adjacent eelgrass beds.

4.2 MATERIALS AND METHODS

SAMPLING PERIODICITY

Samples were collected from August 1992 to May 1994. The sampling periodicity followed that of Chapter 2 except that no eelgrass beds were sampled during the first sampling session in winter 1992.

FIELD SAMPLING

Comparative research between two habitats should ideally utilize a sampling protocol which accurately measures the parameter in question in each region. The majority of sampling designs in comparative ichthyofaunal community studies use the same sampling apparatus in each habitat to reduce species and size selectivity differences between gears. This approach relies on the premise that the gear operates with the same efficiency within both habitats. The unsuitability, due to varying topography, narrow channels, shallow water and high water clarity, of Taylor's creek to sub-sampling techniques such as seine netting and lift traps resulted in a block net being used. Block netting has been used in other salt marsh creek studies (Cain & Dean 1976, Bozeman & Dean 1980) and was found to be the most suitable sampling option available for the very singular characteristics of Taylor's intertidal creek. This technique, which negates the need for subsampling as all the fishes are sampled, avoids problems faced by other procedures such as size and species selectivity, net avoidance and variable towing speeds. Taylor's creek is also ideally suited to block netting as it has only one opening and drains fully at low tide. Block netting was impractical in the adjacent eelgrass beds whereas seine netting has been utilized in numerous South African eelgrass studies (e.g. Beckley 1983, Whitfield et al. 1989). Comparative research into the sampling selectivity of seine and pop nets in eelgrass beds has indicated that seine nets may under sample some species closely associated with the substratum (Connolly 1994b). To counteract this selectivity, the seine net was fitted with a heavily weighted bottom line and spreader poles in order to keep the net from lifting off the bottom. To further reduce the size and species selectivity of the different gears, the seine and block net were constructed from the same netting.

At slack high tide the block net was set across the mouth of the creek (See Materials & Methods Chapter 2) and immediately afterwards the adjoining eelgrass beds were seined. A total of four sites (Figure 4.1) were seined using a 5 m long, 2.5 m deep seine net with a 2.5 mm stretch mesh. The section of eelgrass bed sampled was calculated after each haul with approximately the same area (45 m²) being sampled on each occasion.

Selected physical and chemical parameters were recorded on the high tide at four fixed locations in the creek and at the four seine net stations (Figure 4.1). Water temperature (°C) was measured *in situ* and water samples were collected so that salinity and turbidity (NTU) could be measured in the laboratory using an optical salinometer and turbidimeter.

SAMPLE ANALYSIS

Sample analysis follows that of Chapter 2.

DATA ANALYSIS

Density and standing stock: Fish density and standing stock were calculated by dividing the total number and mass respectively of each species by the area sampled. The area used in the calculation of fish density and standing stock in the creek was that of the unvegetated intertidal creek and not the whole area of inundated marsh. The results of Chapter 3 indicate that on average over 90% of the fishes in the salt marsh are found in the intertidal creek and not on the vegetated flats at slack high tide. A Wilcoxon test (Fowler & Cohen 1993) was undertaken to determine whether there was a significant difference between the density and the standing stock of the ichthyofauna found in the creek compared to that of the adjacent eelgrass beds.

Ichthyofaunal composition: The dominant ichthyofauna utilizing the creek and eelgrass beds were determined as follows. All samples were pooled and the total density, standing stock and percentage frequency of occurrence of each species were ranked. The sum of these three ranks was then ranked to establish which taxa were the most dominant. The estuarine association categories (Table 2.2) assigned to each of the species found in both habitats conform to those proposed by Whitfield (1994b). The percentage, both in terms of density and standing stock, that each estuarine association category made to the total ichthyofauna of each habitat was calculated.

Seasonality: In all seasonal analyses the dawn and dusk samples were pooled for each season. Total fish density and standing stock was calculated per season per habitat. The Shannon-Wiener species diversity index (H') and Pielou's evenness index (J') (Washington 1984) were calculated on a seasonal basis, using confirmed species only, for both the creek and adjacent eelgrass bed fish assemblages.

Classification and ordination: The mean ichthyofaunal density data collected in the salt marsh creek and eelgrass beds (n=30 samples) was root-root transformed. Root-root transformation, as with the log transformation, has the effect of scaling down the scores of abundant species so that they do not swamp the other data, which is desirable for density and biomass data (Field et al. 1982). In addition, the root-root transformation is advantageous in that when similarity is assessed using the Bray-Curtis measure, the similarity coefficient is invariant to a scale change (Field et al. 1982). An association matrix was produced using the Bray-Curtis similarity measure, from which classification and ordination procedures were conducted. The similarity matrix was classified using hierarchical agglomerative clustering with group average linking, while ordination used multidimensional scaling (MDS) techniques (Clarke & Warwick 1994). In order to establish the species responsible for the patterns observed in the ordination and classification, a similarity percentage breakdown (SIMPER) was conducted. This procedure involves computing the average dissimilarity δ between all pairs of inter-group samples (i.e. every sample in the eelgrass paired with every sample in the creek) and then breaking this average down into the separate contributions from each species to this dissimilarity (Clarke & Warwick 1994). All classification and ordination procedures were carried out using the PRIMER 4.0 package.



Figure 4.1 Map of Taylor's salt marsh showing the block net and eelgrass sampling sites.

4.3 RESULTS

Physico-chemical parameters: Seasonal trends were typical with the highest temperatures occurring in the summer months in both habitats (Figure 4.2). The average water temperature in the eelgrass (mean=18.6 °C, SD=3.02) was almost identical to that of the creek (mean=18.4 °C, SD=3.3) and the temperature profiles (Figure 4.2) mirrored one another. Seasonal trends were not discernible in the salinities of either habitat and the average salinity of the eelgrass habitat (mean=34.6, SD=1.0) was identical to that of the creek (mean=34.6, SD=0.8) (Figure 4.2). Seasonal trends in turbidity were not apparent in either the eelgrass or creek environments (Figure 4.2). The average turbidity in the eelgrass (mean=9.4 NTU, SD=3.9) was essentially the same as the intertidal creek (mean=10.1 NTU, SD=3.9).



Figure 4.2 Physico-chemical water parameters sampled in Taylor's intertidal salt marsh creek and adjacent eelgrass beds between August 1992 and May 1994. Variance between water sampling sites in each habitat was very low and is thus not indicated.

Ichthyofaunal density and standing stock: A total of 17 606 individuals were caught in the eelgrass beds while 60 415 were caught in the intertidal creek. The average density of fishes in the eelgrass (65.5 per 10 m², SD=56.0) was substantially higher than that of the intertidal creek (15.4 per 10 m², SD=8.2). There was a significant difference between the median fish densities of the eelgrass and intertidal creek habitats (Wilcoxon test, T=0, P<0.01). Seasonal trends in the densities of fishes in the eelgrass were far more apparent than in the creek (Figure 4.3). The eelgrass habitat showed a clear pattern, with the highest densities of fishes occurring in spring and summer, with considerably lower densities being recorded in winter. Only in the second year of sampling were there any clear seasonal trends in the density of fishes in the creek, with an increase in fish density in spring and summer (Figure 4.3).



Figure 4.3 Mean seasonal fish densities (number per 10 m^2) in Taylor's intertidal salt marsh creek and adjacent eelgrass beds between winter 1992 and autumn 1994. Eelgrass error bars indicate one standard error (n=8).

The total mass of fishes caught in the eelgrass beds was 14.4 kg while 100.1 kg was caught in the creek. The standing stock of fishes, as with density, was higher in the eelgrass (47.8 g per 10 m², SD=28.3) compared to the intertidal creek (25.6 g per 10 m², SD=25.4). There was a significant difference between the median fish standing stock in the eelgrass and creek habitats (Wilcoxon test, T=22, P<0.05). Seasonal trends in the standing stock of fishes in the eelgrass and creek habitats were indistinct (Figure 4.4).



Figure 4.4 Mean seasonal standing stock (grams per 10 m^2) of fishes in Taylor's intertidal salt marsh creek and adjacent eelgrass beds between winter 1992 and autumn 1994. Eelgrass error bars indicate one standard error (n=8).

Ichthyofaunal community composition: A similar number of species were caught in the eelgrass (38 species) and creek habitats (41 species). The dominant taxa in each region, using the ranking index (Table 4.1), differed, with the five dominant species in the eelgrass being *Rhabdosargus holubi*, *Atherina breviceps*, *Caffrogobius natalensis*, *Gilchristella aestuaria* and *Glossogobius callidus*. The creek was dominated by *Liza dumerilii*, Mugilidae (< 20 mm), *Mugil cephalus*, *R. holubi* and *G. aestuaria* (Table 4.1). In both habitats there were only a few species which were both numerically and gravimetrically dominant, with *L. dumerilii* being the most abundant in the creek and *R. holubi* in the eelgrass.

The fish assemblages in the two habitats were dominated by different ichthyofaunal families (Figure 4.5). The eelgrass was dominated by the Sparidae, Clupeidae, Atherinidae and Gobiidae, with the Mugilidae contributing insignificantly to the fish community. Conversely the creek was dominated by the Mugilidae, with the Clupeidae, Sparidae, Atherinidae and Gobiidae being less important (Figure 4.5).



Figure 4.5 Dominant fish families, calculated using density data, found in Taylor's intertidal salt marsh creek and adjacent eelgrass beds between August 1992 and May 1994.

Table 4.1 The fifteen dominant fish taxa and their number per 10 m^2 , percentage of total number, mass per 10 m^2 , percentage of total mass and frequency of occurence in both Taylor's intertidal salt marsh creek and adjacent eelgrass beds for the period August 1992 to May 1994. Groups correspond to estuarine association categories (see Table 2.2).

Taxa	Group	Overall rank	Ave. number per 10 m ²	%	Ave. mass (g) per 10 m ²	%	Frequency of occurence
Intertidal creek							
Liza dumerilii	2b	1	3.7	24.0	17.6	68.9	100.0
Mugilidae (< 20 mm)	-	2	5.0	32.7	0.4	1.5	100.0
Mugil cephalus	5b	3	1.5	9.7	1.5	5.8	86.6
Rhabdosargus holubi	2a	3	0.4	2.3	1.0	3.8	100.0
Gilchristella aestuaria	la	5	2.0	13.1	0.6	2.4	86.6
Atherina breviceps	16	6	0.6	3.6	0.3	1.3	93.3
Psammogobius knysnaensis	la	7	0.5	3.4	0.2	0.7	93.3
Pomadasys commersonnil	2a	7	0.1	0.6	1.1	4.3	86.6
Glossogobius callidus	1b	9	0.1	0.6	<0.1	0.2	100.0
Liza tricuspidens	2b	10	0.2	1.4	0.2	0.8	66.6

Taxa	Group	Overall rank	Ave. number per 10 m ²	%	Ave. mass (g) per 10 m²	%	Frequency of occurence
Table 4.1 continued							
Diplodus sargus	2c	11	0.9	6.0	0.1	0.2	66.6
Liza richardsonii	2c	12	<0.1	0.1	2.2	8.5	60.0
Caffrogobius natalensis	1b	12	<0.1	0.2	0.1	0.2	86.6
Myxus capensis	Sb	14	<0.1	0.2	0.2	0.7	66.6
Terapon jarbua	2a	15	0.1	0.6	<0.1	0.2	73.3
Adjacent eelgrass beds							
Rhabdosargus holubi	2a	1	26.0	39.6	22.5	47.0	100.0
Atherina breviceps	1b	2	9.7	14.8	6.0	12.4	100.0
Caffrogobius natalensis	1b	3	2.4	3.7	2.4	5.0	100.0
Gilchristella aestuaria	Ia	4	18.5	28.2	5.9	12.3	93.3
Glossogobius callidus	1b	5	1.7	2.6	1.2	2.6	100.0
Caffrogobius gilchristi	1b	6	1.7	2.6	2.0	4.4	93.3
Caffrogobius nudiceps	1b	7	0.5	0.7	1.3	2.8	93.3
Diplodus sargus	2c	8	1.0	1.5	0.4	0.8	93.3
Syngnathus acus	1b	9	0.5	0.7	0.4	0.8	93.3
Mugilidae (< 20 mm)	-	10	1.3	1.9	0.1	0.1	100.0
Clinus superciliosus	1b	10	0.4	0.6	1.1	2.4	80.0
Pomadasys olivaceum	3	12	0.1	0.2	0.5	1.1	86.6
Monodactylus falciformis	2a	13	0.1	0.2	0.1	0.2	66.6
Siganus sutor	3	14	0.3	0.5	0.3	0.7	20.0
Solea bleekeri	2b	14	0.1	0.1	0.2	0.4	60.0

Remaining creek fish species and ranks: Pomadasys olivaceum 16; Solea bleekeri 17; Rhabdosargus globiceps 17; Monodactylus falciformis 19; Caffrogobius gilchristi 20; Caffrogobius nudiceps 21; Diplodus cervinus 22; Lithognathus lithognathus 23; Oreochromis mossambicus 24; Sarpa salpa 25; Crenimugil crenilabis 26; Clinus superciliosus 27; Lichia amia 28; Elops machnata 29; Syngnathus acus 30; Ophisurus serpens 30; Periophthalmus sobrinus 32; Gobiopsis pinto 33; Pomatomus saltatrix 34; Arothron hispidus 35; Saurida gracilis 35; Omobranchus woodi 37; Monodactylus argenteus 38; Lactoria fornasini 39; Heteromycteris capensis 40; Ambassis gymnocephalus 41.

Remaining eelgrass fish species and ranks: Diplodus cervinus 16; Saurida gracilis 17; Mugil cephalus 17; Pomatomus saltatrix 19; Pomadasys commersonnii 20; Liza dumerilii 21; Torpedo fuscomaculata 22; Sarpa salpa 22; Rhabdosargus globiceps 24; Psammogobius knysnaensis 25; Stephanolepis auratus 26; Arothron hispidus 27; Heteromycteris capensis 28; Lactoria diaphana 29; Amblyrhynchotes honckenii 30; Pervagor janthinosoma 31; Terapon jarbua 32; Caffrogobius caffer 33; Myxus capensis 34; Elops machnata 35; Lithognathus mormyrus 36; Engraulis japonicus 37; Argyrosomus japonicus 38; Liza richardsonii 39.

The percentage contributions made by the fish species of the various estuarine association categories (Table 2.2) differed between the eelgrass and creek habitats (Figure 4.6). In terms of density, the creek was dominated by marine species, although the estuarine and catadromous

species were also important. In contrast, the eelgrass was dominated by estuarine species with the only other significant group of fish being the marine species. When analysing the estuary association categories in the different habitats using the standing stock of fishes, the dominant category was the marine species in both the creek and the eelgrass habitats. The creek was however overwhelmingly dominated by marine fishes, whereas the eelgrass also had a significant estuarine fish standing stock (Figure 4.6).



Figure 4.6 Estuarine association categories for the ichthyofauna assemblages associated with Taylor's intertidal salt marsh creek and adjacent eelgrass beds for the period August 1992 to May 1994.

The overall diversity of fishes in the eelgrass and creek was similar, with the eelgrass assemblage having a slightly higher diversity (mean Shannon-Wiener index=1.53, SD=0.39) than the creek (mean Shannon-Wiener index=1.43, SD=0.39). Seasonal patterns in fish diversity were reversed (Figure 4.7) with the highest fish diversity and evenness in the intertidal creek occurring in summer and decreasing in winter. In contrast, diversity and evenness in the eelgrass was highest in autumn and winter, with a lower diversity in summer (Figure 4.7).



Seasons (1992 - 1994)

Figure 4.7 Seasonal diversity (Shannon-Wiener) and evenness (Pielou) indices for the fish communities associated with Taylor's intertidal salt marsh creek and adjacent eelgrass beds from winter 1992 to autumn 1994.

The ichthyofaunal communities in both the eelgrass and intertidal creek habitats were dominated by juvenile fishes (Table 4.2), with the same numerically dominant species in each habitat having similar average lengths (Table 4.2). In the eelgrass ichthyofaunal community all the adult fishes were estuarine species. Similarly in the intertidal creek ichthyofaunal assemblage the majority of the adult fishes were estuarine species but adult mullet were also recorded (Table 4.2).

Classification and ordination: Classification of the fish samples collected in both the eelgrass and creek habitats, using the mean densities of each species, resulted in all samples being separated according to those obtained in the creek and those collected in the eelgrass, indicating that the two fish communities were very distinct (Figure 4.8). The MDS ordination results complemented those of the classification with two very clear groups being identified (Figure 4.9). The ANOSIM (Analysis of Similarity) test showed a significant difference (R=0.974, P<0.001) between the eelgrass and creek groupings. The best discriminating species resulting in the two groupings were R. holubi, L. dumerilii, G. aestuaria, A. breviceps, C. gilchristi and S. acus (Table 4.3).

Table 4.2 Average length, standard deviation, range and life-history stages of the fifteen dominant fish taxa in both Taylor's intertidal salt marsh creek and adjacent eelgrass beds for the period August 1992 to May 1994.

Таха	Overall rank	Number	Measured	Average length	SD	Range	Dominant life- history stages
				(mm)			
Intertidal creek							
Liza dumerilii	1	14527	2786	44.2	32.7	20 - 232	Juveniles
Mugilidae (< 20 mm)	2	19746	2090	14.4	5.4	4 - 20	Juveniles
Mugil cephalus	3	5901	1345	23.5	4.8	20 - 64	Juveniles
Rhabdosargus holubi	3	1400	1317	23.0	19.1	6 - 161	Juveniles
Gilchristella aestuaria	5	7911	1068	29.3	4.3	8 - 47	Juveniles / Adults
Atherina breviceps	6	2165	932	33.9	8.5	14 - 68	Juveniles / Adults
Psammogobius knysnaensis	7	2057	1310	25.7	7.4	10 - 73	Juveniles / Adults
Pomadasys commersonnii	7	381	267	49.5	55.5	19 - 196	Juveniles
Glossogobius callidus	9	348	348	27.9	7.0	10 - 63	Juveniles / Adults
Liza tricuspidens	10	840	611	33.1	8.2	20 - 122	Juveniles
Diplodus sargus	11	3637	448	9.6	3.8	4 - 51	Juveniles
Liza richardsonii	12	51	51	169.4	89.7	25 - 305	Juveniles / Adults
Caffrogobius natalensis	12	123	123	39.7	15.8	7 - 93	Juveniles / Adults
Myxus capensis	14	148	139	26.7	28.0	20 - 265	Juveniles
Terapon jarbua	15	345	342	21.7	7.6	6 - 45	Juveniles
Adjacent eelgrass bed	s						
Rhabdosargus holubi	1	6375	3725	18.6	16.3	4 - 130	Juveniles
Atherina breviceps	2	2638	2126	34.1	9.4	8 - 75	Juveniles / Adults
Caffrogobius natalensis	3	605	605	33.5	13.6	14 - 78	Juveniles / Adults
Gilchristella aestuaria	4	5305	2291	28.7	4.3	8 - 79	Juveniles / Adults
Glossogobius callidus	5	449	449	32.8	11.1	10 - 76	Juveniles / Adults
Caffrogobius gilchristi	6	467	467	34.5	13.0	13 - 88	Juveniles / Adults
Caffrogobius nudiceps	7	169	169	45.8	13.3	18 - 84	Juveniles / Adults
Diplodus sargus	8	312	312	15.6	11.6	5 - 64	Juveniles
Syngnathus acus	9	122	122	116.3	41.8	10 - 221	Juveniles / Adults
Mugilidae (< 20 mm)	10	388	388	11.9	10.0	6.3 - 16	Juveniles
Clinus superciliosus	10	122	122	51.7	18.2	17 - 123	Juveniles / Adults
Pomadasys olivaceum	12	42	42	48.7	13.9	36 - 86	Juveniles
Monodactylus falciformis	13	41	41	25.5	16.1	6 - 88	Juveniles
Siganus sutor	14	74	74	25.2	14.1	17 - 81	Juveniles
Solea bleekeri	14	25	25	41.9	12.5	25 - 58	Juveniles / Adults

Taxa	Ave. Ab	undance	Average term	Ratio	Percent	Cumulative	
	No. per	10 m ²				%	
	Creek	Eelgrass					
Rhabdosargus holubi *	0.4	26.0	4.5	1.9	7.4	7.4	
Liza dumerilii *	3.7	<0.1	4.3	3.1	7.1	14.5	
Gilchristella aestuaria *	2.0	18.5	3.8	1.4	6.3	20.8	
Atherina breviceps *	0.6	9.7	3.5	2.0	5.8	26.6	
Caffrogobius gilchristi *	0.1	1.7	3.3	2.5	5.4	32.0	
Caffrogobius natalensis	<0.1	2.4	2.7	1.9	4.5	36.5	
Syngnathus acus *	<0.1	0.5	2.5	2.5	4.2	40.7	
Diplodus sargus	0.9	1.0	2.4	1.7	4.0	44.7	
Mugil cephalus	1.5	0.4	2.4	1.3	4.0	48.7	
Psammogobius knysnaensis	0.5	<0.1	2.3	2.0	3.9	52.6	
Glossogobius callidus	0.1	1.7	2.2	2.0	3.7	56.3	
Mugilidae (< 20 mm)	5.0	1.3	2.2	1.8	3.6	59.9	
Caffrogobius nudiceps	<0.1	0.5	2.2	2.1	3.6	63.5	
Caffrogobius superciliosus	<0.1	0.4	2.0	1.8	3.3	66.8	
Liza tricuspidens	0.2	<0.1	1.6	1.3	2.7	69.5	

Table 4.3. The fifteen dominant species, and related data, contributing to the total average dissimilarity between the eelgrass and creek groupings in Figure 4.8.

The average term is the $\overline{\times}$ Bray-Curtis contribution of each species in distinguishing the two groups. The ratio is the average term divided by its standard deviation. A good discriminating taxon (*) is one which has a high average and a high ratio. The percentage and cumulative percentage are the percent contributions made by each taxon to the dissimilarity between groups.

Using both classification and ordination techniques as well as the ranking index it is apparent that some species were common in both habitats e.g. G. aestuaria, A. breviceps, R. holubi, G. callidus and D. sargus. Some of these generalist species e.g. R. holubi, G. aestuaria and A. breviceps were also good discriminating species (Table 4.3). While being common to both habitats they were found in far higher densities in eelgrass, thus having a greater affinity for this habitat. Several of the other species also showed clear habitat preferences with L. dumerilii, L. tricuspidens, M. cephalus, P. knysnaensis and P. commersonnii being found predominantly in the creek. The dominant eelgrass specific species were all estuarine species, namely C. natalensis, C. gilchristi, C. nudiceps, S. acus and C. superciliosus.





Figure 4.8 Dendrogram showing classification of 30 samples, 15 from Taylor's intertidal salt marsh creek and 15 from the adjacent eelgrass beds, based on densities of fishes from the period August 1992 to May 1994. Two main groups are distinguished at a similarity level of 40%.



Figure 4.9 Ordination of 30 samples, 15 from Taylor's intertidal salt marsh creek and 15 from the adjacent eelgrass beds, using multidimensional scaling on the same similarity matrix as Figure 4.8.

4.4 DISCUSSION

Both Taylor's creek and the adjacent eelgrass beds function as nursery areas for marine and estuarine fishes in the Kariega Estuary. The nursery function of both eelgrass (Beckley 1983, Whitfield *et al.* 1989, Bell & Pollard 1989) and salt marsh creeks (Cain & Dean 1976, Bozeman & Dean 1980, Weinstein & Brooks 1983) in other estuarine systems is well established. The average lengths and dominant life-history stages for the same species occurring in both Kariega habitats was very similar and there was little evidence of ontogenetic distributional changes by any species between the two habitats, as found for spot (*Leiostomus xanthurus*) in Hungars Creek, Chesapeake Bay (Weinstein & Brooks 1983). The contrasting species assemblages within the two environments indicates that each habitat provides a distinctive nursery area for different fish species.

The ichthyofaunal communities associated with the creek and eelgrass habitats differed considerably with respect to total density, total abundance, dominant families and dominant species. While there were generalist species which occurred in both habitats, there were also a number of dominant taxa in each region which exhibited very clear habitat preferences. Other comparative studies between eelgrass and unvegetated regions in estuaries (Ferell & Bell 1991, Connolly 1994a) indicate differences in species assemblages between the two habitats. Similarly, different faunal assemblages have characterized tidal creeks and eelgrass beds (Weinstein & Brooks 1983, Sogard & Able 1991) with both the creek and eelgrass habitats comprising a mixture of habitat specialists as well as ubiquitous species which showed no site specific preferences (Weinstein & Brooks 1983).

The diversity of the fish communities in the eelgrass and creek habitats were very similar, with each supporting a similar number of species. This similarity in diversity is contrary to findings of other comparative works. Weinstein & Brooks (1983) reported that a basic difference between the two habitats was the much higher species diversity associated with the structurally complex sea meadow, while Sogard & Able (1991) found that marsh creeks supported high densities of fishes but only for a few species that were common in other habitats.

There is a close relationship between the life-history style adopted by a fish and its estuarine association category. In general, estuarine species (Table 2.2) possess many stenotopic characteristics. They have a narrow habitat range, narrow distribution, are sedentary, have a small body size, small populations, are precocial and can be broadly classified as specialists (Whitfield 1994d). Marine transient species (Table 2.2) tend towards eurytopy, have a broad habitat tolerance range, wide distribution, high mobility, large body size, large populations, are altricial and can be broadly classified as generalists (Whitfield 1994d). Many of the stenotopic species (e.g. Syngnathus acus and Clinus superciliosus) are closely associated with eelgrass, indicating that the eelgrass habitat is probably one of the more stable habitats in a generally unpredictable environment. Certainly in comparing Taylor's eelgrass and creek as habitats for fishes, the creek is a harsher environment, lacking in cover and the ichthyofauna are forced to move away over the low tide. Although the area available to eelgrass associated fishes may be reduced during low tide they do not have to move into the main channel. When the total ichthyofauna in each habitat is classified using Whitfield's (1994b) estuarine association categories the creek ichthyofauna is dominated by eurytopic marine fishes, which include marine transient and catadromous species (Table 2.2), while the eelgrass is dominated by estuarine fishes. One of the life-history traits which could explain the above differences is the mobility of the different species, with many of the estuarine species being relatively sedentary and consequently restricted to the eelgrass. In contrast eurytopic marine species are far more mobile and thus able to utilize the intertidal creek when it is available.

The mechanism by which different species avoid detection and predation is important in their habitat utilization patterns. Eelgrass is a structurally complex habitat that permits species the opportunity to employ cryptic mechanisms to blend into the background structure, while the creek environment, which is unvegetated, forces fishes to utilize other protective measures such as schooling. Many species (e.g. *Syngnathus acus*) have evolved very specific habitat needs which restrict them to one habitat. As found by Bell and Pollard (1989) in their review of fishes utilizing eelgrass and unvegetated areas, the Kariega eelgrass beds had significant numbers of small species with cryptic habits (e.g. *Clinus superciliosus, Syngnathus acus, Caffrogobius* species), while the creek was frequented by species gaining protection through schooling or by camouflage against the sediments (e.g. Mugilidae, *Psammogobius knysnaensis*).

Significant differences were found in the density and standing stock of fishes in the eelgrass and creek habitats, with the eelgrass having a far higher density and standing stock of fishes. While these two habitats were sampled using different gear types, the trends exhibited are regarded as valid because the eelgrass values (which were a more conservative estimate) were far higher than those of the creek, which utilized an absolute sampling method. Environmental factors such as temperature (Caulton 1978), turbidity (Blaber & Blaber 1980, Cyrus & Blaber 1987a,b) and salinity (Whitfield *et al.* 1994) often structure fish communities. The environmental factors measured in the eelgrass and creek during this study showed very little, if any, differences between the two habitats and were unlikely to have resulted in the differences between the ichthyofaunas.

The higher fish abundance in eelgrass compared to an unvegetated habitat has been borne out by a number of other South African (Branch & Grindley 1979, Beckley 1983) and international studies (reviewed in Bell & Pollard 1989, Orth 1992). Our results do not concur with the studies of Weinstein & Brooks (1983) and Sogard & Able (1991) which dealt specifically with comparisons between tidal creeks and eelgrass beds. These authors found that the eelgrass had a more diverse ichthyofauna but overall abundance was higher in the creek. However, the greater abundance of fishes in these marsh creeks was attributed to the very high densities of only one or two species.

The fact that eelgrass beds are more attractive habitats for fishes and other estuarine nekton than bare substrata (Bell & Pollard 1989, Orth 1992) has been ascribed to characteristics of the seagrass habitat. Seagrass canopies provide shade, reduced water currents and increased surface area (Bell & Pollard 1989), while the rhizome mat of seagrasses provides further habitat complexity (Orth *et al.* 1984, Orth 1992). These attributes, together with high primary productivity, are presumed to provide an abundant and varied supply of food, as well as protection from predators. The refuge function of vegetated and unvegetated habitats to nekton has received a lot of attention, with studies showing positive relationships between vegetation parameters (e.g. shoot density, biomass or complexity) and prey survivorship (Heck & Thoman 1981, Savino & Stein 1982, Gotceitas & Colgan 1987). In explaining large differences in abundances between the ichthyofaunas of an eelgrass bed (vegetated) and creek (unvegetated) habitat, the role that predation or threat of predation plays in structuring the ichthyofaunal assemblages of the two habitats must be questioned.

For predation to be a factor resulting in lower densities of fishes in Taylor's creek in comparison to the nearby eelgrass beds there should be either a higher threat of predation or higher mortalities within the creek habitat. Abundant Eastern Cape piscivorous fishes such as *Argyrosomus japonicus*, *Elops machnata* and *Lichia amia* were however not caught in the intertidal creek, whereas these species were relatively common in the main estuary channel adjacent to the eelgrass beds (Chapter 7). Similarly, large piscivorous fishes were uncommon in samples from other creek studies (Shenker & Dean 1979, Reis & Dean 1981, Rozas & Hackney 1984). This avoidance of the shallow areas in estuaries by large piscivorous fishes may be a consequence of increased vulnerability to avian or mammalian predation, decreased foraging ability or increased physiological stress due to elevated temperatures or reduced oxygen levels (Ruiz *et al.* 1993). An additional reason for the lack of piscivorous fishes in Taylor's creek might be the restricted access to the creek through the narrow mouth. Fish mortalities may also arise from crustacean, conspecific fish predation and bird predation. Results of the feeding and predation studies (Chapter 7) in intertidal creeks in the Kariega Estuary do however indicate that the level of predation by these components is most likely negligible (Chapter 7).

The mechanisms for predation resulting in differences in abundances of nekton in unvegetated and vegetated areas has been intensely debated (Bell & Pollard 1989, Orth 1992). If predation is regarded as a proximate cause of differential abundances between habitats, as suggested by Heck and Orth's (1980) predation model, then differential mortality is needed between the vegetated and unvegetated habitats. Although no direct measure of differential mortality was obtained for the ichthyofauna frequenting Taylor's creek in comparison to the eelgrass, evidence presented above implies a low predation pressure within the intertidal creek habitat even though it is structurally simple. Evidence exists (Bell & Westoby 1986a,b,c, Bell *et al.* 1987) to show that predation is the agent driving selection for correct habitat choice and not the direct cause of low fish abundance in poor cover (Bell & Pollard 1989). If this is true, then the higher abundance of fish in the eelgrass habitat compared to the creek was due to the fish recognising the eelgrass as

a superior refuge and not necessarily due to differential mortalities between each habitat. An interesting finding is the higher densities of fishes in creeks compared to other unvegetated shallow water regions elsewhere in an estuary (Sogard & Able 1991). In the Kariega Estuary the unvegetated sand banks outside Grant's marsh were found to have similar dominant species but far lower ichthyofaunal density than in Grant's creek itself (Paterson & Whitfield unpublished data). These observations indicate that the creek habitat offers some element which is attractive to certain juvenile fishes and is unavailable in the unvegetated shallow water region near the creek. This element could be that fishes recognise the creek as a potential refuge due to the low numbers or absence of predators associated with this environment.

Another reason why there may be higher abundances of fishes in eelgrass beds than in unvegetated areas is food availability. Fish feeding in eelgrass has been well documented (reviewed in Klumpp *et al.* 1989, Bell & Pollard 1989) and for the majority of eelgrass associated species planktonic and epifaunal crustaceans are the important foods. Eelgrass fish communities do not appear to be food limited as the total annual food production in the beds is greater than the total annual food consumption by the eelgrass macrofauna (Adams 1976b). The feeding studies conducted in Taylor's creek indicated that the vast majority of fishes that frequent the system do not feed extensively (Chapter 7). This is in contrast to other studies where fishes were found to feed in tidal creeks and on the marsh surface (Kleypas & Dean 1983, Morton *et al.* 1987, Rozas & LaSalle 1990, Allen *et al.* 1995, Knieb 1997b).

Chapter 5

Spatial variation in the fish assemblages associated with three intertidal salt marsh creeks and their adjacent eelgrass beds

5.1 INTRODUCTION

Research has indicated that intertidal and subtidal salt marsh creeks are utilized by significant numbers of resident estuarine and transient marine fishes with 0+ juveniles forming a very important and conspicuous component of the total ichthyofauna (Cain & Dean 1976, Weinstein 1979, Weinstein *et al.* 1980, Bozeman & Dean 1980, Rountree & Able 1992). In addition, comparative studies between salt marsh creeks and adjacent eelgrass beds (Weinstein & Brooks 1983, Sogard & Able 1991) have demonstrated that salt marsh creeks support a higher density, but lower diversity of fishes than eelgrass beds.

In southern Africa only three studies have been undertaken on salt marsh ichthyofauna and all have been on Taylor's intertidal salt marsh creek (Chapters 2 - 4). The ichthyofauna frequenting Taylor's creek was found to be dominated by juvenile marine species, indicating that this habitat may be an important nursery area for certain families e.g. mugilids. In contrast to other comparative studies (Weinstein & Brooks 1983, Sogard & Able 1991) Taylor's creek was found to have a lower density and standing stock of fishes compared to the bordering eelgrass beds (Chapter 4). The diversity of the ichthyofaunal communities in both the eelgrass and intertidal creek habitats was found to be similar but the species compositions were distinct.

The above results, while being validated over a temporal scale, were spatially restricted as all the studies were confined to one site. This chapter endeavours to examine whether these findings apply to a range of intertidal salt marsh creek systems and their adjacent eelgrass beds within the Kariega Estuary. The specific aims of the study were to:

- Establish whether intertidal salt marsh creeks within the Kariega Estuary have similar ichthyofaunal community structures with respect to species composition, density, standing stock and diversity.
- Verify if eelgrass beds and intertidal creeks are utilized by distinct fish communities with eelgrass beds having a greater overall density but similar diversity of fishes.

5.2 MATERIALS AND METHODS

SAMPLE SITES

Three salt marsh systems were sampled in this study, namely Taylor's, Grant's and Galpin's marshes. Grant's salt marsh is found closest to the estuary mouth and its marsh flats are dominated by *Spartina maritima* and *Sarcocornia perennis*. The intertidal creek is unvegetated, has an area of 3756 m² and consists of three main branches, all of which meet at one single opening to the estuary (Figure 5.1). The creek system is narrow (mean width=8.0 m) and relatively shallow (mean spring high tide depth=74 cm). The intertidal banks adjacent to the creek mouth are unvegetated with the closest eelgrass beds being on the opposite channel bank.

Taylor's salt marsh is the middle marsh and its marsh flats are dominated by Sarcocornia perennis. This marsh is characterized by having a single intertidal creek which has an area of 2608 m² and only one opening into the estuary (Figure 5.2). Taylor's intertidal creek is similar to Grant's creek in that it is narrow (mean width=5.2 m) and shallow (mean spring high tide depth=50 cm). The intertidal creek is unvegetated while the estuary banks adjoining the creek mouth are dominated by the eelgrass Zostera capensis.

Galpin's marsh is unlike Grant's and Taylor's marshes in that it is attached to a small estuarine embayment rather than the main channel (Figure 5.3). The salt marsh flats are dominated by *Spartina maritima* and *Sarcocornia perennis* and there are few high marsh pools. The intertidal creek covers an area of 3343 m² and is wider (mean width=15.2 m) and deeper (mean spring high tide depth=106 cm) than the other two marsh creeks. Unlike the other creeks, Grant's intertidal creek has a number of patches of eelgrass *Zostera capensis* growing in its channel (Figure 5.3). Extensive eelgrass beds are also found in the embayment (Figure 5.3).

SAMPLING PERIODICITY

Samples were collected quarterly over one year between November 1992 and August 1993. On each occasion all three marshes were block netted and their adjacent eelgrass beds seined. Netting occurred over the dawn spring high tide with one creek and adjacent eelgrass bed being sampled daily. Sampling was conducted over three consecutive days in an attempt to limit the effect of temporal variability on physico-chemical and ichthyofaunal parameters.



Figure 5.1 a) Photograph of Grant's salt marsh with the Kariega Estuary in the background. b) Line drawing of Grant's intertidal salt marsh creek.



Figure 5.2 a) Photograph of Taylor's salt marsh with the Kariega Estuary in the foreground.b) Line drawing of Taylor's intertidal salt marsh creek.



Figure 5.3 a) Photograph of Galpin's salt marsh with the Kariega Estuary in the background.b) Line drawing of Galpin's intertidal salt marsh creek.

FIELD SAMPLING

At the slack high tide a block net was placed across the mouth of one of the three creeks and all the fishes were collected as the tide receded (see Chapter 2). Immediately after the block net had been deployed the eelgrass beds adjacent to the creek system were seined. The proximity of the tidal creek and eelgrass beds means that differences in the fish assemblages between the habitats should be due to habitat selection and preference and not random distribution patterns (Weinstein & Brooks 1983). A total of four sites were seined in each eelgrass bed using a 5 m long, 2.5 m deep seine net with a 2.5 mm stretch mesh. The area of eelgrass bed sampled was calculated after each haul.

Selected physical and chemical parameters were recorded on the high tide at four fixed locations in the creek and at the four eelgrass seining sites. Water temperature (°C) was measured *in situ* and water samples were collected so that salinity and turbidity (NTU) could be measured in the laboratory using an optical salinometer and turbidimeter. Water depths (cm) were measured along the centre of the creek as well as in the creek mouth.

SAMPLE ANALYSIS

Sample analysis follows that in Chapter 2.

DATA ANALYSIS

Density and standing stock: Fish density and standing stock were calculated for each creek by dividing the total number and mass of fishes by the creek area. The density of fishes was calculated for each eelgrass bed by dividing the total number of fishes caught by the area seined. Two-way ANOVA tests for single observations (Fowler & Cohen 1993) in conjunction with Tukey multiple range tests (*a posteriori*) were used to determine whether density and standing stock were significantly different between creeks over the four sampling periods. Cochran C tests were undertaken and where the data was found to be heteroscedastic, a log transformation was undertaken.

Ichthyofaunal composition: The dominant ichthyofauna utilizing each of the three creek systems was determined as follows. All samples were pooled for each creek and the total density and standing stock of each species was ranked. The percentage composition of the top fifteen species in each creek was also calculated. The same procedure was adopted for the eelgrass fauna but only density data were used.

Estuarine association categories (Table 2.2) were assigned to each species and the percentage contribution of each estuarine association group was calculated for the fish community in every creek using both density and standing stock data. Diversity indices were calculated for each season for the fish communities found in each creek and eelgrass bed. The Shannon-Wiener species diversity index (H') and Pielou's evenness index (J') were used (Washington 1984). Length frequency histograms were constructed for the dominant estuarine and marine transient fish species which were common in all three of the creeks.

Classification and ordination: The mean ichthyofaunal density data collected in the three creeks and adjacent eelgrass beds (n=24 samples) were root-root transformed. An association matrix was produced using the Bray-Curtis similarity measure, from which classification and ordination procedures were conducted. The similarity matrix was classified using hierarchical agglomerative clustering with group average linking, while ordination used multidimensional scaling (MDS) techniques (Clarke & Warwick 1994). The environmental variables temperature, salinity, turbidity, channel depth and cross-sectional mouth area were superimposed on an ordination produced by the creek fish community. This method, first proposed by Field *et al.* (1982), allows for a simple examination of which environmental parameters may be important in influencing the biotic groupings produced by multidimensional scaling techniques.

A two-way crossed ANOSIM was used to test if there was an overall difference between the ichthyofaunal communities (density data) over time and between the eelgrass and creek habitats in the Kariega Estuary. A two-way ANOSIM (no replication - using weighted Spearman rank) was used to test if there was a significant difference between the fish communities (density data) over time and between each of the three creeks (Clarke & Warwick 1994).

5.3 RESULTS

INTER-CREEK COMPARISON

Physico-chemical: The water parameters measured indicated a high degree of similarity between the creek systems. Water temperature showed a typical seasonal pattern varying between 14 °C and 22 °C (Table 5.1). Full seawater salinities prevailed in all samples except the spring sample in Taylor's creek which was 32 (Table 5.1). The creeks all had very low turbidities which is characteristic of marine dominated southern African estuarine systems (Table 5.1). Average channel water depths varied between the creeks (Table 5.1), with Taylor's creek being the shallowest, Grant's intermediate and Galpin's the deepest. The cross-sectional mouth area followed a similar pattern, with Galpin's creek mouth always having the largest cross-sectional area.

Table 5.1	Physico-chemica	l parameters	(mean and	l standard	deviation)	recorded in	Taylor's,
Grant's an	d Galpin's interti	dal salt marsh	creeks be	ween Nov	ember 199	2 and Augus	t 1993.

Season	Parameter	Taylor's Creek	Grant's Creek	Galpin's Creek
Spring	Temperature (°C)	20.1 (± 0.2)	20.1 (± 0.5)	20.6 (± 0.5)
	Salinity	32.2 (± 0.4)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	16.8 (± 5.0)	14.8 (± 1.9)	14.6 (± 5.2)
	Channel depth (cm)	39.2 (± 10.8)	60.4 (± 10.7)	108.3 (± 12.7)
	Mouth area (m ²)	5.5	9.3	17.0
Summer	Temperature (°C)	22.2 (± 0.4)	19.8 (± 0.2)	22.5 (± 0.1)
	Salinity	34.8 (± 0.4)	35.0 (± 0.0)	34.8 (± 0.4)
	Turbidity (NTU)	9.2 (± 3.3)	5.0 (± 1.6)	10.8 (± 3.0)
	Channel depth (cm)	56.2 (± 10.8)	83.3 (± 10.7)	103.4 (± 12.7)
	Mouth area (m ²)	6.7	12.5	16.2
Autumn	Temperature (°C)	17.4 (± 0.2)	17.5 (± 0.0)	17.5 (± 0.0)
	Salinity	35.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	6.6 (± 1.3)	5.2 (± 1.3)	5.2 (± 2.3)
	Channel depth (cm)	51.2 (± 10.8)	75.2 (± 10.7)	108.7 (± 12.7)
	Mouth area (m ²)	6.3	11.5	17.0
Winter	Temperature (°C)	14.9 (± 0.2)	14.4 (± 0.5)	14.7 (± 0.3)
	Salinity	35.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	7.8 (± 1.5)	5.8 (± 1.3)	13.2 (± 1.3)
	Channel depth (cm)	55.3 (± 10.8)	77.3 (± 10.7)	106.4 (± 12.7)
	Mouth area (m2)	6.6	11.7	16.6

Density and standing stock: A total of 172 940 individuals were caught during this study with 16 979 being netted in Taylor's creek, 37 715 in Grant's creek and 118 246 in Galpin's creek. The total mass of fishes was 462 416 g, with 26 469 g being netted in Taylor's creek, 45 341 g in Grant's creek and 390 606 g in Galpin's creek.

The fish densities in both Taylor's creek (mean=16.3 per 10 m², SD=5.8) and Grant's creek (mean=25.1 per 10 m², SD=12.5) were similar (Figure 5.4). Galpin's creek had a considerably higher fish density than the other two creeks (mean=88.4 per 10 m², SD=81.3) and also displayed the greatest variability (Figure 5.4). A two-way ANOVA indicated that the density of fishes was not significantly different over time (p=0.32) but was significantly different between sites (p=0.03). A Tukey multiple range test indicated that at the 95% confidence level the ichthyofaunal density in Taylor's creek was significantly different to that in Galpin's creek but not significantly different to that of Grant's creek.



Figure 5.4 Density and standing stock of fishes recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks for the period November 1992 to August 1993.

The standing stock of fishes found in each of the creeks followed an analogous trend to that of ichthyofaunal density (Figure 5.4). The standing stocks in Taylor's creek (mean standing stock=25.4 g per 10 m², SD=5.8) and Grant's creek (mean standing stock=30.2 g per 10 m², SD=22.0) were very similar, while Galpin's creek had a considerably higher fish biomass (mean standing stock=292.1 g per 10 m², SD=140.6). A two-way ANOVA indicated that there was no significant difference in the standing stock of fishes in the creeks over time (p=0.74) but a highly significant difference between sites (p=0.001). A Tukey multiple range test indicated that at the 95% confidence level the fish standing stocks found in Taylor's and Grant's creeks were significantly different to those recorded in Galpin's creek.

Ichthyofaunal composition: In terms of numbers, the Mugilidae were the most important family in both Taylor's and Grant's creeks where they comprised 76% (6 species) and 70% (6 species) of the overall fish community. In Galpin's creek the Clupeidae (53%) were dominant, but were represented by only one species (*viz. Gilchristella aestuaria*). The mugilids were the next most dominant family (6 species) in Galpin's creek, comprising 36% of the community. When examining the dominant ichthyofaunal families according to standing stock, the mugilids were by far the dominant family, comprising 78% of the total mass of fishes in Taylor's creek, 84% in Grant's creek and 77% in Galpin's creek.

At the species level *Liza dumerilii* ranked first or second in terms of density in all three creeks (Table 5.2) with the other dominant species being *Gilchristella aestuaria*, *Atherina breviceps*, *Mugil cephalus* and *Rhabdosargus holubi*. In terms of biomass *Liza dumerilii* was also the most dominant species, being ranked first in all three creeks (Table 5.3). The diversity of fishes in the creeks displayed a similar trend to that of density and standing stock, in that Taylor's and Grant's creeks were the most similar (Table 5.4). Taylor's creek had 29 confirmed species and a mean diversity of 1.5 (SD=0.4) while Grant's creek had 30 confirmed species and a mean diversity of 1.5 (SD=0.4) (Table 5.4).

Table 5.2 Mean density, rank and percentage composition of the 15 dominant fish taxa recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks between November 1992 and August 1993 (P=present, A=absent, T=Taylor's creek, Gr=Grant's creek, G=Galpin's creek).

	Tay	lor's Cree	ek	Gra	nt's Creek	c	Galpin's Creek		
Species	No. per 10 m ²	Rank	%	No. per 10 m ²	Rank	%	No. per 10 m ²	Rank	%
Mugilidae (< 20 mm)	7.21	1	44.3	6.39	2	25.4	1.55	5	1.8
Liza dumerilii	4.37	2	26.7	8.80	1	35.0	26.11	2	29.5
Gilchristella aestuaria	1.06	3	6,5		P		47.20	1	53.2
Atherina breviceps	0.91	4	5.6	2.20	4	8.8	0.96	7	1.0
Psammogobius knysnaensis	0.87	5	5.3	3.31	3	13.2	0.14	12	0.2
Mugil cephalus	0.64	6	3.9	0.52	7	2.1	3.12	4	3.5
Rhabdosargus holubi	0.45	7	2.8	0.41	8	1.6	5.74	3	6.5
Liza tricuspidens	0.13	8	0.7	1.61	5	6.4	0.93	8	1.1
Terapon jarbua	0.12	9	0.7		Р		0.14	13	0.2
Glossogobius callidus	0.11	10	0.7	0.09	11	0.4	1.05	6	1.2
Myxus capensis	0.10	11	0.6	0.21	10	0.9		Р	
Diplodus sargus	0.04	12	0.3	0.25	9	1.0		Р	
Pomadasys olivaceum	0.04	12	0.3		А			Р	
Coffrogobius natalensis	0.03	14	0.2	0.05	14	0.2		Р	
Solea bleekeri	0.02	15	0.2		P			Р	
Sarpa salpa		Р		0.91	6	3.6		Р	
Liza richardsonii		Р		0.07	12	0.3	0.15	11	0.2
Monodactylus falciformis		Р		0.06	13	0.2	0.64	9	0.7
Rhabdosargus globiceps		Р		0.03	15	0.1		Р	
Pomadasys commersonnii		Р			Р		0.16	10	0.2
Crenimugil crenilabis		Р			Р		0.11	14	0.1
Caffrogobius gilchristi		Р			Р		0.10	15	0.1

Other species recorded: Acanthopagrus berda ⁽⁰⁾, Ambassis gymnocephalus ⁽⁰⁾, Amblyrhynchotes honckenii ^(Ot.O), Argyrosomus japonicus ^(G), Arothron hispidus ^(G), Caffrogobius nudiceps ^(T,G), Caranx ignobilis ^(O), Caranx sexfasciatus ^(O), Clinus superciliosus ^(T,Gr), Diplodus cervinus ^(T,GT,G), Elops machnata ^(T,Ot.O), Galeichthys feliceps ^(G), Hemiramphus far ^(O), Heteromycteris capensis ^(Gr), Hyporhampus capensis ^(O), Lichia amia ^(G), Lithognathus lithognathus ^(T,Gt,G), Lutjanus fluviflamma ^(O), Lutjanus monostigma ^(O), Monodactylus argenteus ^(O), Ophisurus serpens ^(O), Omobranchus woodi ^(Gt.O), Oreochromis mossambicus ^(T,Ot,O), Pomatomus saltatrix ^(T,G), Saurida gracilis ^(T,O), Scomberoides lysan ^(G), Scomberoides tol ^(Gt), Seriola lalandi ^(G), Siganus sutor ^(Gt,G), Torpedo fuscomaculata ^(O), Trachurus trachurus ^(G). Table 5.3 Mean standing stock, rank and percentage composition of the 15 dominant fish taxa recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks between November 1992 and August 1993 (P=present, A=absent, T=Taylor's creek, Gr=Grant's creek, G= Galpin's creek).

	Tayl	or's Cre	ek	Gra	nt's Creek	c .	Galpin's Creek			
Species	Grams per 10 m²	Rank	%	Grams per 10 m²	Rank	%	Grams per 10 m²	Rank	%	
Liza dumerilii	11.25	1	44.3	21.81	1	72.3	152.90	1	52.3	
Liza richardsonii	4.39	2	17.3	0.16	9	0.5	38.00	2	13.0	
Mugil cephalus	3.73	3	14.7	0.85	6	2.8	32.70	3	11.2	
Rhabdosargus holubi	1.83	4	7.2	1.42	4	4.7	23.91	5	8.2	
Pomadasys commersonnii	1.68	5	6.6	0.09	10	0.3	26.33	4	9.0	
Atherina breviceps	0.68	6	2.7	1.62	3	5.4	0.5	11	0.2	
Mugilidae (< 20 mm)	0.36	7	1.4	0.69	7	2.3	0.32	14	0.1	
Gilchristella aestuaria	0.35	8	1.4		Р		12.70	6	4.4	
Psammogobius knysnaensis	0.31	9	1.2	1.05	5	3.5		Р		
Pomadasys olivaceum	0.29	10	1.2		A			Р		
Liza tricuspidens	0.10	11	0.4	1.74	2	5.8	0.98	7	0.3	
Caffrogobius natalensis	0.07	12	0.3	0.06	12	0.2		Р		
Caffrogobius gilchristi	0.06	13	0.3		Р			Р		
Diplodus cervinus	0.05	14	0.2	0.08	11	0.3		Р		
Diplodus sargus	0.04	15	0.2	0.25	8	0.8		Р		
Glossogobius callidus		Р		0.06	12	0.2	0.72	8	0.3	
Myxus capensis		Р		0.06	12	0.2		Р		
Sarpa salpa		Р		0.05	15	0.2		Р		
Torpedo fuscomaculata		A			A		0.65	9	0.2	
Argyrosomus japonicus		A			A		0.58	10	0.2	
Monodactylus falciformis		Р			P		0.42	12	0.2	
Crenimugil crenilabis		Р			Р		0.36	13	0.1	
Terapon jarbua		Р			Р		0.15	15	<0.1	

Other species recorded: Acanthopagrus berda ^(G), Ambassis gymnocephalus ^(G), Amblyrhynchotes honkenii ^(Gr,G), Arothron hispidus ^(G), Caffrogobius nudiceps ^(T,O), Caranx ignobilis ^(G), Caranx sexfasciatus ^(G), Clinus superciliosus ^(T,Gr), Elops machnata ^(T,Gr,G), Galeichthys feliceps ^(O), Hemiramphus far ^(G), Heteromycteris capensis ^(Gr), Hyporhampus capensis ^(G), Lichia amia ^(G), Lithognathus lithognathus ^(T,Gr,G), Lutjanus monostigma ^(G), Lutjanus fluviflamma ^(O), Monodactylus argenteus ^(O), Omobranchus woodi ^(Gr,G), Ophisurus serpens ^(O), Oreochromis mossambicus ^(T,Gr,G), Pomatomous saltatrix ^(T,G), Rhabdosargus globiceps ^(T,Gr,G), Saurida gracilis ^(T,G), Scomberoides lysan ^(G), Scomberoides tol ^{(Gr,}, Seriola lalandi ^(O), Siganus sutor ^(Gr,G), Solea bleekeri ^(T,Gr,O), Trachurus trachurus ^(G).
Table 5.4 Shannon-Wiener diversity and Pielou evenness indices (mean and standard deviation) for the fish assemblages recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks and their adjacent eelgrass beds between November 1992 and August 1993.

Marsh system		Creek	Eelgrass			
	Diversity	Evenness	Diversity	Evenness		
Taylor's	1.55 (± 0.4)	0.52 (± 0.1)	1.47 (± 0.7)	0.51 (± 0.3)		
Grant's	1.52 (± 0.2)	0.52 (± 0.05)	1.52 (± 0.3)	0.62 (± 0.1)		
Galpin's	1.23 (± 0.4)	0.38 (± 0.1)	1.47 (± 0.1)	0.59 (± 0.02)		

When analysing estuarine association using density data, both Taylor's and Grant's creeks exhibited a similar pattern, with the marine species being the most important grouping followed by the estuarine taxa (Figure 5.5). In Galpin's creek the reverse was evident with the estuarine species being more dominant. This reversal does not occur when the estuarine association categories are calculated using standing stock data, with the marine species always being overwhelmingly dominant in all the creeks (Figure 5.5).

The vast majority of fishes caught in the creeks were 0+ juveniles and subadults. The main cohorts of *Liza dumerilii*, the dominant transient marine species (Table 2.2), were juveniles between 20 and 40 mm SL, which is well below the size at sexual maturity of 180 mm (Wallace 1975) (Figure 5. 6). *Atherina breviceps*, a common estuarine species (Table 2.2) which reaches sexual maturity at 40 mm SL (Ratte 1989), was represented by juveniles and adults (Figure 5.6).

CREEK VERSUS EELGRASS COMPARISON

Physico-chemical: The water parameters measured indicated that physico-chemical conditions in the eelgrass beds (Table 5.5) were all very similar to those of the creeks (Table 5.1). Water temperatures varied between 14 °C and 23 °C and, with the exception of Taylor's spring sample, all samples were full seawater (35). Turbidities measured in the eelgrass beds, as in the creeks, were low, ranging between 5 and 15 NTU.



Figure 5.5 Estuarine association groups (Table 2.2) for fishes recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks, calculated using both density and biomass data, for the period November 1992 to August 1993.



Figure 5.6 Length frequencies of *Atherina breviceps* and *Liza dumerilii* caught in Taylor's, Grant's and Galpin's intertidal salt marsh creeks for the period November 1992 to August 1993.

 Table 5.5 Physico-chemical parameters (mean and standard deviation) recorded in the eelgrass

 beds adjacent to Taylor's, Grant's and Galpin's salt marshes between November 1992 and August

 1993.

Season	Parameter	Taylor's eelgrass	Grant's eelgrass	Galpin's eelgrass
Spring	Temperature (°C)	20.0 (± 0.5)	18.3 (± 0.2)	20.7 (± 0.5)
	Salinity	31.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	15.5 (± 0.5)	14.2 (± 0.9)	16.2 (± 1.2)
Summer	Temperature (°C)	23.0 (± 0.0)	20.7 (± 0.5)	22.3 (± 0.2)
	Salinity	35.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	10.5 (± 1.7)	5.5 (± 1.3)	15.0 (± 1.2)
Autumn	Temperature (°C)	17.3 (± 0.3)	17.7 (± 0.5)	17.5 (± 0.0)
	Salinity	35.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	5.2 (± 0.5)	9.7 (± 2.5)	5.5 (± 2.6)
Winter	Temperature (°C)	14.7 (± 0.5)	14.8 (± 0.3)	14.8 (± 0.5)
	Salinity	35.0 (± 0.0)	35.0 (± 0.0)	35.0 (± 0.0)
	Turbidity (NTU)	7.5 (± 0.6)	7.7 (± 0.5)	9.0 (± 2.3)

Density: Fish density comparisons between eelgrass sites revealed smaller differences than between creek sites (Figure 5.7). The highest density was recorded in Taylor's eelgrass beds (mean density=93.1 per 10 m^2 , SD=89.8) and lowest in Grant's eelgrass beds (mean density=62.3 per 10 m^2 , SD=45.1), with Galpin's eelgrass being intermediate (mean density=79.5 per 10 m^2 , SD=19.9) (Figure 5.7). While densities between sites varied seasonally, fish density in eelgrass sites was consistently higher than in creeks (Figure 5.7). The disparity between fish densities in the two habitats was greatest between Taylor's creek and its adjacent eelgrass beds.

Ichthyofaunal composition: The dominant species (density) in the eelgrass habitats outside all three creeks were *Rhabdosargus holubi*, *Atherina breviceps* and *Gilchristella aestuaria* (Table 5.6). The primary difference between the eelgrass and creek habitats in the Kariega Estuary was the dominance exhibited by the mugilids in the latter habitat (Tables 5.2 and 5.6). Numerically, the mugilids comprised more than 70% of the ichthyofauna in Taylor's and Grant's creeks but less than 12% within their adjacent eelgrass beds.

Table 5.6 Density, rank and percentage composition of the 15 dominant fish taxa recorded in the eelgrass beds found adjacent to Taylor's, Grant's and Galpin's salt marshes between November 1992 and August 1993 (P=present, A=absent, T=Taylor's eelgrass beds, Gr=Grant's eelgrass beds, G=Galpin's eelgrass beds).

	Taylor':	eelgrass	beds	Grant's	eelgrass l	beds	Galpin's eelgrass beds			
Species	No. per 10 m²	Rank	%	No. per 10 m²	Rank	%	No. per 10 m ²	Rank	%	
Rhabdosargus holubi	59.93	1	64.5	17.71	2	28.6	24.08	1	30.7	
Atherina breviceps	12.90	2	13.9	24.48	1	39.6	5.39	5	6.9	
Gilchristella aestuaria	4.98	3	5.4	0.37	13	0.6	14.30	3	18.2	
Caffrogobius natalensis	4.10	4	4.4	1.03	10	1.7	0.60	9	0.7	
Caffrogabius gilchristi	2.20	5	2.3	2.10	6	3.4	1.77	6	2.3	
Glossogobius callidus	1.94	6	2.1	0.05	15	0.1	19.40	2	24.7	
Siganus sutor	1.24	. 7	1.3		Р		0.25	10	0.3	
Diplodus sargus	1.07	8	1.2	1.43	8	2.3	0.20	11	0.2	
Syngnathus acus	0.83	9	0.9		А			Р		
Mugilidae (< 20 mm)	0.82	10	0.9	1.90	7	3.1	0.78	8	0.9	
Caffrogobius nudiceps	0.70	11	0.8	0.21	11	0.3		Р		
Sarpa salpa	0.61	12	0.7	0.52	12	0.8		А		
Clinus superciliosus	0.32	13	0.3	4.11	3	6.7		Р		
Monodactylus falciformis	0.17	14	0.2	2.76	5	4.5	10.09	4	12.8	
Solea bleekeri	0.16	15	0.2		А			А		
Mugil cephalus		Р		0.18	14	0.3		Р		
Liza dumerilii		Р		3.58	4	5.7	0.81	7	1.0	
Liza tricuspidens		A		1.31	9	2.1		A		
Oreochromis mossambicus		A			А		0.17	12	0.2	
Arothron hispidus		Р			A		0.12	15	0.2	
Terapon jarbua		Р			A		0.13	14	0.2	
Psammogobius knysnaensis	-	Р			Р		0.14	13	0.2	

Other species recorded: Amblyrhynchotes honckenii^(T), Argyrosomus japonicus^(T), Diplodus cervinus^(T), Elops machnata^(T), Heteromycteris capensis^(T), Liza richardsonii^(G), Monodactylus argenteus^(G), Pomadasys commersonnii^(T), Pomadasys olivaceum^(T), Pomatomous saltatrix^(T), Pervagor janthisoma^(T), Saurida gracilis^(T), Torpedo fuscomaculata^(T).



Figure 5.7 Fish densities recorded in Taylor's, Grant's and Galpin's intertidal salt marsh creeks and their adjacent eelgrass beds (standard deviation also recorded for eelgrass samples n=4) for the period November 1992 to August 1993.

The three eelgrass habitats all had similar fish diversity values. Taylor's and Grant's eelgrass ichthyofaunal diversities were very similar to those found in their adjacent creek systems whereas Galpin's eelgrass beds had a higher diversity than Galpin's creek (Table 5.4). The number of confirmed species was lower in the eelgrass beds in comparison to the creeks with 26, 17 and 20 confirmed species being caught in Taylor's, Grant's and Galpin's eelgrass beds respectively.

Ordination and classification: The dendrogram constructed using density data (Figure 5.8) clearly demonstrates that the ichthyofaunal communities associated with the eelgrass and creek habitats were quite different. At the 50% similarity level the samples were clustered into two groupings viz. eelgrass and creek (Figure 5.8). A two-way crossed ANOSIM test showed a significant difference between the eelgrass and creek habitats (R=0.852, P < 0.001) but no significant difference over time (R=0.012, P=0.53). This clear distinction between the fish communities associated with the two habitats was also apparent when the density data was standardised, indicating that even when using percentage composition data there is still a clear distinction between the ichthyofaunal communities of the different regions.



Figure 5.8 Dendrogram showing the classification of 24 samples, 12 from Taylor's (T), Grant's (Gr) and Galpin's (G) intertidal salt marsh creeks and 12 from their adjacent eelgrass beds. The classification used fish density data collected between November 1992 and August 1993.

At the 60% similarity level the creek samples formed two groups, one containing all Galpin's samples and the other including both Grant's and Taylor's samples. The eelgrass samples displayed a stronger site affinity, with each site forming its own grouping at the 60% similarity level. A two-way ANOSIM test (no replication) indicated that there was a significant difference between the three creeks (RHO=0.73, P=0.03) but no significant difference over time (RHO=0.036, P=0.34). This dissimilarity of Galpin's creek fish community in comparison to the other two creeks is comparable to trends obtained for the overall density, standing stock and diversity of the ichthyofauna associated with the creeks.

The superimposition of environmental variables on the creek biotic groupings (60% similarity level) indicated consistent relationships between both the creek water depth (Figure 5.9) and mouth area (Figure 5.10) with the two major creek biotic clusters. Water temperature, salinity and turbidity did not display any pattern which could explain the disparity between the two biotic groupings.



Figure 5.9 MDS ordinations of Taylor's (T), Grant's (Gr) and Galpin's (G) intertidal salt marsh creek ichthyofaunal communities, with the superimposition of creek water depths on the plot. The MDS ordination was based on fish density data collected between November 1992 and August 1993, and the 60% similarity level was derived from Figure 5.8.



Figure 5.10 MDS ordinations of Taylor's (T), Grant's (Gr) and Galpin's (G) intertidal salt marsh creek ichthyofaunal communities, with the superimposition of creek cross-sectional mouth areas on the plot. The MDS ordination was based on fish density data collected between November 1992 and August 1993, and the 60% similarity level was derived from Figure 5.8.

5.4 DISCUSSION

The findings of research done in Taylor's creek thus far (Chapter 2,3 & 4) indicated that creeks were important nursery areas for many estuarine and migrant marine fish species. The ichthyofaunal community was found to be dominated by juveniles, in particular the mugilids, and very few piscivorous fish species were present (Paterson & Whitfield 1996). The density and standing stock of fishes in the creek were within the range reported for other estuarine habitats but were generally lower than other creek systems. An expansion of this original work into other creeks within the Kariega Estuary has allowed for these initial findings to be examined on a wider spatial scale.

The current study identified a number of characteristics which were common to all three creeks. The three creeks were found to have similar species compositions, and ordination and classification techniques consistently isolated the creek fish communities from the communities in other habitats. This similarity is noteworthy because use of salt marshes and their creeks by nekton is often highly variable (Shenker & Dean 1979, Varnell *et al.* 1995) and fishes are usually patchily distributed. The dissimilarity with other habitats indicates that creeks form a unique habitat within the estuary and are utilized by a distinct combination of species.

In all three creeks the mullet were the principal taxa when numbers, biomass and species number were taken into consideration. The numerically dominant family in Galpin's creek were the clupeids. However, this family was represented by only one species, *Gilchristella aestuaria*, and very high numbers in the autumn sample may have exaggerated its overall importance. Fish communities associated with all three creeks were dominated by 0+ juveniles, with very few piscivorous species being present.

While there were a number of similarities between the three creeks, (e.g. dominant species, nursery function and lack of piscivorous fishes), the systems differed in terms of density, standing stock and diversity of fishes. Fish densities and standing stocks were similar between Taylor's and Grant's creeks but were considerably greater in Galpin's creek. However, the recorded values in all three creeks fell within the range documented for other marsh creeks (Carr & Giesel 1975, Zimmerman & Minello 1984, Sogard & Able 1991, Minello *et al.* 1994). The overall trend was for the ichthyofaunal communities of Taylor's and Grant's creeks to be the most alike, with Galpin's creek tending to be dissimilar.

The exact mechanisms which regulate the overall density, standing stock and diversity of fishes utilizing salt marsh creeks have not been clearly identified. Weinstein *et al.* (1980) reported that in the Cape Fear Estuary (USA) the distribution of marine transients in shallow marsh habitats was governed primarily by salinity gradients and, to a lesser extent, by substratum characteristics. The physico-chemical variables measured in the Kariega Estuary creeks showed very little variation and could therefore not have resulted in the recorded differences between the ichthyofaunal communities moving into them.

Invertebrate and larval fish research in the Kariega Estuary (Hodgson 1987, Ter Morshuizen & Whitfield 1994) has shown that the density and biomass of biota may vary between the lower, middle and upper reaches of the estuary. Research on fishes associated with eelgrass beds has shown that location in an estuary may override other factors such as leaf density and habitat complexity (Sogard 1989). The three marshes in the Kariega Estuary are all found within a relatively short stretch of the estuary (3 km) and therefore spatial variations in the abundance and diversity of fishes are unlikely to be a major factor.

One of the major differences between the three creeks and their marshes was the topographical characteristics of the different systems. In general terms, Taylor's and Grant's creeks were the most similar as they were relatively shallow, sinuous and had smaller mouth dimensions in comparison to Galpin's creek. This overall topographical similarity between Taylor's and Grant's creeks, and mutual dissimilarity with Galpin's creek in terms of ichthyofaunal density, standing stock and diversity, lends some weight to marsh topography being an important factor in regulating the utilization of creeks by fish. The close association between water depth and creek mouth area with the biotic clusters, produced by the superimposition of abiotic variables on the biotic groupings, further indicates that these two parameters may be important community structure determinants. Water depth and in particular the hydroperiod of a creek or marsh surface have a direct effect on regulating the number and size of fishes entering these habitats (Teal 1986, Rozas 1995). Hydroperiod may also mediate habitat exploitation within the different marsh microhabitats through its influence on other factors such as prey abundance and vegetation density (Rozas 1995). In Taylor's creek there was a modest correlation between water depth and fish standing stock (Paterson & Whitfield 1996), primarily due to schools of large mugilids entering the marsh only during the highest spring tides. When comparing all three creeks, it would appear that the deeper the intertidal creek the greater the standing stock and density of fishes.

The dimension and position of the creek mouth may act together in regulating the numbers and size of fishes moving into creeks. The number of fishes entering a creek or salt marsh system during the high tide can be highly variable (Varnell *et al.* 1995) and, due to the schooling behaviour of many species, may be a more or less random event. The larger mouth of Galpin's creek and the funnelling effect of the adjoining embayment could result in a greater recruitment

zone when compared to the other creeks. This larger recruitment zone would have a greater effect on the less mobile mid-water species (e.g. *Gilchristella aestuaria*) which are easily influenced by water flow and currents.

The influence of submerged aquatic vegetation (SAV) on fish abundance in estuarine environments is well documented (Pollard 1984, Whitfield 1984, Bell & Pollard 1989, Lubbers *et al.* 1990) with SAV generally having a higher density of fishes than unvegetated areas. SAV has been shown to have far higher mean fish densities than unvegetated areas in tidal freshwater creeks (Rozas & Odum 1987c). It has been suggested that fishes select SAV in tidal freshwater creeks since it provides an abundant source of invertebrate prey as well as protection from predators (Rozas & Odum 1987c). Galpin's creek, unlike Taylor's and Grant's creeks, had areas which were covered in *Zostera capensis* and these eelgrass patches may have played a similar function to those in tidal freshwater creeks. Both this and the previous chapter have shown that eelgrass supports a higher density of fishes than creeks. The eelgrass in Galpin's creek undoubtedly increased the overall fish density in the creek and may also have attracted additional species due to the increased physical complexity provided by the eelgrass.

The proportion of fishes in the different estuarine association categories (Whitfield 1994b) varies between habitats. In eelgrass the dominant group is the estuarine residents, whereas in the creek habitat a far greater proportion of the fishes are marine transients (Chapter 4). Numerically Taylor's and Grant's creeks were dominated by transient marine fishes while estuarine residents were the principal estuarine association category in Galpin's creek. This demonstrates the possible influence that the eelgrass in the creek had on the overall ichthyofauna in Galpin's creek.

The highly mixed nature of the water column in Kariega Estuary, along with a small axial salinity gradient (Allanson & Read 1995) and the close proximity of the three salt marshes, offered a unique situation where several physico-chemical parameters were very similar in all three study sites. By excluding these factors, a combination of parameters such as depth, hydroperiod, eelgrass and characteristics of the creek mouth were identified as possible controlling variables which influence fish diversity, abundance and biomass in the creeks. The exact mechanisms by which these factors influence an estuary's nekton to utilize creeks will only be ascertained through carefully constructed field experiments.

In order to understand the importance of a habitat to an estuary's nekton it is necessary to compare it to other regions, so that an overall perspective of its role within that ecosystem can be ascertained. Research comparing unvegetated and vegetated areas in estuaries (Beckley 1983, Bell & Pollard 1989, Lubbers et al. 1990) has shown that vegetated reaches generally have a higher fish density and diversity. This pattern may be due to enhanced refuge from predation, increased availability of food, habitat complexity and general habitat preference (Lubbers et al. 1990). Specific studies comparing creeks with other estuarine habitats have shown that creeks have a lower diversity and higher density of fishes as well as a distinct community composition (Weinstein & Brooks 1983, Sogard & Able 1991). In Chapter 4 it was shown that in a South African salt marsh creek and adjacent eelgrass beds, the two habitats had very similar diversities but the eelgrass had higher fish densities. The study was however limited to one site and, as reported, the standing stock and density of fishes can vary between creeks. Current results have shown that while the density of fishes from both habitats in the Kariega Estuary varied between sites and seasons, the eelgrass habitats in general had a higher density of fishes than the creeks when each habitat pair was examined. The higher density of fishes in eelgrass compared to other unvegetated habitats may result from complex plant-plant, plant-animal, plant-physical environment and animalanimal interactions (Orth 1992).

Similar to other studies comparing vegetated and unvegetated habitats in estuaries (Bell & Pollard 1989), the creeks and eelgrass beds had very distinct fish communities. The division between the two communities in the classification and ordination procedures was distinct with no outliers recorded, despite seasonal and site variations in the ichthyofauna and the transient nature of significant portions of both communities. This significant difference between the two habitats, using both density and percentage composition data, demonstrates that they support two very different fish communities within the Kariega Estuary.

Chapter 6

A comparison between the fishes associated with the benthic and epipelagic channel habitats and those found in Taylor's intertidal salt marsh creek

6.1 INTRODUCTION

The channel environment in estuaries can be broadly partitioned into demersal and open water pelagic habitats. In South African estuaries research into the ichthyofauna associated with the open water pelagic habitat is principally based on gill net data (e.g. Marais 1981, 1983a,b, Plumstead *et al.* 1985, 1989a,b, 1991). Seine net data also exists for a number estuaries (e.g. Great Fish Estuary - Whitfield *et al.* 1994, Ter Morshuizen *et al.* 1996) but the method of deployment of this technique results in a mixture of fishes from both the littoral and open water pelagic habitats, making the interpretation of results from these studies difficult. In addition, there is a paucity of information on the fishes that utilize the demersal habitat, with the only published data being on three small temporarily open/closed estuaries in KwaZulu-Natal (Harrison & Whitfield 1995).

The published ichthyofaunal work on the Kariega Estuary is confined to those taxa associated with salt marshes (Chapter 2), eelgrass beds (Ter Morshuizen & Whitfield 1994, Chapter 4) and the ichthyoplankton in the mouth of the system (Whitfield 1994c). Prior to this study no information was available on the juvenile or adult fishes in either the pelagic or demersal habitats in the channel of the Kariega Estuary.

The Kariega Estuary is situated in a steep sided river valley, resulting in the intertidal area within the system being relatively small in comparison to other types of estuaries (Heydorn & Tinley 1980). Since the channel environment covers the largest surface area within the Kariega Estuary, particularly in the middle and upper reaches of the system, knowledge of what fishes are found within this habitat is imperative to the overall understanding of the ichthyofauna that utilize the estuary. As many fish species are highly mobile and utilize the intertidal habitats of estuaries for feeding and refuges (Orth 1992, Ruiz *et al.* 1993), a potentially important link exists between the subtidal and intertidal reaches. In order to understand these linkages (e.g. the possible export of energy from intertidal habitats such as salt marshes), a knowledge of the fish species and lifehistory stages associated with the different habitats within the Kariega Estuary is required. The aim of this chapter is to compare and contrast the ichthyofauna found in the subtidal and intertidal habitats in the Kariega Estuary, thereby providing the basis from which various ecological links between the salt marshes and main channel in the Kariega Estuary can be evaluated (Chapters 7-9).

6.2 MATERIALS AND METHODS

FIELD SAMPLING

Demersal habitat: The demersal channel habitat of the Kariega Estuary was sampled at ten sites between Grant's and Galpin's marshes from June 1995 to February 1997. Sampling was conducted at night (20h00 - 22h00) during the slack high tide on thirteen occasions using a small otter trawl. A total of 130 trawls were undertaken. The otter trawl consisted of two weighted otter boards (length 42 cm, height 22 cm) which were individually attached by a 20 m line to the boat. The trawl net had a 1.25 m long chain bottom line and a 2 m long head rope with a number of buoys attached to it. The net was conical in shape and consisted entirely of 6 mm stretch mesh netting. In order to standardise the area trawled (100 m^2), a half kilogram weight with an attached graduated line was deployed simultaneously with the net.

Open water pelagic habitat: The open water habitat in the Kariega Estuary was sampled using two methods, gill netting and a surface trawl. While gill netting is an effective method for catching large fishes, it is inadequate for small species, thus necessitating a dual approach.

Surface tows were undertaken in the Kariega channel between Galpin's and Grant's marshes in August, September and October 1995 as well as March 1996. Sampling was conducted at night (20h00 - 22h00) over the slack high tide with ten tows being completed during each sampling occasion (40 samples in total). The surface trawl consisted of a 2 m long conical net (6 mm stretch mesh) attached to a circular metal frame (75 cm diameter). Attached to the top of the metal frame were three floats making the trawl neutrally buoyant. The trawl was deployed from the side of the boat and was towed just below the surface at a constant speed for two minutes. The gill netting study was divided into two separate surveys. The first (piscivore gill net survey) targeted the larger species in the channel and utilized a mesh size which has been shown to be effective in sampling the common piscivorous fishes in Eastern Cape estuaries (Marais 1985). The piscivore gill netting survey was conducted just after the new moon in February, August, October and December 1994, as well as April and May 1996. On each sampling occasion six multifilament nets (20 m long, 3 m deep, 100 mm stretch mesh) were set in the channel outside Taylor's marsh. The nets were laid at 18h00, checked every two hours and retrieved at 06h00.

The second gill net survey was aimed at sampling a greater size range of fishes using two multifilament fleets, each comprising four (50, 70, 80 and 100 mm stretch mesh) 10 m long and 2.5 m deep panels. The sampling was undertaken during the new moon spring high tide in July, September and October 1995, as well as April and May 1996. The nets were set in the channel outside Taylor's and Grant's marshes and were deployed at 18h00, checked at midnight and retrieved at 06h00.

SAMPLE ANALYSIS

In the laboratory all fishes were measured (mm SL), identified to species level and counted. In addition the total preserved wet mass for each species captured in the demersal otter trawl and the surface trawl was measured to the nearest 0.1 g. The estuarine association categories assigned to each species conform to Whitfield (1994b)(Table 2.2).

6.3 RESULTS

DEMERSAL HABITAT - OTTER TRAWL

The otter trawl sampled a total of 4 599 individuals. The average density was 2.4 fish per 10 m² (SE=0.14) and ranged between 0.4 and 5.6 fish per 10 m² (Figure 6.1). A total of 20 species were recorded (Table 6.1) with only three species contributing more than 5% of the total density, *viz.* Solea bleekeri (53%), Glossogobius callidus (25%) and Psammogobius knysnaensis (7%). The soles (55% of total density) and gobies (34% of total density) were the two dominant demersal families. The marine migrants (61%) followed by the estuarine spawners (38%) were the numerically dominant estuarine association groups.

Species	Group	Density	%	Rank	Standing stock	%	Rank
Solea bleekeri	2b	1.29	53.27	1	2.75	48.18	1
Glossogobius callidus	16	0.61	25.08	2	0.47	8.29	4
Psammogobius knysnaensis	la	0.16	6.68	3	0.11	1.89	8
Gilchristella aestuaria	1a	0.10	4.34	4	0.04	0.62	11
Pomadasys commersonnii	2a	0.06	2.83	5	0.88	15.56	2
Heteromycteris capensis	2b	0.05	1.92	6	0.03	0.51	13
Rhabdosargus holubi	2a	0.04	1.57	7	0.22	3.84	7
Pomadasys olivaceum	3	0.03	1.03	8	0.05	0.80	10
Caffrogobius nudiceps	16	0.02	0.91	9	0.03	0.47	14
Caffrogobius gilchristi	1b	0.02	0.87	10	0.03	0.53	12
Argyrosomus japonicus	2Ъ	0.02	0.65	11	0.23	3.98	6
Gobiopsis pinto	1a?	< 0.01	0.28	12	0.01	0.09	15
Torpedo fuscomaculata	2c	< 0.01	0.21	13	0.49	8.57	3
Caffrogobius natalensis	1b	< 0.01	0.17	14	< 0.01	0.03	17
Diplodus cervinus	3	< 0.01	0.10	15	< 0.01	0.02	18
Hyporhamphus capensis	1a	< 0.01	0.04	16	< 0.01	0.01	19
Ophisurus serpens	2c	< 0.01	0.01	17	< 0.01	0.06	16
Dasyatis chrysonota	3	< 0.01	0.01	17	0.08	1.56	9
Platycephalus indicus	2c	< 0.01	0.01	17	0.28	4.96	5
Chelidonichthys kumu	3	< 0.01	0.01	17	< 0.01	< 0.01	20
Total		2 43	100		5.71	100	

Table 6.1 Mean density and standing stock of the fishes sampled during the otter trawl survey of the demersal habitat in the channel of the Kariega Estuary.

(Group=Estuarine association group, Density=numbers of fish per 10 m², Standing stock=grams of fish per 10 m²)

A total of 11 438 g of fish was caught in the otter trawl study with the channel having an average standing stock of 5.7 g per 10 m² (SE=0.53). The standing stock of fishes ranged from 2.8 g per 10 m² in March 1996 to 14.0 g per 10 m² in April 1996 (Figure 6.2). Gravimetrically *S. bleekeri* was the dominant species, contributing 48% of the total standing stock. The other species which contributed over 5% of the total standing stock were *Pomadasys commersonnii* (16%), *Torpedo fuscomaculata* (9%), *Glossogobius callidus* (8%) and *Platycephalus indicus* (5%) (Table 6.1). The dominant estuarine association group, using standing stock data, were the marine migrants (86%) followed by the estuarine spawners (12%).

When examining the life-history stages of the common fish species sampled, all of them were dominated by juveniles and only six species had adult representatives (Table 6.2).



Figure 6.1 Density and standard deviation values for the demersal ichthyofauna in the Kariega Estuary collected using an otter trawl.



Figure 6.2 Standing stock and standard deviation values for the demersal ichthyofauna in the Kariega Estuary collected using an otter trawl.

Table 6.2 Mean lengths and life-history stages of the dominant fish species caught in the otter trawl survey from June 1995 to February 1997.

Species	Number	Mean	SD	Life-history
	measured	length (mm)	_	stages present
Solea bleekeri	1972	45.8	11.4	Juveniles / Adults
Glossogobius callidus	994	35.7	10.5	Juveniles / Adults
Psammogobius knysnaensis	546	30.4	4.2	Juveniles / Adults
Gilchristella aestuaria	93	28.1	7.7	Juveniles / Adults
Pomadasys commersonnii	96	61.6	29.6	Juveniles
Heteromycteris capensis	149	35.4	5.8	Juveniles
Rhabdosargus holubi	51	49.8	28.2	Juveniles
Pomadasys olivaceum	63	39.4	9.1	Juveniles
Caffrogobius nudiceps	55	33.0	7.4	Juveniles / Adults
Caffrogobius gilchristi	58	35.1	5.8	Juveniles / Adults
Argyrosomus japonicus	22	69.7	55.2	Juveniles

OPEN WATER PELAGIC HABITAT - SURFACE TRAWL

A total of 1 731 individuals were caught in the surface trawl survey (\bar{x} CPUE=57.7 fish, SD=51.4). Altogether seven confirmed species were sampled, with *G. aestuaria* being the numerically dominant species (97 %). Almost 99 % of the catch consisted of estuarine spawners (Table 6.3).

Table 6.3 CPUE, percentage composition and rank of the fish species caught in the KariegaEstuary during the surface trawl survey.

			Numb	er		Mass				
Species	Group	z CPUE	SD	%	Rank	× CPUE	SD	%	Rank	
Gilchristella aestuaria	la	55.90	51.93	96.8	1	30.46	30.25	30.6	2	
Atherina breviceps	lb	0.83	1.13	1.4	2	1.16	1.38	1.2	3	
Liza dumerilii	2a	0.67	1.22	1.2	З	67.67	144.68	67.9	1	
Hyporhamphus capensis	la	0.13	0.34	0.2	4	0.27	0.74	0.3	4	
Mugil cephalus	5b	0.07	0.25	0.1	5	0.01	0.04	< 0.1	6	
Mugilidae (< 20 mm)		0.03	0.18	<0.1	6	< 0.01	0.02	< 0.1	7	
Monodactylus falciformis	2a	0.03	0.18	<0.1	6	0.03	0.20	< 0.1	5	
Psammogobius knysnaensis	la	0.03	0.18	<0.1	6	0.02	0.13	< 0.1	6	
Total		57.69		100.0		99.64		100.0		

(Group =Estuarine association group, Number CPUE=number of fish per two minute tow, Mass CPUE=mass (grams) of fish per two minute tow, SD=Standard deviation)

OPEN WATER PELAGIC HABITAT - GILL NETTING

Piscivore survey: A total of 234 individuals were caught in the piscivore gill netting survey (\bar{x} CPUE=39.0 fish, SD=22.3). Altogether 11 species were sampled with the dominant species being *Pomadasys commersonnii* (39%), *Argyrosomus japonicus* (26%), *Elops machnata* (9%), *Galeichthys feliceps* (7%) and *Lichia amia* (6%) (Table 6.4). The fishes caught were almost entirely marine migrants (99%).

 Table 6.4 CPUE, percentage composition and rank of the fishes caught in the piscivore gill

 netting survey of the Kariega Estuary.

Species	Group	₹ CPUE	SD	%	Rank
Pomadasys commersonnii	2a	15.17	14.30	38.9	I
Argyrosomus japonicus	2a	10.00	5.42	25.6	2
Elops machnata	2a	3.50	3.20	9.0	3
Galeichthys feliceps	2b	2.83	4.10	7.2	4
Lichia amia	2a	2.50	1.26	6.4	5
Mugil cephalus	5b	1.50	2.57	3.9	6
Monodactylus falciformis	2a	1.50	2.93	3.9	7
Liza tricuspidens	2b	1.17	1.07	3.0	8
Rhabdosargus holubi	2a	0.50	1.12	1.3	9
Liza richardsonii	2c	0.17	0.37	0.4	10
Dasyatis chrysonota	3	0.17	0.37	0.4	10
Total		39.01		100	

(Group=Estuarine association group, SD=Standard deviation, CPUE=number of fish per sampling occasion)

General survey: A total of 124 individuals were caught in this survey ($\overline{\times}$ CPUE=24.4 fish, SD =0.7). Altogether 12 species were sampled with *A. japonicus* (28%), *Liza dumerilii* (28%) and *Liza tricuspidens* (16%) being the dominant species (Table 6.5). The mugilids were the dominant family (53% of total) and were represented by four species (Table 6.5). As in the piscivore gill netting survey, the majority (97%) of the fishes caught were marine migrants.

Only two species captured in the gill net surveys, A. japonicus and Carcharias taurus, did not have adult components to their sampled populations (Table 6.6). P. commersonnii, L. dumerilii, L. tricuspidens, E. machnata, L. amia, M. falciformis and M. cephalus were all represented by both juveniles and adults (Table 6.6) with the remainder comprising adults only.

Species	Group	▼ CPUE	SD	%	Rank
Argyrosomus japonicus	2a	6.8	4.5	27.9	1
Liza dumerilii	2a	6.8	7.7	27.9	1
Liza tricuspidens	2b	4.0	4.5	16.4	3
Monodactylus falciformis	2a	1.4	1.8	5.8	4
Mugil cephalus	5b	1.4	2.8	5.8	4
Pomadasys commersonnii	2a	1.2	1.5	4.9	6
Valamugil buchanani	2c	0.8	1.2	3.3	7
Elops machnata	2a	0.6	0.8	2.5	8
Lichia amia	2a	0.6	0.5	2.5	8
Carcharias taurus	3	0.4	0.8	1.6	10
Sarpa salpa	2c	0.2	0.4	0.7	11
Hyporhamphus capensis	la	0.2	0.4	0.7	11
Total		24.4		100	

Table 6.5 CPUE, percentage composition and rank of the fishes caught in the general gill nettingsurvey of the Kariega Estuary.

(Group=Estuarine association group, SD=Standard deviation, CPUE=number of fish per sampling occasion)

Table 6.6 Mean length, range and life-history stages of the fish species sampled in both the piscivore and general gill netting surveys conducted in the Kariega Estuary.

Species	Number	Mean	SD	Range	Life-history
	measured	length (mm)		(mm)	stages present
Pomadasys commersonnii	95	295.3	50.7	170 - 520	Juveniles / Adults
Argyrosomus japonicus	93	374.8	74.7	235 - 640	Juveniles
Liza dumerilii	34	160.8	36.8	115 - 321	Juveniles / Adults
Liza tricuspidens	27	315.2	56.4	230 - 420	Juveniles / Adults
Elops machnata	24	575.7	66.6	410 - 752	Juveniles / Adults
Lichia amia	18	423.0	103.8	290 - 725	Juveniles / Adults
Galeichthys feliceps	17	313.7	27.4	280 - 420	Adults
Monodactylus falciformis	11	120.0	63.2	110 - 175	Juveniles / Adults
Mugil cephalus	10	317.5	17.6	290 - 350	Juveniles / Adults
Valamugil buchanani	4	432.5	28.6	410 - 480	Adults
Rhabdosargus holubi	3	213.3	4.7	210 - 220	Adults
Carcharias taurus	2	1025.0	5.0	1120 - 1130	Juveniles
Liza richardsonii	1	265.0			Adult
Sarpa salpa	1	255.0			Adult
Hyporhamphus capensis	1	375.0			Adult
Dasyatis chrysonota	1	450.0*			Adult

6.4 **DISCUSSION**

COMPARISON OF THE KARIEGA ESTUARY'S CHANNEL ICHTHYOFAUNA WITH OTHER SOUTHERN AFRICAN ESTUARIES

Prior to this study the use of otter trawls in South African estuaries was limited to Harrison and Whitfield's (1995) examination of the ichthyofauna in three temporarily open/closed systems in KwaZulu-Natal. The fish caught in the otter trawls in the Damba, Mhlanga and Zotsha estuaries were numerically dominated by Glossogobius callidus and Gilchristella aestuaria, whilst gravimetrically Oreochromis mossambicus was the most dominant species. The Kariega Estuary's demersal ichthyofauna was similar to that found in the three temporarily open/closed systems, in that Glossogobius callidus was also a dominant species. However, the Kariega Estuary differed greatly in that Solea bleekeri was the most dominant fish both gravimetrically and numerically, whereas this sole did not contribute more than 1% of the total composition (numbers or mass) of the fish caught in any of the three systems studied by Harrison and Whitfield (1995). G. aestuaria formed a substantial proportion (62%) of the otter trawl catch in the Mhlanga Estuary whereas very few were caught in trawls conducted in the Kariega Estuary. G. aestuaria were however abundant in the surface trawls, indicating a clear vertical separation in the distribution of this species in the Kariega channel environment. The lack of a vertical distribution pattern exhibited by G. aestuaria in the estuaries in KwaZulu-Natal may be a function of system depth and gear type used. The three estuaries in KwaZulu-Natal are far shallower than the Kariega Estuary and on occasions had an average depth of less than 50 cm (Harrison & Whitfield 1995) whereas the the otter trawl in the Kariega Estuary was usually operated in water more than 2.5 m deep. The shallowness of the temporarily open/closed estuaries in KwaZulu-Natal would have resulted in the otter trawl sampling both the demersal and middle waters, thus masking any vertical distribution of G. aestuaria in those systems. Unfortunately no comparisons could be made between the demersal ichthyofauna in the Kariega Estuary and any of the other permanently open estuaries in southern Africa to establish whether S. bleekeri or other soles (e.g. Heteromycteris capensis) are also important components of these systems.

Ichthyofaunal studies in the surface waters of southern African estuaries have been limited to a number of ichthyoplankton studies (Melville-Smith & Baird 1980, Melville-Smith 1981, Melville-Smith *et al.* 1981, Whitfield 1989a,b,c, Harris & Cyrus 1995) which targeted larvae and not

juvenile or adult fishes. For this reason the surface trawl used in the Kariega Estuary was designed to sample juvenile and adult fishes rather than larvae. The catches using the surface trawl were numerically dominated by juvenile and adult G. *aestuaria* which complements the ichthyoplankton research conducted in the middle and upper reaches of the Kariega Estuary, where G. *aestuaria* was also the dominant species (Whitfield & Paterson unpublished data).

During the 1980s and early 1990s the channel ichthyofauna of a number of permanently open estuaries was studied with the use of gill nets (Marais 1983a,b, Whitfield *et al.* 1994, Plumstead *et al.* 1985, Plumstead *et al.* 1989a,b, 1991), thus providing information on the larger marine migrant fishes which utilize these systems. The gill net catches in these estuaries were dominated by mugilids, in particular *Liza richardsonii* and *Mugil cephalus*, as well as a number of larger piscivorous species, e.g. *Argyrosomus japonicus* and *Lichia amia*. The Kariega Estuary gill net catches were very similar to other Eastern Cape estuaries with mugilids (e.g. *Liza dumerilii, Liza tricuspidens, Mugil cephalus*) and piscivorous fishes (e.g. *A. japonicus* and *L. amia*) being commonly recorded.

Whitfield *et al.* (1994) found that the marine dominated, clear Kowie Estuary had far greater numbers of *L. amia* than the freshwater dominated, turbid Great Fish Estuary. It was hypothesised that *L. amia*, being a visual predator, preferred clear water while the kob (*A. japonicus*) was better suited to the turbid environment. Further evidence for this hypothesis is that studies on the Kromme Estuary, which is also a marine dominated system, indicated the presence of far more *L. amia* than *A. japonicus* (Marais 1983a). Despite it being a marine dominated, clear water system, this hypothesis does not appear to hold true in the Kariega Estuary where *A. japonicus* were more plentiful in the catches than *L. amia*.

COMPARISON BETWEEN THE ICHTHYOFAUNA ASSOCIATED WITH THE CHANNEL

AND THOSE THAT UTILIZE INTERTIDAL SALT MARSH CREEKS AND EELGRASS BEDS

The fish assemblage of the channel environment in the Kariega Estuary differed greatly from that found in the eelgrass beds and intertidal salt marsh creeks. The numerically dominant species in all the various habitats were different, with the creeks being dominated by mullet, the eelgrass beds by *Rhabdosargus holubi*, the demersal channel environment by *S. bleekeri*, the channel surface

waters by G. aestuaria and the channel water column by mullet and larger marine piscivorous fishes. Some species, e.g. G. aestuaria, were common in almost all habitats while others had a more limited distribution. S. bleekeri for example, dominated the demersal channel environment but was absent in the channel surface waters and rare in the eelgrass beds and creeks (Chapter 4). The absence of S. bleekeri in the channel surface waters is to be expected but the creek habitat has a number of similar characteristics to the demersal channel environment. Both are unvegetated and have a sandy/muddy substratum, yet only one habitat is used extensively by flatfish. The reason for this difference in distribution may be due to the sole being cryptic and relatively sedentary and therefore not opting to use high lying intertidal habitats, and/or the lack of suitable food items for fishes in the intertidal salt marsh creek (Chapter 7).

The relative contributions of juvenile mugilids to the ichthyofaunal assemblages of the different Kariega Estuary habitats varied greatly. Within the intertidal region this family was abundant in the creeks (Chapter 2) but scarce in the eelgrass beds (Chapter 4), while in the main channel they were not caught in the demersal environment and seldom recorded in the surface waters. Visual observations in the lower reaches of the Kariega Estuary indicated that juvenile mullet frequent intertidal sandbanks during the high tide and also form schools along the edges of eelgrass beds in the upper reaches of the system. In the nearby Great Fish Estuary, which does not have salt marshes or extensive eelgrass beds in the middle reaches, mugilids are abundant in the littoral intertidal areas of the system (Ter Morshuizen *et al.* 1996). In a comparison between the ichthyofauna associated with the *Zostera* and non-*Zostera* regions in the Kromme Estuary, it was found that the dominant mullet species (*L. dumerilii*) was far more common in the unvegetated areas than in the eelgrass beds (Hanekom & Baird 1984). With limited unvegetated, shallow water habitats along the banks of the middle reaches of the Kariega Estuary, juvenile mugilids are concentrated in the intertidal creeks, avoiding the shallow water vegetated habitats and open channel environment.

A difference in the distribution of life-history stages of fishes was also apparent in the different habitats in the Kariega Estuary. The channel environment was utilized by the adults and subadults of a number of marine species which were only found as juveniles in the creeks, e.g. *P. commersonnii*, *R. holubi*, *L. dumerilii*, *M. cephalus* and *M. falciformis* (Chapter 2).

Piscivorous marine fishes (e.g. L. amia, A. japonicus and E. machnata) form a conspicuous component of the ichthyofaunal assemblage in the Kariega Estuary but have a limited distribution within the whole system. Very few piscivorous fishes were recorded in either the salt marsh creeks or eelgrass beds of the Kariega Estuary (Chapters 2 & 4), whereas in the main channel both adults and juveniles were caught in the otter trawl and gill nets. Avoidance of the littoral zone by piscivorous fishes may be linked to increased vulnerability to predation or decreased foraging ability and stranding (Ruize *et al.* 1993). At present the exact mechanisms which result in these distribution patterns remain unclear and further research is needed to elucidate them.

Chapter 7

The role of the Kariega salt marshes as feeding and refuge areas for fish

7.1 INTRODUCTION

International research has shown that salt marsh creeks act as nursery areas for many marine and estuarine fish species (Cain & Dean 1976, Morton *et al.* 1987, Knieb 1997b, Mathieson *et al.* in press a) and Chapters 2 to 5 have corroborated this general trend in a southern African context. While descriptive studies on ichthyofaunal composition and distribution are the necessary building blocks that lay the foundations for future research, they do not provide information as to why fishes utilize these habitats.

Two of the more commonly quoted criteria for a habitat to have a nursery function are that it should provide food and refuge. Despite this, the relative roles that food and refuge play in the structuring and functioning of nursery habitats are poorly understood (Baltz *et al.* 1993). Boesch and Turner (1984) state that 'implicit in the concept of salt marsh systems acting as nurseries for fish is that the shallow waters associated with the marsh provide protection for critical life-history stages'. In comparison to eelgrass and tidal freshwater marshes, little is known about the refuge function of intertidal creeks and salt marsh flats. While some studies report low densities of piscivorous fishes in tidal creeks (Shenker & Dean 1979, Reis & Dean 1981, Morton *et al.* 1987), others have shown that predatory fish species, e.g. perch and bass are caught (Hackney & de la Cruz 1981, Josselyn 1983, Teal 1986, Rountree & Able 1997). Research in the Kariega Estuary has indicated that very few primarily piscivorous fish are caught in the intertidal salt marsh creeks (Chapters 2 to 5) while these species are common in the main estuary channel (Chapter 6). One of the aims of this chapter was to validate or refute these results by simultaneously examining the distribution of piscivorous fishes in Galpin's creek and adjacent shallow and deep water habitats.

The role of salt marsh habitats in the nourishment of fishes and the provision of nutrients for both estuarine and nearshore ecosystems has been a topic of intense debate for the last three decades. The outwelling hypothesis (Odum 1980) suggests that there is a nett export of organic material from salt marshes to adjacent waters. Due largely to the conception that physical processes dominate biological ones, research was concentrated on the tidal flux of nutrients and energy rather than the role that nekton may play in their export (Deegan 1993). Salt marshes have been found to vary in their capacity to export organic matter and nutrients. Taylor and Allanson (1995) for example demonstrated the inapplicability of the outwelling hypothesis to Taylor's salt marsh.

Numerous studies have shown that fishes feed both in salt marsh creeks and on the vegetated salt marsh surface and many authors have suggested that these fishes play a role in the 'outwelling' of energy from salt marsh systems to adjacent estuarine and nearshore environments (Valiela *et al.* 1977, Bozeman & Dean 1980, Weinstein *et al.* 1980, Weinstein & Walters 1981, Weisberg & Lotrich 1982, Talbot & Able 1984, Knieb & Wagner 1994, Allen *et al.* 1995). While it has been established that there is no significant tidal export of organic carbon from Taylor's salt marsh (Taylor & Allanson 1995), this chapter aims to examine the potential that the dominant fish species frequenting Taylor's salt marsh and intertidal creek have in the transport of nutrients and energy.

7.2 MATERIALS AND METHODS

PREDATION

Sampling periodicity: Sampling was conducted in Galpin's creek as the adjacent bay and channel provided a gradation between a number of shallow and deep water sites which were both vegetated and unvegetated. Gill netting was conducted between sunset and sunrise four days prior to the new moon spring tide in January, February, March, April, May, September and October 1995. Sampling four days prior to the spring tide allowed for a nocturnal netting period of four hours in the intertidal habitats. Diurnal sampling was avoided as the clear nature of the marine dominated Kariega Estuary would have resulted in gear avoidance by most fish species.

Sampling technique: A total of eight 20 m long gill nets were set in four habitats in and adjacent to Galpin's salt marsh with two nets being set in each of the following habitats: the main estuary channel, the bay leading into Galpin's creek, the eelgrass beds adjacent to Galpin's salt marsh and Galpin's creek. The nets were set two hours prior to the spring high tide and retrieved two hours after the high tide, resulting in each net fishing the water column for a standard four hours. The nets fished the entire water column in each habitat and were constructed of green multifilament twine with a stretch mesh of 100 mm. Experimental gill netting conducted by Marais (1985) demonstrated that a 100 mm stretch mesh was very effective at catching the common piscivorous fish species inhabiting Eastern Cape estuaries.

At high tide the water depth and temperature were measured and a water sample collected so that turbidity and salinity could be measured back at the laboratory. When the nets were lifted all the fishes were removed, identified and measured.

Data analysis: The number of fishes caught were counted and a percentage species composition was calculated for each habitat. The distribution of each species between the different habitats was examined by calculating what percentage of each species was caught in each area. A Chi squared test (Fowler & Cohen 1993) was used to determine if there was a significant difference between the numbers of fish (all species, piscivorous species only, *Argyrosomus japonicus* and *Lichia amia*) caught in the different habitats. Spearman rank correlation tests (Fowler & Cohen 1993) were undertaken between the numbers of fish caught (all species and piscivorous species only) and water depth, temperature, salinity and turbidity.

FEEDING

Sampling periodicity: Two sets of block net fish samples, one dawn and one dusk, were taken per season in Taylor's creek from winter 1992 to autumn 1993 (see sampling periodicity - Chapter 2). Stomach fullness estimates were conducted on dawn and dusk samples from all four seasons while stomach content analyses were limited to winter and summer.

Sampling technique: The fishes were measured to the nearest 0.1 mm after which their stomachs were removed. The stomachs were analyzed using a modified points system (Ricker 1968, Hyslop 1980) which involved a subjective estimation of stomach fullness, after which the stomach contents were sorted into food groups according to their taxonomic similarity. Points were then allocated to each group according to the proportion they represented in relation to other groups present and the fullness of the gut. The maximum total points which could be allocated was 100 for a full stomach (Harrison 1991). The frequency of occurrence method (Hyslop 1980) was also used. This involved recording the number of stomachs in which each food item occurred and expressing it as a percentage of the total number of stomachs examined. Only the top six numerically dominant fish species caught in Taylor's creek, which accounted for over 90% of the ichthyofaunal caught, were examined.

Subjective analysis of gut fullness and food proportions has been used in salt marsh and intertidal creek studies before (Morton *et al.* 1987, 1988). However, this simple and rapid method has been criticized because of its inherent subjectivity (Hynes 1950). In order to reduce this subjectivity a number of checks and balances were employed to reduce bias in estimating stomach fullness or in the allocation of points to any food items.

- Prior to the analysis, a sample of fish from the dominant cohorts of each species were collected from different habitats in the estuary and their stomachs were removed and examined in order for the evaluator to familiarize himself with varying degrees of fullness.
- A graduated glass plate with a cover slip was used, allowing for the stomach contents to be leveled and a more accurate estimation of relative volume to be made. Similar methods were employed by Gibson & Ezzi (1978) and Rozas & La Salle (1990).

7.3 RESULTS

PREDATION

Physico-chemical parameters

The salinity and temperature of the water in the four habitats were very similar (Table 7.1) and there was no correlation between either of these two parameters and the number of fishes caught (all species and piscivorous species only). The turbidity was similar between the channel and bay and eelgrass but was higher in the creek (Table 7.1). There was also no correlation between turbidity and the numbers of fishes caught (all species and piscivorous species only). Depth did vary between the habitats, with the channel being the deepest followed by the bay, eelgrass and creek respectively (Table 7.1). There was a positive correlation between depth and the number of fishes caught (all species) on four of the seven sample periods (r_s ranged between 0.73 and 0.96, p < 0.05). A stronger correlation existed between depth and number of piscivorous fishes caught with a significant positive correlation being present on each sampling occasion (r_s ranged between 0.77 and 0.89, p < 0.05).

Composition

Channel: A total of 84 individuals representing eight species were caught in the channel, with the dominant species being *Argyrosomus japonicus*, *Lichia amia* and *Pomadasys commersonnii*. The only shark, *Carcharias taurus*, comprised 2% of the channel ichthyofauna (Table 7.2).

	Salinity		Tempera	Temperature		lity	Depth	
			(°C)		(NTI	U)	(cm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Channel	30.1	4.1	20.1	2.9	22.3	7.4	316.4	44.8
Bay	28.7	6.9	19.8	3.1	21.5	8.0	123.7	20.6
Eelgrass	30.3	3.9	19.7	2.9	24.0	8.1	90.7	18.0
Creek	30.4	3.6	19.8	2.9	30.5	11.8	74.8	16.5

Table 7.1 Physico-chemical parameters measured in Galpin's intertidal salt marsh creek and adjacent habitats from January to October 1995.

Table 7.2 Number (n), percentage composition (% C) and percentage distribution (% D) of fish species caught in Galpin's intertidal salt marsh creek and adjacent habitats from January to October 1995.

	Channel				Bay			Eelgrass			Intertidal creek		
Species	n	%D	%C	n	%D	%C	n	%D	%C	n	%D	%C	
Argyrosomus japonicus	31	77.5	36.9	7	17.5	16.6	2	5	7.2				
Elops machnata	1	50.0	1.2	1	50.0	2.3							
Carcharias taurus	2	100.0	2.4										
Galeichthys feliceps	1	4.1	1.2	12	50.0	28.5	10	41.6	35.7	1	4.1	20.0	
Lichia amia	20	86.9	23.8	3	13.0	7.1							
Mugil cephalus	11	40.7	13.0	8	29.6	19.0	7	25.9	25.0	1	3.7	20.0	
Platycephalus indicus				2	66.6	4.7	1	33.3	3.6				
Pomadasys commersonnii	16	50.0	19.0	9	28.1	21.4	5	15.6	17.8	2	6.3	40.0	
Rhabdosargus holubi							2	66.6	7.2	1	33.3	20.0	
Torpedo fuscomaculata							1	100.0	3.6				
Valamugil buchanani	2	100.0	2.4										

Bay: A total of 42 individuals representing seven species were caught in the bay, with the dominant species being Galeichthys feliceps, Mugil cephalus, Pomadasys commersionnii and Argyrosomus japonicus (Table 7.2).

Eelgrass: A total of 28 individuals representing seven species were caught in the eelgrass, with the dominant species being very similar to those in the bay, namely *Galeichthys feliceps*, *Mugil cephalus* and *Pomadasys commersonnii* (Table 7.2).

Creek: Only 5 individuals representing four species were caught in the creek, with *Pomadasys* commersonnii being the dominant species (Table 7.2).

Distribution

Different species and components of the overall catch showed significant differences in their distributions between the four habitats sampled (Table 7.2). The overall distribution of fishes was significantly different (χ^2 =78.8, P < 0.001) between the habitats, with most fishes being caught in the channel followed by the bay, eelgrass and creek (Figure 7.1). There was also a significant difference in the distribution of piscivorous fishes (χ^2 =104.8, P < 0.001) with the vast majority being caught in the channel, considerably fewer in the bay and eelgrass, and none being caught in the creek. The distributions of the two dominant piscivorous species (*Lichia amia* and *Argyrosomus japonicus*) in the study were also highly skewed (*A. japonicus* χ^2 =59.3, P < 0.001; *L. amia* χ^2 =84.8, P < 0.001). *A. japonicus* was found predominantly in the channel with smaller proportions being caught in the bay and eelgrass and none in the creek (Figure 7.1), while *L. amia* was only caught in the channel and bay (Figure 7.1).

FEEDING

Rhabdosargus holubi

Stomach fullness: Of the 189 stomachs examined 10% were empty. The remainder had a mean stomach fullness of 60% (SD=31.8). No clear seasonal trends were evident and the mean stomach fullness per sample period ranged between 44% and 64% (Figure 7.2). Of the six dominant species examined in this study *Rhabdosargus holubi* had the highest mean stomach fullness.



Figure 7.1 Catch per unit effort (average number of fish per 20 m gill net) of all species, piscivorous fish only, *Lichia amia* and *Argyrosomus japonicus* from Galpin's intertidal salt marsh creek and adjacent habitats (error bars represent one standard error).

Stomach contents: The dominant food items in the stomachs of both the winter and summer samples were amphipods (predominantly *Grandidierella* sp.), anomurans (*Upogebia africana*), crabs and polychaetes (Table 7.3). A broad range of food items were eaten, with the crustaceans forming the dominant component.

Psammogobius knysnaensis

Stomach fullness: Of the 210 stomachs examined 15% were empty. The mean stomach fullness ranged between 45% and 55% during the sample period (Figure 7.2) with the overall mean stomach fullness being 51% (SD=35.7). Of the species examined in this study *Psammogobius knysnaensis* had the second highest mean stomach fullness.

Stomach contents: A wide range of food items was consumed with the dominant prey during both winter and summer being polychaetes, copepods (predominantly *Pseudodiaptomus hessei*) and ostracods (Table 7.3). Fish were also present in the gut but formed a very small proportion of the overall stomach contents (Table 7.3).

Gilchristella aestuaria

Stomach fullness: Of the 240 stomachs examined only a small proportion were empty (17%) with the average stomach fullness being 37% (SD=30.4). The mean stomach fullness over the sample period had a greater range (24 - 46%) in comparison to *R. holubi* and *P. knysnaensis*, although few trends were discernible (Figure 7.2).

Stomach contents: The winter samples were dominated by copepods (predominantly *Pseudodiaptomus hessei*) while in summer thalassid larvae (most likely *Upogebia africana*) were the dominant item in the stomach contents (Table 7.4).

Atherina breviceps

Stomach fullness: A total of 189 stomachs were examined and 55% of these were empty. The mean stomach fullness was only 22% (SD=2.8) and ranged considerably between sample periods (Figure 7.3). *A. breviceps* were only feeding during two of the seven occasions that fish were sampled.



Figure 7.2 Stomach fullness (%) of *Rhabdosargus holubi*, *Psammogobius knysnaensis* and *Gilchristella aestuaria* collected in Taylor's intertidal salt marsh creek from winter 1992 to autumn 1993 (error bars represent one standard error).
Table 7.3 Percentage frequency of occurrence (% F) and percentage points (% P) of food items in the diet of *Rhabdosargus holubi* and *Psammogobius knysnaensis* collected in Taylor's intertidal salt marsh creek.

		Rhabdosargus holubi			Psammogobius knysnaensis				
		Win	iter	Sum	mer	Wint	er	Summer	
Number of stomachs examined		n = 30		n = 60		n = 30		n = 60	
Number of stor	achs with contents	n = 28 26 - 82		n = 54 19 - 77		n = 29 29 - 42		n = 55 19 - 44	
Lengths of fish	examined (mm)								
		% F	% P	% F	% P	% F	%P	% F	% P
Sand particles:				5.5	0.4	3.4	0.1	20.0	2.8
Particulate orga	nic matter:	21.4	7.8	1.8	0.4	6.9	1.3	23.6	3.4
Macrophytes:	Aquatic	14.2	3.9	14.8	8.8				
Algae:	Filamentous	17.8	3.9			1			
Annelida:	Polychaeta			33.3	8.6	48.2	34.4	49.0	40.0
Crustacea;	Copepoda	10.7	5.5	14.8	3.0	82.7	17.7	27.2	10.2
	Ostracoda	14.2	10.2	9.2	1.5	58.6	8.5	5.4	0.8
	Isopoda	3.5	0.7	5.5	0.7			3.6	0.5
	Amphipoda	32.1	24.5	35.1	7.1	51.7	7.9	21.8	3.9
	Tanaidacea					13.7	2.3	47.2	19.8
	Mysidacea			12.9	5.1	17.2	1.4	1.8	0.5
	Macrura			9.2	4.9	3.4	0.6	7.2	3.8
	Anomura	7.1	3.4	27.7	21.6	3.4	0.3		
	Anomura larvae			5.5	0.6				
	Brachyura	21.4	32.6	33.3	23.0			12.7	10.9
	Unidentified	32.1	3.5	50.0	11.1	44.8	7.0		
	remains								
Insecta:	Unidentified					3.4	0.3		
Mollusca:	Gastropoda	7.1	2.3	7.4	1.7				
	Pelecypoda	17.8	1.7			37.9	4.8		
Nemertea:	Unidentified			5.5	1.1				
Pisces:	Unidentified					6.9	12.8	3.6	3.4
	Eggs	_		1.8	0.4	6.9	0.6		



Figure 7.3 Stomach fullness (%) of *Atherina breviceps*, *Liza dumerilii* and Mugilidae (< 20 mm) collected in Taylor's intertidal salt marsh creek from winter 1992 to autumn 1993 (error bars represent one standard error).

Table 7.4 Percentage frequency of occurrence (% F) and percentage points (% P) of food items in the diet of *Gilchristella aestuaria* and *Atherina breviceps* collected in Taylor's intertidal salt marsh creek.

		Gilchristell		a aestua	ria	Atl	ierina br	eviceps	5
		Wir	iter	Sum	mer	Wint	er	Sumn	ner
Number of stomachs examined Number of stomachs with contents		n = 60 n = 55		n = 60 n = 53		n = 39 n = 6		n = 30 n = 11	
		% F	% P	% F	% P	% F	%P	% F	% P
Particulate organ	uc matter:	49.0	9.5	7.5	1.3			9.0	5.0
Macrophytes:	Terrestrial	9.0	1.1	1.8	0.8				
	Aquatic	16.3	2.2					18.0	25.0
Algae:	Filamentous	3.6	0.8						
	Diatoms	43.6	12.6	7.5	1.9				
Annelida:	Polychaeta								
Crustacea:	Copepoda	78.0	55.6	62.0	6.5			36.3	12.5
	Ostracoda	21.8	3.9	64.1	7.1			36.3	10.0
	Isopoda			15.0	2.4				
	Amphipoda	16.3	2.3	54.7	14.8			18.0	7.5
	Tanaidacea			7.5	0.8				
	Mysidacea			9.4	1.9			9.0	10.0
	Anomura larvae			81.0	56.1			9.0	5.0
	Brachyura larvae			28.3	4.7				
	Unidentified remains	30.9	5.1	7.5	1.4				
Insecta:	Insecta	12.7	3.9	7.5	0.5	100.0	100.0	36.3	25.0
Mollusca:	Pelecypoda	21.8	2.5						
Pisces:	Eggs	3.6	0.5						

Table 7.5 Percentage frequency of occurrence (% F) and percentage points (% P) of food items in the diet of Mugilidae (< 20 mm SL) and *Liza dumerilii* collected in Taylor's intertidal salt marsh creek.

		Mugilidae (< 20 mn		m)		Liza du	merilii		
		Win	iter	Sum	mer	Wint	er	Summer	
Number of stomachs examined Number of stomachs with contents		n = 100 n = 29		n = 100 n = 42		n = 100 n = 7		n = 100 n = 28	
		% F	% P	% F	% P	% F	%P	% F	% P
Sand particles:		93.1	52.3	54.7	9.2			85.8	56.1
Particulate organi	ic matter:	89.6	19.0	57.1 19.1		57.1	50.7	85.7	11.4
Macrophytes:	Aquatic	55.1	15.4	16.6	2.5	71.4	18.4	17.2	4.7
Algae:	Filamentous	6.9	1.6	2.3	0.1			17.8	9.6
	Unicellular							7.2	1.0
	Diatoms	82.7	11.7	30.9	3.2	85.7	29.2	78.0	13.4
Annelida:	Polychaeta			2.3	0.6				
Crustacea:	Copepoda			54.7	41.0	14.2	1.7	14.3	2.8
	Ostracoda			52.3	14.7				
	Isopoda			2.3	0.5				
	Amphipoda			2.3	0.2			3.6	1.0
Insecta:	Insecta			7.1	3.2				
Mollusca:	Gastropoda			0.4	5.7				

Atherina breviceps cont.

Stomach contents: The winter samples were dominated entirely by insects but this result was based on only six individuals. During summer insects formed the dominant part of the diet, with aquatic macrophytes and copepods also contributing significantly. As with *G. aestuaria*, thalassid larvae were present in the stomach contents of *A. breviceps* in the summer samples (Table 7.4).

Mugilidae (< 20 mm)

Stomach fullness: The majority (68%) of the 400 stomachs examined were empty with the mean stomach fullness being very low 7% (SD=16.2) (Figure 7.3).

Stomach contents: In the winter samples the stomach contents were dominated by sand particles, particulate organic matter and aquatic macrophyte detritus while in summer the stomach contents had less sand particles and noticeably more copepods and ostracods (Table 7.5).

Liza dumerilii

Stomach fullness: Of the 400 stomachs examined the vast majority (88%) were empty with the mean stomach fullness being extremely low 4% (SD=15.3). L. dumerilii had the lowest gut fullness of all the species examined and at no time were these mullet feeding (Figure 7.3). Stomach contents: The stomach contents were dominated by sand particles, particulate organic matter, aquatic macrophyte detritus and diatoms (Table 7.5).

7.4 DISCUSSION

PREDATION

One of the factors influencing fish utilization of salt marshes and their tidal creeks may be the refuge function that this habitat provides from large piscivorous fishes (Shenker & Dean 1979, Reis & Dean 1981, Boesch & Turner 1984, Rozas & Hackney 1984, Morton et al. 1987, Paterson & Whitfield 1996). Conclusive evidence for the refuge function of salt marshes and their tidal creeks has been limited, but research into tidal freshwater creeks and marshes has provided some insight into the distribution of piscivorous fishes and levels of predation on the marsh surface, intertidal creeks and subtidal environments as well as identifying some of the factors that may affect predation levels e.g. stream order and aquatic vegetation (Rozas & Odum 1987a,b,c, Rozas & Odum 1988, Rozas et al. 1988, McIvor & Odum 1988). While some of these broad principles may be applied to more saline marsh systems, since the structure and functioning of tidal freshwater marshes and creeks is similar to that of salt marsh systems, research specifically on salt marshes and their creeks is needed to corroborate much of this work. Recent studies on fish utilization of a New Jersey salt marsh creek (Rountree & Able 1997) has shown that a number of relatively large predatory fish (e.g. Pomatomus saltatrix) appear to use shallow bay and marsh creek habitats during nocturnal hours. The presence of these predatory fishes in shallow marsh creeks (subtidal and intertidal) weakens the hypothesis that shallow marsh habitats serve as refuges to 0+ juveniles (Rountree & Able 1997).

In this study no piscivorous fish were recorded in the marsh intertidal creek and very few in the other two shallow water habitats immediately adjacent to the salt marsh, viz. the eelgrass beds and shallow bay environment. The converse was true for the channel environment where high numbers of piscivorous fishes (e.g. Argyrosomus japonicus and Lichia amia) were caught (also see Chapter 6). The hypothesis that 0+ juvenile fishes in the Kariega Estuary utilize salt marsh creeks as refuges because of the low level of predation, or low threat of predation, is also supported by other evidence e.g. extensive block netting studies in these creeks which documented very few piscivorous fishes (Chapters 2 and 5). While Rountree and Able (1997) maintain that the low catches of large predatory fishes in other studies may be due to gear avoidance, block netting in the Kariega salt marsh creeks was successful in catching significant numbers of large highly mobile species such as Liza dumerilii and Pomadasys commersonnii. While catches of piscivorous fishes were always negligible in the block net samples (Chapter 2), there was always the possibility that piscivorous fishes moved into the creek to feed for very short periods during the flood tide and then moved out again before the block net was set. The results of the gill netting study, however, refute this idea as the gill nets sampled the ichthyofauna over an extended period of time, thus giving a time integrated representation of the fish community.

Predation on juvenile fishes that utilize salt marshes and their creeks is not only limited to large predatory fishes. Other possibilities include predation by juvenile conspecifics, crustaceans and birds. The stomach content analyses of the six dominant fish species found in Taylor's creek demonstrated that the majority of fishes were not feeding, while the stomach contents of those species which were feeding (e.g. *Rhabdosargus holubi* and *Gilchristella aestuaria*) did not contain any fish. In addition, a literature review of the feeding ecology of the top 20 fish species (99% of the total catch) in Taylor's creek (Table 7.6) indicated that these taxa seldom consumed fish. The dominant macro-crustaceans found on the marsh were *Paratylodiplax edwardsii*, *Sesarma catenata, Palaemon pacificus, Upogebia africana* and *Scylla serrata*, all of which are either detritivores or filter feeders. Birds have been shown to be important predators in many South African estuarine systems (Whitfield & Blaber 1979a,b,c, Siegfried 1981) and are able to feed extensively in vegetated and unvegetated shallow water areas. Avian predation was not examined but field observations during this study indicated that the majority of piscivorous birds were concentrated in the lower reaches of the estuary. Very few birds were seen feeding on the

salt marshes, which could possibly be due to their location within the estuarine system and the fact that the salt marshes are generally surrounded by high cliffs and dense vegetation. Further research is required in order to clarify the possible role of piscivorous birds in the trophic structure of the Kariega Estuary salt marshes.

It has been suggested that the low numbers of piscivorous fishes in shallow water areas within estuaries is a function of unfavourable physical conditions such as high temperatures, the physical constraint of the shallow water, or both (Rozas & Odum 1987a). Water temperature, salinity and turbidity were not found to be correlated to the distribution of piscivorous fish species in this study, while water depth was found to show a strong positive correlation with the number of piscivores recorded. The low numbers of large piscivorous fishes in the shallow areas may also be a result of increased vulnerability to predation and/or decreased foraging ability (Ruiz *et al.* 1993).

FEEDING

The results of the feeding study have shown that the mugilids, which were the dominant fishes caught in Taylor's creek, had very low stomach fullness values. This result is in contrast to a number of other studies which have shown that fishes frequenting salt marshes and their creeks in both Australia and North America foraged in these habitats (Knieb & Stiven 1978, Byrne 1978, Kleypas & Dean 1983, Morton *et al.* 1987, Rozas & LaSalle 1990, Allen *et al.* 1995). Feeding studies on mullet in southern African estuaries have shown that these fishes are detritivores with benthic micro-algae forming an important component of their diet (Masson & Marais 1975, Blaber 1976). Benthic micro-algal surveys conducted on the creek surface as well as the main creek shallows indicated a considerably lower concentration of micro-algal availability in the creek compared to the estuary channel (Adams pers.comm.), which may have accounted for the lack of feeding by mullet in the former area. In Taylor's creek no fish were found to feed directly on detrital matter as was found for menhaden in some North American salt marshes in North Carolina feed primarily on vascular plant detritus, demonstrating an efficient direct link from marsh primary production to fishery utilization (Lewis & Peters 1984).

Table 7.6 A literature review of the dominant food items recorded for the 20 most common fish species caught in Taylor's intertidal salt marsh creek. Food items recorded from the literature were from the same size range of fish as those caught in Taylor's intertidal salt marsh creek.

Species	Dominant food items	References
Liza dumerilii	Particulate organic matter, diatoms, macrophytic plant material, foraminiferans and gastropods.	Masson & Marais 1975, Blaber 1976, 1977, Blaber & Whitfield 1977.
Gilchristella aestuaria	Copepods, ostracods, mysids, macruran larvae, amphipods, chironomid larvae and diatoms.	Coetzee 1982a, White & Bruton 1983, Talbot 1982, Bennett 1989, Cyrus et al.
Mugil cephalus	Particulate organic matter, diatoms, macrophytic plant material, foraminiferans and gastropods.	1993. Masson & Marais 1975, Blaber 1977.
Diplodus sargus capensis	Harpacticoid copepods, polychaetes and amphipods.	Whitfield 1985.
Atherina breviceps	Copepods, amphipods, isopods, ostracods, gastropods and insect larvae.	Blaber 1979, Coetzee 1982a, Bennett 1989, Bennett & Branch 1990, Hecht & van der Lingen 1992.
Psammogobius knysnaensis	Amphipods, polychaetes, isopods, insect larvae, decapods, copepods and ostracods.	Whitfield 1988, Bennett 1989, Bennett & Branch 1990.
Rhabdosargus holubi	Filamentous algae, aquatic macrophytes and epibenthic invertebrates.	Blaber 1974, Whitfield 1984, 1985, de Wet & Marais 1990.
Liza tricuspidens	Filamentous algae, macrophytic plant material, epiphytic diatoms and foraminiferans.	Masson & Marais 1975, Blaber 1976, 1977.
Rhabdosargus globiceps	Isopods, amphipods, decapods and copepods.	Talbot 1955, Bennett 1989.
Pomadasys commersonnii	Pelagic copepods and mysids.	Wooldridge & Bailey 1982.
Glossogobius callidus	Amphipods and chironomid larvae.	Whitfield 1988.
Terapon jarbua	Copepods and amphipods,	Whitfield 1985.
Myxus capensis	Particulate organic matter, pennate diatoms, terrestrial plant debris and filamentous algae.	Blaber 1976, 1977.
Caffrogobius natalensis	No data - possibly similar to Caffrogobius gilchristi.	
Pomadasys olivaceum	Amphipods, polychaetes, brachyurans and anomurans.	Day et al. 1981.
Monodactylus falciformis	Copepods, isopods, amphipods and insects.	Whitfield 1984.
Caffrogobius gilchristi	Amphipods, isopods, brachyurans, insect larvae, macrurans, anomurans, poychaetes and small fish.	Whitfield 1988, Bennett & Branch 1990.
Liza richardsonii	Particulate organic matter, diatoms, aquatic macrophytes, filamentous algae and unicellular algae.	Masson & Marais 1975, Whitfield 1988.
Solea bleekeri	Benthic crustaceans.	Cyrus & Martin 1991.
Sarpa salpa	Harpacticoid copepods.	Whitfield 1985.

Knieb and Wagner's (1994) examination of nekton use of vegetated marsh habitats at different stages of tidal inundation revealed that fish species have differing potentials for exporting intertidal salt marsh production to other estuarine and coastal environments because of different life-histories and intertidal migration patterns. While Knieb & Wagner's study documented how far fishes penetrated the vegetated marsh surface, similar principles could be applied to the distance that different fish species move up an intertidal creek. Those species which were found to be feeding in Taylor's creek (*viz. Rhabdosargus holubi* and *Gilchristella aestuaria*) had a limited distribution. Both *R. holubi* and *G. aestuaria* were found predominantly in the lower or middle reaches (Chapter 3) with few individuals occurring in the upper reaches of the creek. Therefore their limited distribution would restrict their ability to export intertidal salt marsh production. Ironically the mullet, which were more widely distributed and would have a greater potential to export organic material and nutrients, did not feed within the creek. The only common species which fed in and was distributed throughout the creek system was *Psammogobius knysnaensis*.

Numerous studies have shown that salt marsh creeks are the conduits for many fish species to reach the salt marsh surface itself. It has been established that when tides are high enough to inundate marshes, killifish move over the marsh surface where they feed extensively on the marsh fauna before returning to the creek as the tide falls (Rozas & La Salle 1990). It has also been demonstrated that some fish allowed access to the marsh surface have far higher growth rates than those individuals of the same species denied access (Weisberg & Lotrich 1982). While many studies have documented fishes moving onto and feeding on both tidal freshwater marshes and salt marsh vegetated flats (Harrington & Harrington 1961, Weisberg *et al.* 1981, Weisberg & Lotrich 1982, Kleypas & Dean 1983, Morton *et al.* 1988, Rozas & La Salle 1990, Knieb 1997b), such foraging behaviour does not appear to apply to Taylor's salt marsh where only a small percentage of the overall ichthyofauna were ever found over the vegetated flats (Chapter 3).

While the premise that salt marshes and their creeks act as important foraging areas to juvenile fishes, and in so doing form an important link between salt marshes and other estuarine and nearshore habitats, appears to be true for regularly flooded North American marsh systems (Knieb 1997b), it does not seem to be applicable to Taylor's salt marsh. The fact that few fishes venture

onto the vegetated salt marsh flats, that the dominant species do not feed extensively in the creek, and that those taxa which do so have a limited distribution, precludes the possibility of fishes acting as a significant conduit for the extensive export of nutrients and energy out of Taylor's salt marsh. Further research concentrating on other transient nekton, such as invertebrates, that may venture onto Taylor's creek needs to be undertaken to establish whether they may facilitate the transport of nutrients and energy.

Chapter 8

A stable carbon isotope study of the food web in the Kariega Estuary, with particular emphasis on the fishes

8.1 INTRODUCTION

In many aquatic food webs more energy flows through detritus pathways than through grazer food chains (Mann 1988). Until recently it was assumed that in salt marsh dominated estuaries vascular plants supported food webs both within the marsh and in the adjacent water column via detritus based food chains (Sullivan & Moncrieff 1990). The importance of salt marshes as an energy source for estuarine nekton was regarded as being dependent on the amount of detritus that the marsh produced and the ability of the nekton to assimilate the energy bound within that detritus. Initial research into salt marsh dominated estuaries indicated that the high productivity of marshes may contribute significantly to the detrital pool within the estuary through the exportation of organic matter (Teal 1962, Odum & de la Cruz 1967). This export of organic material from salt marshes into estuaries and coastal waters formed the basis for the outwelling hypothesis (Odum 1980). However, further research (Dame *et al.* 1986, Roman & Daiber 1989, Dame *et al.* 1991, Baird & Winter 1992, Taylor & Allanson 1995) into the interactions between salt marshes and their adjacent waters has shown that salt marshes vary in their ability to export organic matter.

Due to the nature of detritus, the composition and assimilation of its various fractions by estuarine nekton has been difficult to ascertain. Stable isotopic ratios of an organism's tissues provide a measure of the assimilated (not just ingested) time integrated diet of an animal. When these isotope ratios of an animal's tissue are compared to the ratios of the dominant primary producers in a system, both allochthonous and autochthonous, source and process data on the animal's diet can be inferred. This technique therefore offers a unique way to study detrital food webs in estuaries (Peterson & Fry 1987). Since the initial stable isotope studies on the nekton of the tidal creeks and rivers of Sapelo Island, Georgia USA, first showed that the deposit feeding crabs, mud snails and filter feeding bivalves did not have carbon isotope ratios which corresponded to those of the dominant salt marsh grass (*viz. Spartina*) but rather an algal based diet, there has been an ongoing debate as to the importance of vascular plant detritus to estuarine nekton (Haines 1976, 1977, Haines & Montague 1979, Peterson *et al.* 1980, Sherr 1982, Hughes & Sherr 1983, Peterson *et al.* 1986, Couch 1989, Sullivan & Moncreiff 1990, Currin *et al.* 1995, Kwak & Zedler 1997, Page 1997).

Stable carbon isotope analysis in South African estuaries has been limited (de Villiers 1990, Jerling & Wooldridge 1995, Schlacher & Wooldridge 1996). The work of Jerling & Wooldridge (1995) and Schlacher & Wooldridge (1996) on the Sundays and Gamtoos systems, both of which have a perennial freshwater input, phytoplankton blooms and limited aquatic macrophyte resources, has emphasized the importance of phytoplankton as a carbon source for nekton. In the marine dominated Kariega Estuary, de Villiers (1990) found that the infaunal bivalve *Solen cylindraceus* utilized a depleted source of carbon, most likely terrestrial plant detritus rather than that of the enriched dominant estuarine macrophytes *Zostera capensis* and *Spartina maritima*. This chapter aims, through the use of carbon isotopes, to ascertain the extent to which the dominant salt marsh plants are utilized as an energy source by the fishes and invertebrates in the Kariega Estuary.

8.2 MATERIALS AND METHODS

Samples for carbon isotope analysis were collected in September 1993 and October 1994. All sampling was restricted to the middle reaches of the Kariega Estuary between Galpin's and Grant's salt marshes.

SAMPLE COLLECTION AND PREPARATION

Fish

All fishes were collected in the main channel. Where possible fish were kept overnight in filtered estuarine water to allow for gut clearance. If this was not possible, or if the fish died during the overnight purging period, the contents of the stomach and intestine were removed. At least 10 individuals of a given species were then pooled, homogenised and freeze dried. In the case of larger species, which could not be homogenised whole, approximately equal weights of dorsal muscle were collected from each individual, pooled and then freeze dried. Muscle tissue was selected as it is easy to sample and is known to have a carbon isotope ratio similar to that of whole fish (Fry 1977).

As many fish species utilize estuaries for only part of their life-history, sampling was restricted to those cohorts known to have spent the majority of their life within the confines of the Kariega Estuary. Thus both juvenile and adult members of the resident estuarine fish fauna were analysed, whereas only juveniles were analysed for those marine species which are known to use estuaries as nursery areas. The adults of these transitory species were excluded as they may have spent substantial periods of time in the marine environment.

Invertebrates

All invertebrates, with the exception of the zooplankton, were kept overnight in filtered estuarine water to allow for gut clearance. The samples of *Upogebia africana*, *Palaemon pacificus*, *Sesarma catenata* and *Paratylodiplax edwardsii* comprised more than 50 individuals which were pooled, homogenised whole and freeze dried. Due to the large size of *Scylla serrata*, only the muscle tissue of 9 specimens were pooled and analysed. Although the estuarine invertebrates sampled have a short marine larval stage, with *S. serrata* and *P. pacificus* also having a marine breeding phase, all specimens collected were of a size where they would have spent the majority of their life-history in the estuary. The zooplankton was sampled using a 200 μ m mesh conical plankton net. After the removal of detritus the samples were homogenised and freeze dried. The flesh of 25 *Solen cylindraceus* was dissected out of the shell, pooled, homogenised and then freeze dried.

Vegetation and epiphytes

All vegetation samples were rinsed in filtered estuarine water and oven dried at 50°C to a constant mass. The dried material was then ground up using a mortar and pestle. *Spartina maritima*, *Chenolea diffusa*, *Sarcocornia perennis* and *Zostera capensis* were all harvested just above the sediment surface. Tidal wrack collected along the high water mark and leaves from the overhanging terrestrial vegetation were also sampled. Epiphytes were carefully collected from submerged *Zostera capensis*, concentrated by centrifugation and then freeze dried.

Sediments

Sediment samples were collected from the intertidal creek in Taylor's salt marsh and from the main estuary channel. Ten 1.5 cm diameter core samples were removed from each area and the top 3 mm of sediment scraped onto a glass slide. The scrapings from each region were pooled and then freeze dried.

CARBON ISOTOPES

Because of the relatively small size of the carbon atom and of CO₂, biological discrimination between the two carbon isotopes ¹²C and ¹³C occurs either by passive diffusion or enzymatic selectivity (Jackson *et al.* 1986). Higher plants fall into two categories *viz.* those with low δ^{13} C values (-24 to -34‰) and those with high δ^{13} C values (-6 to -19‰), whereas algae have intermediate δ^{13} C values of between -12 to -23‰ (Smith & Epstein 1971). With the detritus of most plants retaining their isotope signature and given that the isotopic composition of an animal reflects the composition of its diet (De Niro & Epstein 1978), the carbon isotope ratio of an animal will indicate its primary food source no matter which trophic pathway it was derived from.

As with any technique, there are a number of limitations e.g. enrichment may occur between different trophic levels due to isotopic fractionation during assimilation and respiration (Fry & Sherr 1984) and one must be cautious when interpreting isotope values. This enrichment in carbon isotopes is small, typically ranging between zero and 1.0‰ per trophic level (De Niro & Epstein 1978, Fry & Sherr 1984, Peterson & Fry 1987). Changes in the δ^{13} C of plants undergoing either aerobic on anaerobic decomposition is generally low (Fry & Sherr 1984). However, *Spartina* decomposing in the sediment has a lighter δ^{13} C value than living tissue but this observed shift is typically 2‰ or less (Currin *et al.* 1995).

Estuaries are suited to carbon isotope analysis as they generally have both C_3 and C_4 plants and therefore have very distinct end members. However, ambiguity may arise when intermediate sources e.g. benthic microalgae are also available. Clarification can nonetheless be derived by the combination of more conventional techniques with stable isotope analysis.

Analysis

All carbon isotope analyses were performed by the CSIR in Pretoria, South Africa. The analytical variation of replicate analyses in this laboratory is less than 0.2‰ (A.S. Talma, pers. comm.) All samples were pre-treated with dilute HCl, washed, dried and combusted in a closed system with ultra high pressure O_2 . Resultant CO_2 was frozen out and isotope ratios measured against an internal standard calibrated to the Chicago Pee Dee belemnite standard on a VG SIRA 24 mass spectrometer. The results are reported as δ^{13} C in ‰, where δ^{13} C=(¹³C/¹²C_{sample})/(¹³C/¹²C_{PDB}) -1 X 10³.

8.3 RESULTS

STABLE ISOTOPE VALUES OF PRODUCERS

The δ^{13} C‰ values of the vegetation sampled differed greatly, with the plants either being enriched or depleted in δ^{13} C (Table 8.1 and Figure 8.1). The δ^{13} C enriched species were the eelgrass *Zostera capensis* and salt marsh cordgrass *Spartina maritima*. The δ^{13} C values of *Z. capensis* (-7.8‰ and -9.5‰) fell well within the range reported for other seagrasses (Fry *et al.* 1977, McConnaughey & McRoy 1979, Fry *et al.* 1982) and were similar to the values recorded by de Villiers (1990). The δ^{13} C values for *S. maritima* (-13.3‰ and -13.5‰) are comparable to those found for other C₄ plants and *Spartina* species (Haines 1976, Haines & Montague 1979, Sullivan & Moncrieff 1990, Currin *et al.* 1995). Although comparatively enriched in δ^{13} C (Figure 8.1), the tidal wrack material was slightly more depleted in δ^{13} C when compared to either *S. maritima* or *Z. capensis*, its major constituents (Table 8.1). The epiphytic material found on *Z. capensis*, which was a composite of both algae and other flocculated material, had a relatively enriched δ^{13} C value (-9.1‰).

The terrestrial and C₃ salt marsh plants were depleted in δ^{13} C (Figure 8.1). The three terrestrial plant species analysed had δ^{13} C values ranging from -26.2‰ to -27.8‰ (Table 8.1), well within the range of -23‰ and -30‰ which Smith and Epstein (1971) reported for terrestrial C₃ plants. Terrestrial vegetation collected by de Villiers (1990) on the mud surface in the middle reaches of the Kariega Estuary had δ^{13} C values of -23.2‰ and -25.1‰. The salt marsh plants *Chenolea diffusa* and *Sarcocornia perennis* had δ^{13} C values of -25.8‰ and -24.9‰ respectively (Table 8.1). The δ^{13} C values for the different fractions of suspended particulates ranged from -20.8‰ to -24.6‰ (de Villiers 1990)(Table 8.1). The 10-20µm fraction (-24.6‰) most closely represented the phytoplankton of the Kariega Estuary (de Villiers 1990). The sediment scrapings (Table 8.2) had intermediate δ^{13} C values, with the scrapings from the salt marsh being slightly more enriched (-18.7‰) in δ^{13} C than the channel sediment scrapings (-20.2‰).



Figure 8.1 $\delta^{13}C$ (%) values and ranges (-) of the dominant carbon sources, invertebrates and ichthyofauna found within the Kariega Estuary.

Table 8.1 δ^{13} C values (‰) of the dominant primary producers in the Kariega Estuary. Suspended particulate values after de Villiers (1990).

Plant species	Habitat	Number of samples	Mean ¹³ C values (‰)	Range
Chenolea diffusa	Salt marsh	2	-25.8	-25.426.3
Sarcocornia perennis	Salt marsh	2	-24.9	-23.926.0
Spartina maritima	Salt marsh	2	-13.4	-13.313.5
Zostera capensis	Eelgrass	2	-8.7	-7.89.5
Zostera epiphytes	Eelgrass	1	-9.1	
Peterocelastrus tricuspidatus	Terrestrial	1	-26.2	
Pittosporum viridiflorum	Terrestrial	1	-26.5	
Schotia affra	Terrestrial	1	-27.8	
Tidal wrack	Mixed	1	-14.1	
Suspended particulates:				
>20µm	Channel	1	-20.8	
10-20µm	Channel	1	-24.6	
<10µm	Channel	. 1	-21.4	

STABLE ISOTOPE VALUES OF CONSUMERS

Invertebrates

The majority of the invertebrates either had intermediate or enriched δ^{13} C values (Table 8.2 and Figure 8.1). Only two species, the mud crab *Scylla serrata* and bivalve *Solen cylindraceus*, had δ^{13} C values less than -20‰. De Villiers (1990) also reported relatively depleted δ^{13} C values (-21.6‰ and -25.3‰) for *S. cylindraceus*. The zooplankton samples were also found to be δ^{13} C depleted (-19.8‰). The most δ^{13} C enriched invertebrates were the shrimps *Alpheus crassimanus* and *Palaemon pacificus* with δ^{13} C values of -11.5‰ and -12.6‰ respectively (Table 8.2). The salt marsh crabs *Paratylodiplax edwardsii* and *Sesarma catenata* both had similar δ^{13} C values of approximately -15‰. The estuarine mudprawn *Upogebia africana* from within the salt marsh had δ^{13} C values of -15.3‰ and -15.7‰, whereas those from the channel were less enriched in δ^{13} C (-18.0‰).

Taxon	Invertebrate species and sediment samples	Estuarine habitat	Number of samples	Mean ¹³ C values <u>(</u> ‰)	Range
Macrura	Palaemon pacificus	Eelgrass	2	-12.6	-12.213.1
Macrura	Alpheus crassimanus	Eelgrass	1	-11.5	
Brachyura	Sesarma catenata	Salt marsh	2	-14.9	-14.515.3
Brachyura	Paratylodiplax edwardsii	Salt marsh	1	-15.2	
Brachyura	Scylla serrata	Channel	1	-20.7	
Anomura	Upogebia africana	Channel	1	-18.0	
Anomura	Upogebia africana	Salt marsh	2	-15.5	-15.315.7
Pelecypoda	Solen cylindraceus	Channel	1	-22.4	
	Zooplankton	Channel	2	-19.8	-19.220.4
	Sediment	Salt marsh	1	-18.7	
	Sediment	Channel	1	-20.2	

Table 8.2 δ^{13} C values (‰) of the dominant invertebrate species in the Kariega Estuary.

Fish

No fish were found to have highly depleted δ^{13} C values, with the majority of the ichthyofauna having either enriched (Group A - littoral) or intermediate (Group B - channel) δ^{13} C values (Table 8.3 and Figure 8.1). The littoral fishes all had δ^{13} C values which fell within a narrow range and were comparatively enriched in δ^{13} C (Figure 8.1). This group consisted of the gobies *Caffrogobius gilchristi* (-12.6‰), *Caffrogobius natalensis* (-11.7‰) and *Psammogobius knysnaensis* (-12.0‰); the mugilids *Liza dumerilii* (-12.6‰) and *Liza richardsonii* (-11.0‰), and the sparid *Rhabdosargus holubi* (-12.4‰). The channel group, which included the dominant piscivorous and zooplanktivorous fishes in the system, had intermediate δ^{13} C values ranging between -15.1‰ and -21.5‰. The piscivorous *Argyrosomus japonicus* (-18.7‰), *Lichia amia* (-18.8‰) and *Elops machnata* (-18.1‰) and the zooplanktivorous *Hyporhamphus capensis* (-16.9‰), *Atherina breviceps* (-17.0‰) and *Gilchristella aestuaria* (-18.9‰) all had similar δ^{13} C values (Figure 8.1). The haemulid *Pomadasys commersonnii* had δ^{13} C values ranging from -16.1‰ to -17.4‰. *Monodactylus falciformis* had the most depleted δ^{13} C values which ranged between -18.2‰ and -21.5‰.

Family	Fish species	Life-history category	Number of samples	Mean ¹³ C values (‰)	Range
Clupeidae	Gilchristella aestuaria	Estuarine	2	-18.9	-18.219.7
Atherinidae	Atherina breviceps	Estuarine	3	-17.0	-15.118.1
Gobiidae	Caffrogobius gilchristi	Estuarine	3	-12.6	-12.713.1
Gobiidae	Caffrogobius natalensis	Estuarine	1	-11.7	
Gobiidae	Psammogobius knysnaensis	Estuarine	3	-12.0	-11.712.2
Hemiramphidae	Hyporhamphus capensis	Estuarine	1	-16.9	
Sciaenidae	Argyrosomus japonicus	Marine	1	-18.7	
Carangidae	Lichia amia	Marine	3	-18.8	-18.219.5
Monodactylidae	Monodactylus falciformis	Marine	4	-19.8	-18.221.5
Sparidae	Rhabdosargus holubi	Marine	3	-12.4	-11.613.0
Haemulidae	Pomadasys commersonnii	Marine	3	-16.9	-16.117.4
Mugilidae	Liza dumerilii	Marine	3	-12.6	-11.013.6
Mugilidae	Liza richardsonii	Marine	2	-11.0	-10.511.6
Elopidae	Elops machnata	Marine	1	-18.1	

Table 8.3 δ^{13} C values (‰) of the dominant fish species in the Kariega Estuary.

8.4 DISCUSSION

The study by de Villiers (1990) on the pencil bait Solen cylindraceus in the Kariega Estuary demonstrated that this bivalve assimilated a food source depleted in δ^{13} C. This result was surprising as it had previously been assumed that the fauna in this C₄ macrophyte dominated estuary utilized the detritus from these vascular plants as their primary food source. Results from this study indicate that *S. cylindraceus* in fact has the most depleted δ^{13} C value of the 21 invertebrate and fish taxa sampled (Figure 8.1). The majority of the aquatic animals in the Kariega Estuary appear to be utilizing food resources based on more enriched forms of δ^{13} C.

The δ^{13} C values for the majority of the crustaceans and littoral fishes (Figure 8.1) indicate that they most likely assimilate enriched δ^{13} C food sources derived from Zostera capensis and its associated epiphytes as well as Spartina maritima. Although carbon isotope analysis cannot indicate the relative proportions of the different enriched carbon sources being utilized, the most likely scenario is that of a mixture of S. maritima, Z. capensis and epiphytes. With enrichment values of between 0‰ and 1‰ per trophic level (De Niro & Epstein 1978), S. maritima could be interpreted as their dominant carbon source. However, unlike most other plants, the decomposition of *Spartina* has been shown to produce detritus which is slightly more depleted in δ^{13} C relative to its living tissue (Benner *et al.* 1987, Currin *et al.* 1995). Consequently, the δ^{13} C values for the majority of the crustaceans and fishes (littoral group) indicate that they assimilate a mixture of enriched δ^{13} C food sources. Many of the species which utilize this C₄ macrophyte detrital and associated epiphytic carbon sources are also found in abundance within these habitats. All of the fishes in the littoral grouping are known to utilize either salt marshes (Paterson & Whitfield 1996) or eelgrass beds (Whitfield *et al.* 1989, Ter Morshuizen & Whitfield 1994, Chapter 4). The marsh crabs *S. catenata* and *P. edwardsii* are also known to be abundant in *Spartina* and *Zostera* stands respectively (Hodgson 1987, Taylor 1987).

Previous studies (Fry & Parker 1979, McConnaughey & McRoy 1979) have shown that rooted plants in seagrass meadows are nutritionally important for animals, but the importance of epiphytic material has generally been overlooked. Epiphytic algae may be a primary food source in seagrass meadows (Kitting *et al.* 1984). A likely candidate within the littoral group of fishes in the Kariega Estuary that may partially utilize epiphytic algae is *Rhabdosargus holubi*. This fish species is known to feed on epiphytic material by ingesting *Zostera capensis* and stripping the epiphytic layers off the leaf blades which are then passed through the gut undigested (Blaber 1974, de Wet & Marais 1990). The δ^{13} C values for *R. holubi* (Figure 8.1) support the contention that they may assimilate the epiphytic flora associated with *Z. capensis*.

Recent studies have shown that benthic microalgae may contribute significantly to salt marsh primary production (Sullivan & Moncrieff 1988, Pickney & Zingmark 1993) as well as being important components in salt marsh food webs (Sullivan & Moncreiff 1990, Currin *et al.* 1995). Research along the South African Cape coast has indicated that estuarine benthic microalgal biomass may be two to three orders of magnitude higher than that of the phytoplankton (Rodriguez 1993). Mugilidae in South African estuaries are known to feed on detritus as well as on unicellular algae and meiofauna associated with sand and mud (Blaber & Whitfield 1977, Masson & Marais 1975). The two mullet species analysed in this study, *L. dumerilii* and *L. richardsonii*, have isotope values (Table 8.3) which fall well within the range of values for benthic microalgae reported by Currin *et al.* (1995). As the Kariega Estuary has very low microbenthic algae concentrations in comparison to other South African estuaries (Adams *pers. comm.*), the C_4 macrophytes and epiphytes are probably a more significant carbon source than benthic microalgae.

The channel group of fishes, the zooplankton, Solen cylindraceus and Scylla serrata all have carbon isotope values which are more depleted in δ^{13} C than the other crustaceans or the littoral fishes. These taxa utilize food chains which are based on greater proportions of δ^{13} C depleted carbon sources, e.g. C₃ marsh plants, C₃ terrestrial vegetation or phytoplankton. The carbon isotope values of the channel group of fishes are very similar (Figure 8.1) and this group is a good example of the simple premise on which much isotope research is based, "you are what you eat". Feeding studies in South African estuaries have shown that *L. amia*, *E. machnata* and *A. japonicus* all prey extensively on small fishes such as *A. breviceps*, *G. aestuaria* and *H. capensis* (Coetzee 1982b, Smale & Kok 1983, Marais 1984) which in turn are known to feed on zooplankton (Blaber 1979, Whitfield 1980, Coetzee 1982a). The similarity in the δ^{13} C values of the fishes in the channel group and their prey, as well as the analogous conclusions of independent feeding studies, indicate how two different techniques are able to validate one another.

Although the interpretation of middle of the range carbon isotope values of consumers can be ambiguous, it has been postulated that the primary carbon source for food chains in estuarine and salt marsh channels is based mainly on phytoplankton (Peterson *et al.* 1986, Sullivan & Moncrieff 1990, Jerling & Wooldridge 1995, Schlacher & Wooldridge 1996). There is, however, evidence to suggest that this may not be the case in the macrophyte dominated Kariega Estuary. On first examination, the δ^{13} C values reported by de Villiers (1990) for suspended particulate matter (-20.8 to - 24.6‰) fall within the range for estuarine phytoplankton (Fry & Sherr 1984, Peterson & Fry 1987) and allowing for a 1‰ enrichment, match the δ^{13} C values obtained for zooplankton (Figure 8.1). However, de Villiers (1990) suggests that phytoplankton most closely matches the 10 - 20 µm fraction of the suspended particulates (-24.6‰) which, even with enrichment through a number of trophic levels, is too depleted to be a significant carbon source for the zooplankton (-19.8‰). Carbon isotope studies on other Eastern Cape estuaries have also reported depleted δ^{13} C values for phytoplankton. Jerling and Wooldridge (1995) found that in the Sundays Estuary the POC fraction with the greatest concentration of phytoplankton had δ^{13} C values of -27.0 to

-29.5‰, while Schlacher and Wooldridge (1996) calculated highly depleted δ^{13} C values (-31.2‰) for suspended particulate matter in the Gamtoos Estuary. These far more depleted δ^{13} C values for phytoplankton in the Sundays and Gamtoos estuaries, in comparison to the Kariega Estuary, can be ascribed partially to the depleted DIC values found in estuaries with a significant freshwater input.

Suspended particulate matter is composed of a complex mixture of phytoplankton, detritus, bacteria and organic particles which varies considerably both temporally and spatially with respect to size, distribution, composition and nutritional potential (Grange & Allanson 1995). In the Kariega Estuary the seston is dominated by detritus with phytoplankton stocks being extremely low (Grange & Allanson 1995). Allanson and Read (1995) demonstrated that in the Kariega Estuary only 35% of the variation in TOC was accounted for by changes in chlorophyll a, thus indicating that other sources of carbon are important. Although feeding on phytoplankton may be preferable to detritus, due to reduced fibrous material and higher nitrogen value (Mann 1988), the zooplankton in the Kariega Estuary may be limited in their selective feeding capabilities. Since the phytoplankton and detrital particles in the Kariega all fall within the nanoplanktonic size range (Grange & Allanson 1995), the zooplankton are likely to consume a mixture of these components. A number of possibilities exist in terms of the origin of the detrital portion of the seston on which the zooplankton graze. The enriched portion is undoubtedly derived from C4 macrophytes and epiphytes, while the depleted fraction could come from a mixture of C3 salt marsh plants, terrestrial vegetation and phytoplankton. The contribution made by C₃ salt marsh plants is likely to be very small as these areas are seldom inundated and organic export from Taylor's salt marsh in the Kariega Estuary, which has large stands of Chenolea diffusa and Sarcocornia perennis, has been shown to be limited (Taylor & Allanson 1995). This is in contrast to Stribling and Cornwell's (1997) study of a low salinity wetland in Chesapeake Bay where C3 plants were found to be important primary producers. As the Kariega Estuary has a very low riverine input this precludes the conventional source of terrestrial material from being considered as a major detrital source. Nonetheless, even without this riverine source terrestrial material might still be important in the Kariega Estuary. The terrestrial vegetation overhanging the intertidal zone in the middle and upper reaches could deposit a substantial amount of leaf litter into the system. In addition, the strong easterly and westerly winds which blow in summer and winter respectively may also aid in depositing terrestrial plant litter into the estuary. The Kariega River is known to flood every few years and the contribution that these pulses of freshwater have on the input of terrestrial plant material should not be underestimated. Allanson and Read (1995) demonstrated that in the nearby Keiskamma Estuary there were considerable increases in POC after flood events.

Although the Kariega Estuary is a hydrodynamically well mixed system, the location of an organism can have a profound effect on the food sources that it utilizes (Peterson *et al.* 1986). The difference in the δ^{13} C values of the detritivore *Upogebia africana* (mud prawn) between the main channel (-18.0‰) and an adjoining salt marsh (-15.5‰) can be ascribed to the composition of the detrital mixture available in each region. The mud prawns which were collected in the salt marsh were located in a stand of *Spartina maritima* and therefore had an abundant supply of δ^{13} C enriched *Spartina* detritus, whereas those collected in the main channel had a detrital source which would have included more δ^{13} C depleted sources of carbon such as phytoplankton. The sediment scrapings mirror this result, with the scrapings in the salt marsh having more enriched δ^{13} C values in comparison to those taken in the channel (Table 8.2). These results concur with those of Sherr (1982) who found that *Spartina* carbon was more important in the intertidal compared to subtidal sediments of a Georgia salt marsh estuary.

Pomadasys commersionnii is known to feed extensively on U. africana (van der Westhuizen & Marais 1977, Marais 1984) and the similar δ^{13} C (Figure 8.1) values of predator and prey support this link. This haemulid is uncommon on Taylor's salt marsh (Paterson & Whitfield 1996) but abundant in the channel of the Kariega and other Eastern Cape estuaries (Baird & Marais 1980, Plumstead *et al.* 1989a, Whitfield *et al.* 1994). Allowing for trophic enrichment, the δ^{13} C values of P. commersionnii match those of the U. africana found in the channel (Table 8.2).

The role of macrophytes in the food web of the freshwater deprived Kromme Estuary, which is similar to the Kariega in terms of size and extent of salt marshes, has recently been studied by Heymans & Baird (1995). Within the Kromme system, marsh macrophytes and halophytes were the dominant primary producers, with phytoplankton contributing very little to the overall energy flow. In addition, very little of this macrophyte and halophyte production enters the grazing food

web but it does contribute substantially to the detrital food chain. The Kromme study did not, however, discern whether only some or all of these salt marsh detrital sources were assimilated by the different estuarine organisms.



Figure 8.2 Diagrammatic representation of carbon flows within the Kariega Estuary food web.

In conclusion (Figure 8.2), a mixture of both the C4 macrophytes, Z. capensis and S. maritima are very important primary food sources for many of the dominant invertebrate and fish species in the Kariega Estuary. The relative importance of these two macrophytes does however differ with respect to the two dominant food chains within the system. The littoral pathway, which includes the littoral group of fishes as well as the majority of the crustaceans, is a δ^{13} C enriched pathway which utilizes a mix of detritus from Z. capensis and S. maritima as well as epiphytes. In the channel pathway, C₄ macrophytes counterbalanced the more depleted sources of δ^{13} C arising from a mixture of phytoplankton and terrestrial detritus. Studies elsewhere (Haines & Montague 1979, Hughes & Sherr 1983, Peterson et al. 1986) suggest that whereas the littoral fauna are more reliant on Spartina detritus, phytoplankton are more important to the filter feeding and subtidal fauna. In answering the initial question as to the importance of salt marshes in the Kariega Estuary, it would appear that the C3 salt marsh plants S. perennis and C. diffusa are not utilized as a primary food source by the nekton in the Kariega Estuary while the C₄ salt marsh plant S. maritima may be utilized by the estuarine fauna. The relative importance of the two dominant C_4 vascular plant sources Z. capensis and S. maritima to the nekton of the Kariega Estuary will only be established through a multiple isotope study. The most promising approach would be to use a combination of carbon, nitrogen and sulphur stable isotopes, but unfortunately this technique is currently unavailable in South Africa.

Chapter 9

Concluding discussion

9.1 STRUCTURE AND FUNCTION OF ICHTHYOFAUNAL ASSEMBLAGES ASSOCIATED

WITH SALT MARSHES IN THE KARIEGA AND OTHER ESTUARIES

Most ichthyofaunal salt marsh research has been conducted along the east and Gulf coasts of North America (90%) which makes worldwide comparisons between systems difficult (Connolly in press). While salt marshes in North America vary from region to region they are generally very different to those found in the Kariega Estuary as they are usually an order of magnitude larger, have a more complex network of tidal creeks and are inundated more frequently and for longer periods. Australian and European salt marshes are similar to those in the Kariega Estuary in that the vegetated salt marsh surface is only accessible to fishes on spring high tides and they have short hydroperiods (Cattrijsse *et al.* 1994, Connolly *et al.* in press, Knieb 1997b). However, Australian salt marshes differ from South African systems in that they often occupy the zone landward of mangroves (Connolly *et al.* in press).

Despite the differences in marsh size, hydroperiod, complexity and location there were a number of similarities in the characteristics of fish assemblages associated with salt marshes in the Kariega Estuary and those found elsewhere in the world. Differences were however apparent in the manner and extent to which fishes utilized salt marshes and their creeks in the various regions.

Composition: The composition of the ichthyofauna that frequented the intertidal salt marsh creeks in the Kariega Estuary (Figure 9.1) had a number of similarities to shallow tidal marsh creeks studied in North America. For example, many tidal marsh creeks in North America had a significant percentage of marine transient fish species; the fish assemblages were generally only dominated by a few species and the majority of fishes were 0+ juveniles, indicating that the habitat may serve as a nursery area (Cain & Dean 1976 - South Carolina, Weinstein 1979 - North Carolina, Bozeman & Dean 1980 - South Carolina, Weinstein & Brooks 1983 - Virginia, Smith *et al.* 1984 - Virginia, Rountree & Able 1993 - New Jersey). Research in Australia (Morton *et al.* 1987 - Queensland) and Europe (Mathieson *et al.* in press b - Scotland) also indicated that the fish fauna associated with shallow tidal salt marsh creeks in these regions were dominated by a few species of which the majority were juveniles. A study comparing the structure and functioning of fish assemblages in European salt marshes (Mathieson *et al.* in press a) has also demonstrated that salt marsh creeks in the Mira and Forth estuaries were dominated by juvenile marine taxa. South Africa's east coast is dominated primarily by an Indo-Pacific ichthyofauna (Smith & Heemstra 1986). However very few salt marsh fish studies have been conducted in this region, making geographical comparisons between the fish species and families that use these habitats difficult. One of the few studies of fishes on salt marshes indicated that a tidal creek in Moreton Bay, Australia, was dominated by mugilids and sparids (Morton *et al.* 1987), the same two families which dominated Taylor's creek (Chapter 2).

As with the Kariega creeks (Figure 9.1), the Moreton Bay tidal creek (Morton *et al.* 1987) was dominated by juvenile fishes with very few piscivorous fishes being recorded. The occurrence of large piscivorous fishes in tidal marsh creeks varies from system to system but many studies have found that shallow tidal fresh and salt water creeks have few piscivorous fishes and may therefore offer some refuge to juvenile fishes (Shenker & Dean 1979, Reis & Dean 1981, Rozas & Hackney 1984, Morton *et al.* 1987, Paterson & Whitfield 1996). On the other hand, some investigations in shallow tidal creeks have recorded piscivorous fishes e.g. sea trout, bluefish and bass (Hackney & de la Cruz 1981, Josselyn 1983, Teal 1986, McMichael & Peters 1989, Rountree & Able 1997). An examination of the feeding guilds of fishes frequenting the salt marsh creeks in the following estuarine systems, Kariega (South Africa), Cadiz Bay (Spain), Mira (Portugal), Loire (France), Westerschelde (Netherlands), Humber (United Kingdom) and Forth (United Kingdom), indicated an almost complete absence of primarily piscivorous fishes in all sites (Mathieson *et al.* in prep). This finding supports the view that tidal marshes containing fish assemblages with high proportions of juvenile individuals may provide significant refugia for life-stages vulnerable to predation (Mathieson *et al.* in prep).

Distribution: North American studies have shown that fishes frequent both tidal salt and freshwater marshes, and that within these systems there are differences in the ichthyofaunal assemblages associated with the various physiographic features e.g. creeks, vegetated marsh edge, marsh interior and high marsh pools (Zimmerman & Minello 1984, Talbot & Able 1984, Rozas & Odum 1987a, Hettler 1989, Rozas & Reed 1993, Baltz *et al.* 1993, Knieb & Wagner 1994, Peterson & Turner 1994). Fishes have been found to utilize the vegetated marsh surface in both high (Talbot & Able 1984) and low marshes (Rozas & Reed 1993). The transition zone between creeks and the vegetated marsh surface has also been shown to be very important, with many

species being concentrated in the first few metres of the marsh (Peterson & Turner 1994, Minello *et al.* 1994). In general it has been established that fishes utilizing the vegetated marsh surface are mainly resident on or near the marsh surface for their entire life cycle while those species that congregate around the marsh edge are juveniles of transient species, which spawn elsewhere in the estuary or nearshore zone (Peterson & Turner 1994).

In contrast to the findings reported above, the vegetated habitats in the salt marshes of the Kariega Estuary do not appear to be significantly utilized by fish (Figure 9.1) and no species actively seek out this habitat on the flood tide (Chapter 3). The species that stray into the *Sarcocornia perennis* and *Spartina maritima* flats were predominantly marine transient species (Chapter 3). A recent study on an inundated salt marsh flat in a temperate Australian estuary has also shown that vegetated salt marsh flats have very low densities of fishes and far fewer species than the adjacent intertidal creeks (Connolly *et al.* in press). The fishes and crustaceans in European salt marsh flats (Cattrijsse *et al.* 1994, Knieb 1997b).

These differences in the distribution of fishes in South African, European and Australian salt marshes in comparison to the North American systems is thought to be related to the hydroperiods of the marshes in the different regions (Cattrijsse *et al.* 1994, Knieb 1997b, Connolly *et al.* in press). Hydroperiod (frequency and duration of flooding) influences access to the different marsh habitats and thus controls potential habitat use (Knieb & Wagner 1994, Rozas 1995, Knieb 1997b). In comparison to North American salt marshes the dominant salt marsh vegetation occurs higher up the tidal profile in South African, Australian and European estuaries (Goodman 1958, Pierce 1979, McKee & Patrick 1988, O'Callaghan 1994, Adams & Bate 1998) and thus these marshes are only flooded during high amplitude spring tides, limiting the availability of the vegetated marsh surface as refuge and feeding areas. Other factors which may result in low utilization of the vegetated salt marsh flats in the Kariega Estuary are the lack of piscivorous fishes in the creek habitat, the difference in morphology and distribution of *Spartina maritima* in comparison to *Spartina alterniflora* and the possibility of the structurally complex, widely distributed eelgrass (*Zostera capensis*) fulfilling any ichthyofaunal need for a shallow water vegetated habitat in the Kariega Estuary (Chapter 4).

The distribution of fishes within Taylor's creek also showed distinctive species specific patterns and while the system is structurally simple, with only a single intertidal creek (stream order 1), the different reaches of the creek had substantially different fish assemblages (Chapter 3). The distribution patterns exhibited by many of the fish species in Taylor's creek is probably related to depth and the distance from the adjacent eelgrass beds. North American studies have also revealed longitudinal distribution patterns within tidal creeks, e.g. Weinstein (1979) showed that fishes tend to congregate in the upper reaches of tidal creeks in the Cape Fear River, North Carolina and Haplin (1997) demonstrated that *Fundulus heteroclitus* was found predominantly in the upper reaches of intertidal creeks in New England. Stream order has also been shown to greatly influence the distribution of fishes in a tidal freshwater marsh (Rozas & Odum 1987a) but the salt marsh creeks in the Kariega Estuary are not complex, making comparable studies difficult.

One of the biggest differences in ichthyofaunal utilization of the Kariega salt marshes, and many of those in North America, is that the former's salt marsh vegetated surface and intertidal creek are fully drained at low tide which results in almost no standing water in the system and therefore no permanent marsh residents (Chapter 3). In contrast, many salt marshes in North America have tidal creek systems and pools that do not drain fully at low tide (Peterson & Turner 1994, Knieb 1997a). The availability of standing water over low tide has resulted in many species being able to reside in the marsh system throughout the tidal cycle and their entire life-histories (Knieb 1997a,b). Indeed, many of their classification systems of fish utilization of salt marshes are orientated around whether fishes are resident on the marsh and how far they penetrate into the vegetation at high tide (Peterson & Turner 1994).



Figure 9.1 Diagrammatic representation of the characteristics of the fish assemblages associated with the dominant habitats in the Kariega Estuary.

Comparative studies in North America have found that salt marsh creeks have a distinctive ichthyofaunal assemblage when compared to other estuarine habitats e.g. eelgrass, sea lettuce, macroalgae, channels and open bay areas (Weinstein & Brooks 1983 - Delmarva Peninsula, Virginia; Sogard & Able 1991 - Little Egg Harbour Great Bay system, New Jersey; Szedlmayer & Able 1996 -Little Egg Harbour Great Bay system, New Jersey). In comparisons between tidal creeks and adjacent eelgrass beds the tidal creeks were found to have a lower diversity but higher density of fishes (Weinstein & Brooks 1983, Sogard & Able 1991). In contrast, the eelgrass beds adjacent to the salt marshes in the Kariega Estuary generally had a similar diversity but higher density and standing stock of fishes compared to the salt marsh creeks (Figure 9.1)(Chapter 4). The fish assemblage that frequented the salt marsh creeks in the Kariega Estuary was also different to that found in the main channel (Chapter 6), with the two regions having different dominant species and life-stages of fish (Figure 9.1).

Feeding and predation: The fish utilization of Taylor's salt marsh differed from findings in other systems in that the dominant fish species which occurred in the marsh did not feed (Figure 9.1). Those species which did forage were confined to the lower and middle reaches of the intertidal creek (Chapter 7). Studies in North American (Knieb & Stiven 1978, Kleypas & Dean 1983, Lewis & Peters 1984, Rozas & LaSalle 1990, Miltner *et al.* 1995, Allen *et al.* 1995), Australian (Morton *et al.* 1987, 1988) and European (Cattrijsse *et al.* 1994) estuaries have shown that fishes feed extensively in tidal marshes and their creeks. Experiments have even shown that species (e.g. *Fundulus heteroclitus*) which are experimentally restricted from foraging on the vegetated marsh surface lose weight (Weisberg & Lotrich 1982).

The role that shallow tidal creeks play as refuge areas has been widely debated. Some studies have shown low abundances of piscivorous fish (e.g. Shenker & Dean 1979, Reis & Dean 1981, Rozas & Hackney 1984, Morton *et al.* 1987, Mathieson *et al* in prep) while others have shown that predatory transient marine species are found in shallow marsh creeks and that the refuge role of shallow tidal creeks is questionable (e.g. Rountree & Able 1997). This study has shown that tidal creeks in the Kariega Estuary are areas of low fish predation as very few piscivorous fishes are found in these habitats (Figure 9.1). The dominant fish species which do frequent the salt marshes do not feed on fish and there is limited avian, conspecific and crustacean predation on fish.

Many studies (Valiela et al. 1977, Bozeman & Dean 1980, Weinstein et al. 1980, Weinstein & Walters 1981, Weisberg & Lotrich 1982, Talbot & Able 1984, Knieb & Wagner 1994, Allen et al. 1995) have cited fish as being important links through which the high production associated with marshes is exported into the adjacent estuary and nearshore zone. The lack or restricted distribution of fishes feeding on the Kariega salt marshes, as well as the refuge which this habitat provides for juvenile fishes, casts some doubt on the above scenario being the case in the Kariega salt marshes. Knieb's (1997b) 'trophic relay' hypothesis, which demonstrates how fishes are part of a mechanism by which marsh production moves horizontally across the marsh surface into the estuary, is not valid for the Kariega salt marshes as key elements of the hypothesis (e.g. that resident fishes forage on the vegetated marsh surface and that predatory fishes move into the salt marsh creeks to feed on these resident fish and other nekton) are not present in the Kariega salt marsh systems. The possible route through which marsh production could be exported out of the Kariega salt marshes by fishes is by way of those species which feed in the lower and middle reaches of the intertidal creek. However, there are also constraints on this route as one of the dominant species that forage in this region, Gilchristella aestuaria, feeds extensively on zooplankton which may be imported into the system from the main channel during the high tide. Carbon isotope values for G. aestuaria indicate that this species corresponds to those taxa which belong to the channel grouping of nekton and use a wide range of primary carbon sources including phytoplankton (Chapter 8). The role that Kariega Estuary fishes may play in transporting production off local salt marsh systems where there is limited access to the highly productive vegetated marsh must therefore be questioned.

9.2 A PRELIMINARY MODEL OF THE IMPORTANCE OF SALT MARSHES AS ENERGY SOURCES TO THE ICHTHYOFAUNA OF THE KARIEGA ESTUARY

Salt marshes are one of the most productive habitats on earth (Mitsch & Gosselink 1993, Vernberg 1993) and the role that these systems play in estuaries and the nearshore zone has been debated for over three decades. In particular the question as to whether salt marshes export organic material into estuaries, therefore providing important food sources for primary consumers and thus trophic support to adjacent estuarine and nearshore waters, has been widely investigated (Teal 1962, Odum & de la Cruz 1967, Nixon 1980, Odum 1980, 1984). A range of techniques have been employed to examine this question (see Odum 1984) with two of the major thrusts

being flux and isotope studies. The flux studies have concentrated primarily on the exchange of POC and DOC between salt marshes and the adjacent estuary through tidal action, and gave little cognisance to the functional role of nekton (Deegan 1993, Knieb 1997b). The results of these studies have shown that salt marshes vary greatly in their ability to export authochthonous production (Dame *et al.* 1986, Roman & Daiber 1989, Dame *et al.* 1991, Baird & Winter 1992, Taylor & Allanson 1995, Murray & Spencer 1997). Similarly, isotope studies which centred on whether the vascular detritus produced by salt marshes is actually assimilated (directly or indirectly) by the estuarine nekton have also come to varying conclusions as to the importance of this resource in the functioning of estuarine systems (Haines 1976, Haines & Montague 1979, Peterson *et al.* 1986, Currin *et al.* 1995, Paterson & Whitfield 1997, Stribling & Cornwell 1997).

The Kariega Estuary, its salt marshes and the fishes associated with them have been the focus of a number of studies, e.g. POC and DOC fluxes out of Taylor's marsh (Taylor & Allanson 1995); a carbon isotope analysis examining the importance of salt marshes to fishes (Paterson & Whitfield 1997, Chapter 8); the distribution and abundance of fishes in a variety of habitats (Paterson & Whitfield 1996, Chapters 2 - 6) and an appraisal of the potential for fishes to export marsh production (Chapters 7 & 9). This range of studies, using different techniques, affords the possibility to develop a conceptual model indicating:

- the principal sources of primary production;
- where this production is situated;
- whether it is exported;
- and finally if it is utilized (directly or indirectly) by the fishes in the Kariega Estuary.

The assimilation of organic carbon originating from the primary producers is predominantly indirect as few fish feed directly on living or detrital plant tissue.

Odum (1984) developed a model of the carbon sources available to primary consumers along a marsh stream order gradient. A fundamental difference between the two models is that the proposed model incorporates both the availability of organic carbon produced by the primary producers as well as whether fishes utilize it, while Odum's model concentrated only on availability. The proposed model is a generalised one as fish feeding behaviour and distribution

is complex and some species may be found in one habitat yet feed in another. In addition, the exact ratios of the carbon derived from the primary producers may differ amongst fish species due to their varying feeding habits. The model is aimed specifically at the fishes in the middle reaches of the Kariega Estuary and the role of other nekton e.g. crustaceans is not included.



Figure 9.2 Conceptual model of the availability and utilization of organic carbon derived from the dominant primary producers by 0+ juvenile fishes in the middle reaches of the Kariega Estuary.
C₃ SALT MARSH PLANTS - Sarcocornia perennis and Chenolea diffusa

Importance to fish: C_3 salt marsh plants do not form an important habitat (Chapter 3) nor act as a significant energy source to fishes in the Kariega Estuary.

Rationale: The availability of C₃ detritus is high within the salt marsh habitat (Figure 9.2) but very few fishes frequent the S. perennis or C. diffusa beds. Limited feeding occurs in the salt marsh habitat as a whole and thus the utilization of this detrital source within the system is low (Chapters 3 & 7). While it has been hypothesised that salt marshes may export organic matter into their adjacent estuary, the export of detrital material into the Kariega channel by tidal action was found to be minimal as the short hydroperiod associated with the Kariega salt marshes facilitates exchanges of gaseous carbon with the atmosphere rather than organic carbon with the estuary (Taylor & Allanson 1995). Furthermore, both S. perennis and C. diffusa form dense horizontal mats and are therefore more likely to trap detached plant material, in comparison to plants with vertical copies, resulting in decomposition within the marsh rather than export into the adjacent estuary (Taylor & Allanson 1995). The limited export of C₃ detrital matter out of the salt marsh results in low availability of this detrital source within the main channel environment (Figure 9.2). The insignificant role that both S. perennis and C. diffusa play as energy sources to the Kariega Estuary fishes is further illustrated by these plants having a highly depleted carbon isotope signature, while the majority of ichthyofauna in the estuary have an enriched signature. The considerable difference in the signatures indicates that the organic carbon originating from these primary producers is not extensively utilized by the fishes in the Kariega Estuary (Chapter 8). In contrast to the Kariega salt marshes, C₃ marsh plants have been found to be important primary producers in low salinity tidal creek systems in Chesapeake Bay (Stribling & Cornwell 1997).

C₄ SALT MARSH PLANTS - Spartina maritima

Importance to fish: Spartina maritima is not an important habitat but may be a significant energy source for fishes in the littoral reaches of the Kariega Estuary. Further research must however be undertaken to fully assess the importance of this primary producer.

Rationale: The availability of Spartina maritima detritus is high within the salt marshes of the Kariega Estuary but decreases as one moves down the intertidal zone into the main estuary channel (Figure 9.2). Despite the high availability, utilization of this detritus is low. Few fishes are found in the *S. maritima* beds and the dominant ichthyofaunal species which frequent the salt

marshes do not forage there (Chapter 7). Utilization may however be slightly higher in the lower reaches of the intertidal creek (Figure 9.2) as some fish (e.g. *R. holubi*) are found to feed there (Chapter 7).

Within the intertidal and channel regions of the estuary the role of S. maritima is questionable. Carbon isotope ratios of the dominant fishes in the Kariega Estuary indicate that some fish species which are generally found in the littoral reaches of estuaries (e.g. Caffrogobius gilchristi, Caffrogobius natalensis and Rhabdosargus holubi) utilize an isotopically enriched source of carbon which is probably derived from a mixture of S. maritima and Z. capensis (Chapter 8). Unfortunately carbon isotopes on their own cannot establish the extent to which each primary producer is being used. One hypothesis is that S. maritima detritus is a relatively important organic carbon source to fishes in the littoral reaches, but contributes less to fishes that are associated with the pelagic channel environment (Figure 9.2). This hypothesis is partly supported by the isotope study conducted on the Kariega Estuary but until a multiple isotope study is conducted it cannot be confirmed (Chapter 8). In contrast to this, a second hypothesis is that S. maritima detritus does not act as an important energy source to fishes in the Kariega Estuary at all. Taylor's salt marsh which has S. maritima beds in its lower reaches showed very little export of POC or DOC and the S. maritima marshes in the nearby Swartkops Estuary were also shown to contribute very little detritus to the estuary (Baird & Winter 1992). The salt marshes in both the Kariega and Swartkops estuaries appear to retain the bulk of their production and function as independent sub-compartments within those systems. As the majority of S. maritima in the lower and middle reaches of the Kariega Estuary is found in distinct salt marshes (rather than in thin strips along the banks of the estuary) and there is little export out of these marshes, the availability and utilization of the organic carbon derived from this primary producer will decrease rapidly as one moves away from the salt marshes and into the subtidal environment.

Other evidence indicating that *S. maritima* is not a natural energy source in South African estuaries is that this species is thought to have originated in the Northern hemisphere and may be an exotic first translocated to South Africa in the 1800s (Pierce 1979, 1982). Furthermore it can be argued that the 'Spartina paradigm' which promotes the importance of Spartina alterniflora in the functioning of many North American estuarine systems may not be valid in the South African context.

The reasons for this are that:

- S. maritima has far lower production values in comparison to S. alterniflora (Pierce 1979);
- export of macro-detritus and POC out of S. maritima salt marshes is low (Pierce 1979, Baird & Winter 1992, Winter et al. 1996);
- very few fishes are found to frequent or feed in S. maritima beds (Chapter 3 and 7);
- and it may be a relatively recently introduced plant and is thus not well integrated ecologically.

EELGRASS - Zostera capensis

Importance to fish: Zostera capensis (including its associated epiphytes) is a very important habitat and energy source to fishes in the Kariega Estuary.

Rationale: The availability of Zostera capensis as an energy source is highest in the intertidal reaches where extensive beds are found, decreasing as one moves into the subtidal environment (Figure 9.2). Fish utilization of eelgrass beds in the littoral areas of South African estuaries is high (Beckley 1983, Whitfield *et al.* 1989, Ter Morshuizen & Whitfield 1994) and many species have been shown to feed within and on this macrophyte (Blaber 1974, de Wet & Marais 1990, Whitfield 1988). Carbon isotope signatures of the dominant nekton in the Kariega Estuary have indicated that Zostera capensis and its associated epiphytes are most likely an important primary food source to fishes that are associated with the littoral reaches of the system (e.g. *C. gilchristi, C. natalensis* and *R. holubi*). Eelgrass however contributes only partially to the organic carbon utilized by fishes in the subtidal pelagic channel environment (e.g. *L. amia* and *E. machnata*) (Chapter 8).

PHYTOPLANKTON

Importance to fish: Phytoplankton is a relatively important primary producer to fish in the pelagic channel environment.

Rationale: In the Kariega Estuary the seston is dominated by detritus, with low phytoplankton stocks (Grange & Allanson 1995) resulting in the system being regarded as oligotrophic (Allanson & Read 1995). The availability of this phytoplankton is highest in the well mixed subtidal channel and then decreases towards the intertidal zone (Figure 9.2). Fish utilization of phytoplankton is

greatest by those species associated with the pelagic channel environment, declining markedly in the littoral zone. The carbon isotope signature of the phytoplankton fraction of the suspended particulates was too depleted to be a significant carbon source for many of the littoral fish species (e.g. *Rhabdosargus holubi*). However phytoplankton probably contributes to the detrital pool utilized by nekton in the channel environment (e.g. *Gilchristella aestuaria* and *Hyporhamphus capensis*) (Chapter 8).

TERRESTRIAL PLANTS

Importance to fish: In comparison to estuaries with high freshwater inputs, terrestrial plant detritus is not an important carbon source within the Kariega Estuary.

Rationale: As the intertidal reaches of the Kariega Estuary are overhung by terrestrial vegetation, terrestrial plant detritus availability is highest in this region and then decreases towards the salt marsh and subtidal channel environments (Figure 9.2). In comparison to freshwater dominated systems, the attenuated river flow associated with the Kariega Estuary results in low quantities of terrestrial plant detritus in the subtidal channel habitat. The carbon isotope signatures of fishes associated with the littoral zone (e.g. *Rhabdosargus holubi* and *Psammogobius knysnaensis*) are more enriched in comparison to the highly depleted terrestrial plants, thus eliminating terrestrial detritus as a significant contributer to the littoral organic carbon pool utilized by nekton (Chapter 8). Terrestrial plant detritus may however be one of the more isotopically depleted carbon sources utilized by nekton in the channel pathway (Chapter 8).

BENTHIC MICROALGAE

Importance to fish: Benthic microalgal availability is low throughout the Kariega Estuary and does not appear to be a dominant energy source in this system.

Rationale: In comparison to other Eastern Cape estuaries, the Kariega Estuary had very low benthic algal concentrations (Adams pers. comm.). The distribution of benthic microalgae in this estuary indicated that all the habitats sampled had reduced benthic microalgal levels, with the lowest concentrations being found in the intertidal salt marsh creeks (Adams & Paterson unpublished data). While carbon isotope values are not available for the benthic microalgae in the Kariega Estuary, carbon isotope values from the literature indicate that they could be an important energy source for mugilids (Chapter 8). The difference in availability and utilization of the energy associated with different primary producers in the various habitats within the Kariega Estuary (Figure 9.2) emphasises the need for a cautionary approach when interpreting a primary producer's importance in the functioning of a system. The fact that there is little export of macro-detritus, POC and DOC out of the salt marshes studied thus far in southern Africa, and that few fishes move into these systems to feed, indicates that the role that salt marshes play as an energy source to the adjacent estuary may be minimal. Heymans & Baird's (1995) study on the Kromme Estuary, another marine dominated Eastern Cape estuary, contends that the main primary producers within that system are the dominant salt marsh plants, with the majority of production being broken down into sediment detritus which is then utilized within the estuary. Their study did not however consider the availability of that detritus to the nekton of the system, and whether it was assimilated (directly or indirectly) or not. The results of this thesis indicate that the assumption that the majority of salt marsh detritus is available and is/can be assimilated by the nekton may be flawed.

9.3 FUTURE RESEARCH

With this project representing the commencement of ichthyofaunal research on salt marshes in southern Africa, there are a number of questions that were either not addressed or have arisen from this study. This thesis has provided fundamental information on the fish species, age structure, estuarine dependence and distribution of taxa that frequent salt marshes in the Kariega Estuary. It has also examined the possible roles that salt marshes perform as feeding and refuge areas for juvenile fishes, as well as the importance of salt marsh vegetation to the functioning of the estuarine system as a whole. However, the research was confined to one estuary and further comparative studies are needed so that the current results may be interpreted in a regional perspective. While there are a range of questions that need to be answered regarding the interaction between fish and salt marshes in South Africa, there are five areas of future research that should be concentrated on:

- The influence that both the physical attributes of salt marshes and the physico-chemical nature of the tidal water have on fish utilization of such habitats.
- Diurnal and tidal effects on the ichthyofauna that frequent salt marshes and their tidal creeks, in particular the influence of hydroperiod.

- Carbon isotope research (Chapter 8) indicated that C₃ marsh plants were not important primary producers for nekton in the Kariega Estuary. However the technique did not provide unequivocal answers about the role of the C₄ salt marsh plant *Spartina maritima*. A multiple stable isotope study using carbon, nitrogen and sulphur isotopes needs to be undertaken to establish the extent to which *S. maritima* detritus is being assimilated by the nekton in the littoral reaches of the Kariega Estuary.
- Recent research (Varnell *et al.* 1995) has indicated that high variability in the nektonic assemblages on salt marshes may occur on a daily basis. This variation in the numbers, biomass and types of fishes needs to be thoroughly investigated before a detailed appraisal of seasonal, tidal and diurnal trends in the utilization of salt marshes can be conducted.
- A thorough understanding of the utilization of salt marshes by fishes in South African estuaries can only be attained once the other components of the fauna (e.g. crustaceans) have also been studied.

In conclusion, southern African research into the utilization of salt marshes by fishes has only just begun. Hopefully this thesis has provided the foundation upon which a second generation of wider ranging investigations may be based.

References

- Adams, J.B. & Talbot, M.M. 1992. The influence of river impoundment on the estuarine seagrass Zostera capensis Setchell. Botanica Marina 35: 69-75.
- Adams, J.B. & Bate, G.C. 1998. Primary producers. In: Estuaries of South Africa (ed. B.R. Allanson & D. Baird). Cambridge University Press, Cape Town.
- Adams, S.M. 1976a. The ecology of eelgrass, Zostera marina (L.), fish communities. 1. Structural analysis. Journal of Experimental Marine Biology and Ecology 22: 269-291.
- Adams, S.M. 1976b. Feeding ecology of eelgrass communities. Transactions of the American Fisheries Society 4: 514-519.
- Allanson, B.R. & Read, G.H.L. 1995. Further comment on the response of Eastern Cape Province estuaries to variable freshwater inflows. South African Journal of Aquatic Science 21: 56-70.
- Allen, D.M., Johnson, W.S. & Ogburn-Matthews, V. 1995. Trophic relationships and seasonal utilization of salt marsh creeks by zooplanktivorous fishes. Environmental Biology of Fishes 42: 37-50.
- Baird, D. & Marais, J.F.K. 1980. Seasonality, abundance, distribution and catch per unit effort of fishes in the Swartkops Estuary. South African Journal of Zoology 15: 66-71.
- Baird, D. & Winter, P.E.D. 1992. Flux of inorganic nutrients and particulate carbon between a Spartina maritima salt marsh and the Swartkops Estuary, Eastern Cape. South African Journal of Aquatic Science 18: 64-73.
- Baltz, D.M., Rakoncinski, C. & Fleeger, J.W. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36: 109-126.
- Beckley, L.E. 1983. The ichthyofauna associated with Zostera capensis Setchell in the Swartkops estuary, South Africa. South African Journal of Zoology 18: 15-24.

- Bell, J.D. & Pollard, D.A. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In: Biology of Seagrasses (ed. A.W.D. Larkum, A.J. McComb & S.A. Shepard), pp. 565-609. Elsevier, Amsterdam.
- Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C. & Middleton, M.J. 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Australian Journal of Marine and Freshwater Science 35: 33-46.
- Bell, J.D. & Westoby, M. 1986a. Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. Journal of Experimental Biology and Ecology 90: 171-177.
- Bell, J.D. & Westoby, M. 1986b. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. Journal of Experimental Biology and Ecology 104: 249-274.
- Bell, J.D. & Westoby, M. 1986c. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68: 205-209.
- Bell, J.D., Westoby, M. & Steffe, A.S. 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? Journal of Experimental Biology and Ecology 111: 133-144.
- Benner, R., Fogel, M.L., Sprague, E.K. & Hodson, R.E. 1987. Depletion of ¹³C in lignin and its implications for stable carbon isotope studies. Nature 22: 708-710.
- Bennett, B.A. 1989. The diets of fish in three south-western Cape estuarine systems. South African Journal of Zoology 24: 163-177.

- Bennett, B.A. & Branch, G.M. 1990. Relationships between production and consumption of prey species by resident fish in the Bot, a cool temperate South African estuary. Estuarine, Coastal and Shelf Science 31: 139-155.
- Blaber, S.J.M. 1974. Field studies of the diet of *Rhabdosargus holubi* (Pisces: Teleostei: Sparidae). Journal of Zoology London 173: 407-417.
- Blaber, S.J.M. 1976. The food and feeding ecology of Mugilidae in the St Lucia Lake system.
 Biological Journal of the Linnean Society 8: 267-277.
- Blaber, S.J.M. 1977. The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. Biological Journal of the Linnean Society 9: 259-275.
- Blaber, S.J.M. 1979. The biology of filter feeding teleosts in Lake St Lucia, Zululand. Journal of Fish Biology 15: 37-59.
- Blaber, S.J.M. & Blaber, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17: 143-162.
- Blaber, S.J.M., Brewer, D.T. & Salini, J.P. 1989. Species composition and biomasses of fishes in different habitats of a tropical Northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence. Estuarine, Coastal and Shelf Science 29: 509-531.
- Blaber, S.J.M. & Whitfield, A.K. 1977. The feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. Biological Journal of the Linnean Society 9: 277-284.
- Boesch, D.F. & Turner, R.E. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460-468.
- Bozeman, E.L. & Dean, J.M. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. Estuaries 3: 89-97.

- Branch, G.M. & Grindley, J.R. 1979. Ecology of southern African estuaries Part XI. Mngazana: A mangrove estuary in the Transkei. South African Journal of Zoology 14: 149-170.
- Byrne, D.M. 1978. Life history of the spotfin killifish, *Fundulus luciae* (Pisces: Cyprinodontidae), in Fox Creek marsh, Virginia. Estuaries 1: 211-227.
- Cain, R.L. & Dean, J.M. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Marine Biology 36: 369-379.
- Carr, W.E.S. & Giesel, J.T. 1975. Impact of thermal effluent from a stream-electric station on a marshland nursery area during the hot season. Fishery Bulletin 73: 67-80.
- Cattrijsse, A., Makwaia, E.S., Dankwa, H.R., Hamerlynck, O. & Hemminga, M.A. 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. Marine Ecology Progress Series 109: 195-208.
- Caulton, M.S. 1978. The importance of habitat temperatures for growth in the tropical cichlid *Tilapia rendalli* Boulenger. Journal of Fish Biology 13: 99-112.
- Chamberlain, R.H. & Barnhart, R.A. 1993. Early use by fish of a mitigation salt marsh, Humboldt Bay, California. Estuaries 16: 769-783.
- Chong, V.C., Sasekumar, A., Leh, M.U.C. & Cruz, R.D. 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. Estuarine, Coastal and Shelf Science 31: 703-722.
- Clarke, K.R. & Warwick, R.M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth, UK, 144pp.

- Coetzee, D.J. 1982a. Stomach content analyses of *Gilchristella aestuarius* and *Hepsetia* breviceps from the Swartvlei system and Groenvlei, southern Cape. South African Journal of Zoology 17: 59-66.
- Coetzee, D.J. 1982b. Stomach content analysis of the leervis, *Lichia amia* (L.), from the Swartvlei system, southern Cape. South African Journal of Zoology 17: 177-181.
- Connolly, R.M. 1994a. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Australian Journal of Marine and Freshwater Research 45: 1033-1044.
- Connolly, R.M. 1994b. Comparison of fish catches from a buoyant pop net and beach seine net in a shallow seagrass habitat. Marine Ecology Progress Series 109: 305-309.
- Connolly, R.M. in press. A review of studies of saltmarsh as habitat for fish and nektonic crustaceans. Australian Journal of Ecology.
- Connolly, R.M., Dalton, A. & Bass, D.A. in press. Fish use of an inundated saltmarsh flat in a temperate Australian estuary. Journal of Marine and Freshwater Science.
- Couch, C.A. 1989. Carbon and nitrogen stable isotopes of meiobenthos and their food resources. Estuarine, Coastal and Shelf Science 28: 433-441.
- Currin, B.M., Reed, J.P. & Miller, J.M. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and nontidal nursery areas. Estuaries 7: 451-459.
- Currin, C.A., Newell, S.Y. & Paerl, H.W. 1995. The role of standing dead Spartina alterniflora and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Marine Ecology Progress Series 121: 99-116.

- Cyrus, D.P. & Blaber, S.J.M. 1987a. The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. Continental Shelf Research 7: 1411-1416.
- Cyrus, D.P. & Blaber, S.J.M. 1987b. The influence of turbidity on juvenile fishes in estuaries. Part
 2. Laboratory studies, comparisons with field data and conclusions. Journal of Experimental
 Biology and Ecology 109: 71-91.
- Cyrus, D.P. & Martin, T.J. 1991. The importance of estuaries in the life histories of flatfish species on the southern coast of Africa. Netherlands Journal of Sea Research 27: 255-260.
- Cyrus, D.P., Wellmann, E.C. & Martin, T.J. 1993. Diet and reproductive activity of the estuarine roundherring *Gilchristella aestuaria* in Cubhu, a freshwater coastal lake in northern Natal, South Africa. South African Journal of Aquatic Sciences 19: 3-13.
- Dame, R.F., Chrzanowski, T., Bildstein, K., Kjerfve, B., McKellar, H., Nelson, D., Spurrier, J., Stancyk, S., Stevenson, H., Vernberg, J. & Zingmark, R. 1986. The outwelling hypothesis and North Inlet, South Carolina. Marine Ecology Progress Series 33: 217-229.
- Dame, R.F., Spurrier, J., Williams, T.M., Kjerfve, B., Zingmark, R.G., Wolaver, T.G., Chrzanowski, T.H., McKellar, H.N. & Vernberg, F.J. 1991. Annual material processing by a salt marsh estuarine basin in South Carolina, USA. Marine Ecology Progress Series 72: 153-166.
- Day, J.H. 1967. The biology of the Knysna Estuary, South Africa. In: Estuaries (ed. G.H. Lauff). American Association for the Advancement of Science Publication No. 83: 397-407.
- Day, J.H., Blaber, S.J.M. & Wallace, J.H. 1981. Estuarine fishes. In: Estuarine Ecology with particular reference to southern Africa (ed. J.H. Day). pp.197-222. Balkema, Cape Town.
- Deegan, L.A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Canadian Journal of Fish and Aquatic Science 50: 74-78.

- De Niro, M.J. & Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.
- de Villiers, C.J. 1990. Aspects of the biology of the infaunal bivalve mollusc Solen cylindraceus in the Kariega Estuary. Ph.D. thesis, Rhodes University, Grahamstown, South Africa. 194 pp.
- de Wet, P.S. & Marais, J.F.K. 1990. Stomach content analysis of juvenile Cape stumpnose *Rhabdosargus holubi* in the Swartkops estuary, South Africa. South African Journal of Marine Science 9: 127-133.
- Drake, P. & Arias, A.M. 1991a. Ichthyoplankton of a shallow coastal inlet in South-west Spain: factors contributing to colonization and retention. Estuarine, Coastal and Shelf Science 32: 347-364.
- Drake, P. & Arias, A.M. 1991b. Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S.W. Spain). Journal of Fish Biology 39: 245-263.
- Eleuterius, L.N. & Eleuterius, C.K. 1979. Tide levels and salt marsh zonation. Bulletin of Marine Science 29: 394-400.
- Ferell, D.J. & Bell, J.D. 1991. Differences among assemblages of fish associated with Zostera capricorni and bare sand over a large spatial scale. Marine Ecology Progress Series 72: 15-24.
- Field, J.G., Clarke, K.R. & Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8: 37-52.
- Fowler, J. & Cohen, L. 1993. Practical statistics for field biology. Wiley and Sons, New York. 213 pp.

- Fry, B. 1977. Stable carbon isotope ratios a tool for tracing food chains. M.Sc. thesis, University of Texas, Austin. 126 pp.
- Fry, B., Lutes, R., Northam, M. & Parker, P.L. 1982. A ¹³C/¹²C comparison of food webs in Caribbean seagrass meadows and coral reefs. Aquatic Botany 14: 389-398.
- Fry, B. & Parker, P.L. 1979. Animal diet in Texas seagrass meadows: δ¹³C evidence for the importance of benthic plants. Estuarine and Coastal Marine Science 8: 499-509.
- Fry, B., Scalan, R.S. & Parker, P.L. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. Geochimica et Cosmochimica Acta 41: 1875-1877.
- Fry, B. & Sherr, E.B. 1984. δ¹³C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27: 13-47.
- Gibson, R.N. & Ezzi, I. A. 1978. The biology of a Scottish population of Fries' goby, Lesueurigobius friesii. Journal of Fish Biology 12: 371-389.
- Goodman, P.J. 1958. Biological flora of the British Isles. List of British Vascular Plants 716: 285-297.
- Gosselink, J.G. 1984. The ecology of delta marshes of coastal Louisiana: a community profile. Fish and Wildlife Service, U.S. Department of the Interior. FWS/OBS - 84/09.
- Gotceitas, V. & Colgan, P. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. Transactions of the American Fisheries Society 116: 40-49.
- Grange, N. 1992. The influence of contrasting freshwater inflows on the feeding ecology and food resources of zooplankton in two Eastern Cape estuaries, South Africa. Ph.D. thesis, Rhodes University, Grahamstown, South Africa. 230 pp.

- Grange, N. & Allanson, B.R. 1995. The influence of freshwater flow on the nature, amount and distribution of seston in estuaries of the Eastern Cape, South Africa. Estuarine, Coastal and Shelf Science 40: 403-420.
- Grange, N., Whitfield, A.K., Allanson, B.R. & de Villiers, C.J. in press. The response of two estuaries on the Eastern Cape coast of South Africa to varying freshwater inflow: implications for environmental management of freshwater resources. Aquatic Conservation: Marine and Freshwater Ecosystems.
- Hackney, C.T. & de la Cruz, A.A. 1981. Some notes on the macrofauna of an oligohaline tidal creek in Mississippi. Bulletin of Marine Science 31: 658-661.
- Haines, E.B. 1976. Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt marsh. Estuarine and Coastal Marine Science 4: 609-616.
- Haines, E.B. 1977. The origins of detritus in Georgia salt marsh estuaries. Oikos 29: 254-260.
- Haines, E.B. & Montague, C.L. 1979. Food sources of estuarine invertebrates analyzed using ¹³C/¹²C ratios. Ecology 60: 48-56.
- Hanekom, N. & Baird, D. 1984. Fish community structures in *Zostera* and non-*Zostera* regions in the Kromme estuary, St Francis Bay. South African Journal of Zoology 19: 295-301.
- Haplin, P.M. 1997. Habitat use patterns of the mummichog, *Fundulus heteroclitus*, in New England. 1. Intra marsh variation. Estuaries 20: 618-625.
- Harrington, R.W. & Harrington, E.S. 1961. Food selection among fishes invading a high subtropical salt marsh: from onset of flooding through the progress of a mosquito brood. Ecology 42: 646-666.

- Harris, S.A. & Cyrus, D.P. 1995. Occurrence of fish larvae in the St Lucia Estuary, KwaZulu-Natal, South Africa. South African Journal of Marine Science 16: 333-350.
- Harrison, T.D. 1991. A note on the diet and feeding selectivity of juvenile riverbream, Acanthopagrus berda (Forskal, 1775), in a subtropical mangrove creek. South African Journal of Zoology 26: 36-41.
- Harrison, T.D. & Whitfield, A.K. 1995. Fish community structure in three temporarily open/closed estuaries on the Natal coast. Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology 64: 80pp.
- Hecht, T. & van der Lingen, C.D. 1992. Turbidity-induced changes in feeding strategies of fish in estuaries. South African Journal of Zoology 27: 95-107.
- Heck, K.L., Able, K.W., Fahay, M.P. & Roman, C.T. 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: Species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuaries 12: 59-65.
- Heck, K.L. & Orth, R.J. 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Estuarine Perspectives (ed. V.S. Kennedy), pp. 449-464. Academic Press, New York.
- Heck, K.L. & Thoman, T.A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology 53: 125-134.
- Herke, W.H., Knudsen, E.E., Knudsen, P.A. & Rogers, B.A. 1992. Effects of semi-impoundment of a Louisiana marsh on fish and crustacean nursery use and export. North American Journal of Fisheries Management 12: 151-160.
- Hettler, W.F. 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. Marine Ecology Progress Series 56: 111-118.

- Heydorn, A.E. F. & Tinley, K.L. 1980. Estuaries of the Cape. Part1. Synopsis of the Cape Coast natural features, dynamics and utilization. C.S.I.R. Report No. 380: 97 pp.
- Heymans, J.J. & Baird, D. 1995. Energy flow in the Kromme estuarine ecosystem, St Francis Bay, South Africa. Estuarine, Coastal and Shelf Science 41: 39-59.
- Hodgson, A.N. 1987. Distribution and abundance of the macrobenthic fauna of the Kariega estuary. South African Journal of Zoology 22: 153-162.
- Hoese, H.D. & Konikoff, M. 1995. Effects of marsh management on fisheries organisms: the compensatory adjustment hypothesis. Estuaries 18: 180-197.
- Hughes, E.H. & Sherr, E.B. 1983. Subtidal food webs in a Georgia estuary: δ¹³C analysis. Journal of Experimental Marine Biology and Ecology 67: 227-242.
- Hynes, H.B.N. 1950. The food of freshwater sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius) with a review of methods used in studies of the food in fishes. Journal of Animal Ecology 19: 36-58.
- Hyslop, E.J. 1980. Stomach content analysis a review of methods and their application. Journal of Fish Biology 17: 411-429.
- Jackson, D., Harkness, D.D., Mason, C.F. & Long, S.P. 1986. Spartina anglica as a carbon source for salt marsh invertebrates: a study using δ¹³C values. Oikos 46: 163-170.
- Jerling, H.L. & Wooldridge, T.H. 1995. Relatively negative δ¹³C ratios of mesozooplankton in the Sundays River estuary, comments on potential carbon sources. South African Journal of Aquatic Science 21: 71-77.
- Josselyn, M. 1983. The ecology of San Francisco Bay tidal marshes: a community profile. Fish and Wildlife Service FWS/OBS 83/23, 102pp.

- Kelley, D.F. & Reay, P.J. 1988. The shallow creek fish communities of south west England and west Wales estuaries. Journal of Fish Biology 33: 221.
- Kitting, C.L., Fry, B. & Morgan, M.D. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. Oecologia 62: 145-149.
- Kleypas, J. & Dean, J.M. 1983. Migration and feeding of the predatory fish, *Bairdiella chrysura* (Lacepede), in an intertidal creek. Journal of Experimental Marine Biology and Ecology 72: 199-209.
- Klumpp, D.W., Howard, R.K. & Pollard, D.A. 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Biology of Seagrasses (ed. A.W.D. Larkum, A.J. McComb & S.A. Shepard), pp. 394-437. Elsevier, Amsterdam.
- Knieb, R.T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* and *Fundulus luciae*. Journal of Marine Biology and Ecology 83: 41-51.
- Knieb, R.T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. Ecology 68: 379-386.
- Knieb, R.T. 1997a. Early life stages of resident nekton in intertidal marshes. Estuaries 20: 214-230.
- Knieb, R.T. 1997b. The role of tidal marshes in the ecology of estuarine nekton. Oceanography and Marine Biology: an annual review 35: 163-220.
- Knieb, R.T. & Stiven, A.E. 1978. Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. Journal of Experimental Marine Biology and Ecology 31: 121-140.

- Knieb, R.T. & Wagner, S.L. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. Marine Ecology Progress Series 106: 227-238.
- Kwak, T.J. & Zedler, J.B. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110: 262-277.
- Lewis, V.P. & Peters, D.S. 1984. Menhaden a single step from vascular plant to fishery harvest. Journal of Experimental Marine Biology and Ecology 84: 95-100.
- Lipcius, R.N. & Subrahmanyam, C.B. 1986. Temporal factors influencing killifish abundance and recruitment in Gulf of Mexico salt marshes. Estuarine, Coastal and Shelf Science 22: 101-114.
- Loneragan, N.R., Potter, I.C., Lenanton, R.C.J. & Caputi, N. 1986. Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. Marine Biology 92: 575-586.

Long, S.P. & Mason C.F. 1983. Saltmarsh Ecology. Blackie, London, 160pp.

- Lotrich, V.A. 1975. Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. Ecology 56: 191-198.
- Lubbers, L., Boynton, W.R. & Kemp, W.M. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology Progress Series 65: 1-14.
- Mann, K.H. 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnology and Oceanography 33: 910-930.
- Marais, J.F.K. 1981. Seasonal abundance, distribution and catch per unit effort using gill-nets, of the fishes in the Sundays estuary. South African Journal of Zoology 16: 144-150.

- Marais, J.F.K. 1983a. Seasonal abundance, distribution and catch per unit effort of fishes in the Krom estuary, South Africa. South African Journal of Zoology 18: 96-102.
- Marais, J.F.K. 1983b. Fish abundance and distribution in the Gamtoos estuary with notes on the effects of floods. South African Journal of Zoology 18: 103-109.
- Marais, J.F.K. 1984. Feeding ecology of major carnivorous fish from four eastern Cape estuaries. South African Journal of Science 19: 210-223.
- Marais, J.F.K. 1985. Some factors influencing the size of fishes caught in gill nets in eastern Cape estuaries. Fisheries Research 3: 251-261.
- Masson, H. & Marais, J.F.K. 1975. Stomach content analyses of mullet from the Swartkops estuary. Zoologica Africana 10: 193-207.
- Mathieson, S., Cattrijsse, A., Costa, M.J., Drake Moyano, P., Elliott, M., Gardner, J. & Marchand, J. in press a. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Marine Ecology Progress Series.
- Mathieson, S., Cuthbert, J., Dale, K., Swift, R. & Telfer, S. in press b. Seasonal and diel variation in the nekton assemblage of an intertidal salt marsh creek in the Forth Estuary, Scotland. Estuarine, Coastal and Shelf Science.
- Mathieson, S., Paterson, A.W., Cattrijsse, A., Costa, M.J., Drake, P., Elliott, M. & Marchand,J. in prep. A comparison of the structure and function of fish assemblages in European andSouth African tidal marshes. Transactions of the Royal Society South Africa.
- McConnaughey, T. & McRoy, C.P. 1979. ¹³C label identifies eelgrass *Zostera marina* carbon in an Alaskan estuarine food web. Marine Biology 53: 263-269.

- McIvor, C.C. & Odum, W.E. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69: 1341-1351.
- McKee, K.L. & Patrick, W.H. 1988. The relationship of smooth cordgrass (Spartina alterniflora) to tidal datums. Estuaries 11: 143-151.
- McMichael, R.H. & Peters, K.M. 1989. Early life history of spotted seatrout, Cynoscion nebulosus (Pisces: Sciaenidae) in Tampa Bay, Florida. Estuaries 12: 98-110.
- Melville-Smith, R. 1981. The ichthyoplankton of the Kromme River estuary. South African Journal of Zoology 16: 71-72.
- Melville-Smith, R. & Baird, D. 1980. Abundance, distribution and species composition of fish larvae in the Swartkops estuary. South African Journal of Zoology 15: 72-78.
- Melville-Smith, R., Baird, D. & Wooldridge, T. 1981. The utilization of tidal currents by the larvae of estuarine fish. South African Journal of Zoology 16: 10-13.
- Minello, T.J. & Webb, J.W. 1997. Use of natural and created Spartina alterniflora salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. Marine Ecology Progress Series 151: 165-179.
- Minello, T.J., Zimmerman, R.J. & Medina, R. 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands 14: 184-198.

Mitsch, W.J. & Gosselink, J.G. 1993. Wetlands. 2nd edition. Van Nostrand Reinhold, New York.

Morton, R.M. 1990. Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. Marine Biology 105: 385-394.

- Morton, R.M., Beumer, J.P. & Pollock, B.R. 1988. Fishes of a subtropical Australian saltmarsh and their predation upon mosquitoes. Environmental Biology of Fishes 21: 185-194.
- Morton, R.M., Pollock, B.R. & Beumer, J.P. 1987. The occurrence and diet of fishes in a tidal inlet to a saltmarsh in southern Moreton Bay, Queensland. Australian Journal of Ecology 12: 217-237.
- Moy, L.D. & Levin, L.A. 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries 14: 1-16.
- Miltner, R.J., Ross, S.W. & Posey, M.H. 1995. Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthurus*) in tidal nurseries. Canadian Journal of Fishery and Aquatic Science 52: 971-982.
- Murray, A.L. & Spencer, T. 1997. On the wisdom of calculating annual material budgets in tidal wetlands. Marine Ecology Progress Series 150: 207-216.
- Nixon, S.W. 1980. Between coastal marshes and coastal waters A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, In: Estuarine and Wetland Processes (ed. R. Hamilton & K.B. MacDonald), pp. 437-525. Plenum Press, New York.
- O'Callaghan, M. 1994. Saltmarshes of the Cape (South Africa): Vegetation dynamics and interactions. Ph.D. thesis, University of Stellenbosch, Stellenbosch, South Africa.
- Odum, E.P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling and detritus-based food chains. In: Estuarine Perspectives (ed. V. Kennedy), pp. 437-525. Academic Press, New York.
- Odum, E.P. 1984. Dual-gradient concept of detritus transport and processing in estuaries. Bulletin of Marine Science 35: 510-521.

- Odum, E.P. & de la Cruz, A.A. 1967. Particulate organic detritus in a Georgia salt marshestuarine ecosystem. In: Estuaries (ed. G.H. Lauff), pp.383-388. American Association for the Advancement of Science Publication 83.
- Orth, R.J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: Plant-animal Interactions in the Marine Benthos, (ed. D.M. John, S.J. Hawkins & J.H. Price). Systematics Association special volume 46: 147-164.
- Orth, R.J., Heck, K.L. & van Montfrans, J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator prey relationships. Estuaries 4: 339-350.
- Page, H.M. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. Estuarine, Coastal and Shelf Science 45: 823-834.
- Paterson, A.W. & Whitfield, A.K. 1996. The fishes associated with an intertidal salt marsh creek in the Kariega Estuary, South Africa. Transactions of the Royal Society South Africa 51: 195-218.
- Paterson, A.W. & Whitfield, A.K. 1997. A stable carbon isotope study of the food web in a freshwater deprived South African estuary, with particular emphasis on the ichthyofauna. Estuarine, Coastal and Shelf Science 45: 705-715.
- Paterson, A.W. & Whitfield, A.K. in press. A comparison between the ichthyofauna associated with an intertidal salt marsh creek and adjacent eelgrass beds in the Kariega Estuary, South Africa. Environmental Biology of Fishes.
- Peterson, B.J. & Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293-320.

- Peterson, B.J., Howarth, R.W. & Garritt, R.H. 1986. Sulphur and carbon isotopes as tracers of salt marsh organic matter flow. Ecology 67: 865-874.
- Peterson, B.J., Howarth, R.W., Lipschultz, F. & Ashendorf, D. 1980. Salt marsh detritus: an alternative interpretation of stable carbon isotope ratios and the fate of *Spartina alterniflora*. Oikos 34: 173-177.
- Peterson, G.W. & Turner, R.E. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17: 235-262.
- Pickney, J. & Zingmark, R.J. 1993. Modeling intertidal benthic microalgal annual production in an estuarine ecosystem. Journal of Phycology 29: 396-407.
- Pierce, S.M. 1979. The contribution of Spartina maritima (Curtis) to the primary production of the Swartkops Estuary. M.Sc. thesis, Rhodes University, Grahamstown, South Africa. 135 pp.
- Pierce, S.M. 1982. What is *Spartina* doing in our estuaries? South African Journal of Science 78: 229-230.
- Pierce, S.M. 1983. Estimation of the non-seasonal production of *Spartina maritima* (Curtis) Fernald in a South African estuary. Estuarine, Coastal and Shelf Science 16: 241-254.
- Plumstead, E.E., Prinsloo, J.F. & Schoonbee, H.J. 1985. A survey of the fish fauna of Transkei estuaries. Part 1. Kei River estuary. South African Journal of Zoology 20: 213-220.
- Plumstead, E.E., Prinsloo, J.F. & Schoonbee, H.J. 1989a. A survey of the fish fauna of Transkei estuaries. Part 2. The Mbashe estuary. South African Journal of Zoology 24: 273-281.
- Plumstead, E.E., Prinsloo, J.F. & Schoonbee, H.J. 1989b. A survey of the fish fauna of Transkei estuaries. Part 3: The Mtata River estuary. South African Journal of Zoology 24: 282-289.

- Plumstead, E.E., Prinsloo, J.F., Schoonbee, H.J. 1991. A survey of the fish fauna of Transkei estuaries. Part 4: The Mntafufu and Mzamba River estuaries. South African Journal of Zoology 26: 153-163.
- Pollard, D.A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany 18: 3-42.
- Rakocinski, C.F., Baltz, D.M. & Fleeger, J.W. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. Marine Ecology Progress Series 80: 135-148.
- Ratte, T.H. 1989. Population structure, production, growth, reproduction and ecology of Atherina breviceps (Valenciennes, 1935) (Pisces: Atherinidae) and Gilchristella aestuaria (Gilchrist, 1914) (Pisces: Clupeidae), from two southern Cape coastal lakes. Ph.D. thesis, University of Port Elizabeth, Port Elizabeth, South Africa. 319 pp.
- Reddering, J.S.V. & Rust, I.C. 1990. Historical changes and sedimentary characteristics of southern African estuaries. South African Journal of Science 86: 425-428.
- Reis, R.R. & Dean, J.M. 1981. Temporal variation in the utilization of an intertidal creek by the Bay Anchovy (Anchoa mitchilli). Estuaries 4: 16-23.
- Ricker, R.E. 1968. Methods of assessment of fish production in fresh waters. Blackwells Scientific Publications, Oxford.
- Robertson, A.I. & Duke, N.C. 1990. Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Marine Biology 104: 369-379.

- Rodriguez, F.D.G. 1993. The determination and distribution of microbenthic and chlorophyll *a* in selected South Cape estuaries. M.Sc. thesis, University of Port Elizabeth, Port Elizabeth, South Africa. 134 pp.
- Rogers, S.G., Targett, T.E. & Van Sant, S.B. 1984. Fish-nursery use in Georgia salt-marsh estuaries: The influence of springtime freshwater conditions. Transactions of the American Fisheries Society 113: 595-606.
- Roman, C.T. & Daiber, F.C. 1989. Organic carbon flux through a Delaware Bay salt marsh: tidal exchange, particle size distribution and storms. Marine Ecology Progress Series 54: 149-156.
- Rountree, R.A. & Able, K.W. 1992. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. Estuaries 15: 171-185.
- Rountree, R.A. & Able, K.W. 1993. Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. Estuarine, Coastal and Shelf Science 37: 181-201.
- Rountree, R.A. & Able, K.W. 1997. Nocturnal fish use of a New Jersey marsh creek and adjacent bay shoal habitats. Estuarine, Coastal and Shelf Science 44: 703-711.
- Rozas, L.P. 1992a. Comparison of nekton habitats associated with pipeline canals and natural channels in Louisiana salt marshes. Wetlands 12: 136-146.
- Rozas, L.P. 1992b. Bottomless lift net for quantitatively sampling nekton on intertidal marshes. Marine Ecology Progress Series 89: 287-292.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. Estuaries 18: 579-590.
- Rozas, L.P. & Hackney, C.T. 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. Estuaries 7: 213-224.

- Rozas, L.P. & La Salle, M.W. 1990. A comparison of the diets of Gulf Killifish, Fundulus grandis Baird and Girard, entering and leaving a Mississippi brackish marsh. Estuaries 13: 332-336.
- Rozas, L.P., McIvor, C.C. & Odum, W.E. 1988. Intertidal rivulets and creek banks: corridors between tidal creeks and marshes. Marine Ecology Progress Series 47: 303-307.
- Rozas, L.P. & Minello, T.J. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20: 199-213.
- Rozas, L.P. & Odum, W.E. 1987a. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. Estuaries 10: 36-43.
- Rozas, L.P. & Odum, W.E. 1987b. The role of submerged aquatic vegetation in influencing the abundance of nekton on contiguous tidal freshwater marshes. Journal of Experimental Marine Biology and Ecology 114: 289-300.
- Rozas, L.P. & Odum, W.E. 1987c. Fish and macro-crustacean use of submerged plant beds in tidal freshwater marsh creeks. Marine Ecology Progress Series 38: 101-108.
- Rozas, L.P. & Odum, W.E. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69: 1341-1351.
- Rozas, L.P. & Reed, D.J. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. Marine Ecology Progress Series 96: 147-157.
- Ruiz, G.M., Hines, A.H. & Posey, M.H. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Marine Ecology Progress Series 99: 1-16.

- Rulifson, R.A. 1991. Finfish utilization of man initiated and adjacent natural creeks of South Creek Estuary, North Carolina using multiple gear types. Estuaries 14: 447-464.
- Savino, J.F. & Stein, R.A. 1982. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environmental Biology of Fishes 24: 287-293.
- Schlacher, T.A. & Wooldridge, T.H. 1996. Origin and trophic importance of detritus evidence from stable isotopes in the benthos of a small, temperate estuary. Oecologia 106: 382-388.
- Shenker, J.M. & Dean, J.M. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2: 154-163.
- Sherr, E.B. 1982. Carbon isotope composition of organic seston and sediments in a Georgia salt marsh estuary. Geochimica et Cosmochimica Acta 46: 1227-1232.
- Siegfried, W.R. 1981. The estuarine avifauna of southern Africa. In: Estuarine Ecology with Particular Reference to southern Africa (ed. J.H. Day). Balkema, Cape Town.
- Smale, M.J. & Kok, H.M. 1983. The occurrence and feeding of *Pomatomus saltatrix* (elf) and *Lichia amia* (leervis) juveniles in two Cape south coast estuaries. South African Journal of Zoology 18: 337-342.
- Smith, K.J. & Able, K.W. 1994. Salt-marsh tide pools as winter refuges for the mummichog *Fundulus heteroclitus*, in New Jersey. Estuaries 17: 226-234.
- Smith, S.M. & Epstein, S. 1971. Two categories of ¹³C/¹²C ratios for higher plants. Plant Physiology 47: 380-384.
- Smith, M.M & Heemstra, P.C. (ed.) 1986. Smiths' Sea Fishes. Macmillan South Africa, Johannesburg, 1048 pp.

- Smith, S.M., Hoff, J.G., O'Neil, S.P. & Weinstein, M.P. 1984. Community and trophic organisation of nekton utilizing shallow marsh habitats, York River, Virginia. Fisheries Bulletin 82: 455-467.
- Sogard, S.M. 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. Journal of Experimental Marine Biology and Ecology 133: 15-37.
- Sogard, S.M. & Able, K.W. 1991. A comparison of eelgrass, sea lettuce, macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuarine, Coastal and Shelf Science 33: 501-519.
- Stout, J.P. 1984. The ecology of irregularly flooded salt marshes of the Northeastern Gulf of Mexico: a community profile. U.S. Department of the Interior Biological Report 85 (7.1).
- Stribling, J.M. & Cornwell, J.C. 1997. Identification of important primary producers in Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. Estuaries 20: 77-85.
- Subrahmanyam, C.B. & Coultas, C.L. 1980. Studies on the animal communities in two North Florida salt marshes Part III. Seasonal fluctuations of fish and macroinvertebrates. Bulletin of Marine Science 30: 790-818.
- Subrahmanyam, C.B. & Drake, S.H. 1975. Studies on the animal communities in two North Florida salt marshes. Bulletin of Marine Science 25: 445-465.
- Sullivan, M.J. & Moncreiff, C.A. 1988. Primary production of edaphic algal communities in a Mississippi salt marsh. Journal of Phycology 24: 49-58.

- Sullivan, M.J. & Moncreiff, C.A. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. Marine Ecology Progress Series 62: 149-159.
- Szedlmayer, S.T. & Able, K.W. 1996. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. Estuaries 19: 697-709.
- Talbot, C.W. & Able, K.W. 1984. Composition and distribution of larval fishes in New Jersey high marshes. Estuaries 7: 434-443.
- Talbot, F.H. 1955. Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein River Estuary. Transactions of the Royal Society of South Africa 34: 387-407.
- Talbot, M.M.J. 1982. Aspects of the ecology and biology of *Gilchristella aestuarius* (Pisces: Clupeidae) in the Swartkops estuary, Port Elizabeth. M.Sc. thesis, University of Port Elizabeth, South Africa. 128 pp.
- Taylor, D.I. 1987. Tidal exchanges of carbon, nitrogen and phosphorus between a Sarcocornia salt marsh and the Kariega estuary, and the role of salt marsh brachyura in this transfer. Ph.D. thesis, Rhodes University, Grahamstown, South Africa. 188pp.
- Taylor, D.I. 1992. The influence of upwelling and short-term changes in concentrations of nutrients in the water column on fluxes across the surface of a salt marsh. Estuaries 15: 68-74.
- Taylor, D.I. & Allanson, B.R. 1995. Organic carbon fluxes between a high marsh and estuary, and the inapplicability of the Outwelling hypothesis. Marine Ecology Progress Series 120: 263-270.

- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.
- Teal, J.M. 1986. The ecology of regularly flooded salt marshes of New England. U.S. Department of the Interior, Fish and Wildlife Service, Biological Report 85(7.4).
- Ter Morshuizen, L.D. & Whitfield, A.K. 1994. The distribution of littoral fish associated with eelgrass *Zostera capensis* beds in the Kariega Estuary, a southern African system with a reversed salinity gradient. South African Journal of Marine Science 14: 95-105.
- Ter Morshuizen, L.D., Whitfield, A.K. & Paterson A.W. 1996. Distribution patterns of fishes in an Eastern Cape estuary and river with particular emphasis on the ebb and flow region. Transactions of the Royal Society South Africa 51: 257-280.
- Thayer, G.W., Colby, D.R. & Hettler, W.F. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. Marine Ecology Progress Series 35: 25-38.
- Thayer, G.W., Hoffman Stuart, H., Kenworthy, W.J., Ustach, J.F. & Hall, A.B. 1978. Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. American Water Research Association, November: 235-247.
- Valiela, I., Wright, J.E., Teal, J.M. & Volkmann, S.B. 1977. Growth, production and energy transformations in salt marsh killifish *Fundulus heteroclitus*. Marine Biology 40: 135-144.
- van der Westhuizen, H.C. & Marais, J.F.K. 1977. Stomach content analyses of *Pomadasys* commersonnii from the Swartkops estuary. Zoologica Africana 12: 500-504.
- Varnell, L.M., Havens, K.J. & Hershner, C. 1995. Daily variability in abundance and population characteristics of tidal salt-marsh fauna. Estuaries 18: 326-334.
- Vernberg, J.F. 1993. Salt marsh processes: A review. Environmental Toxicology and Chemistry 12: 2167-2195.

- Wallace, J.H. 1975. The estuarine fishes of the east coast of South Africa. Part 3. Reproduction. Investigational Report of the Oceanographic Research Institute 41: 1-48.
- Washington, H.G. 1984. Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. Water Research 18: 653-694.
- Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fisheries Bulletin 77: 339-357.
- Weinstein, M.P. & Brooks, H.A. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Marine Ecology Progress Series 12: 15-27.
- Weinstein, M.P. & Davis, R.W. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. Estuaries 3: 98-105.
- Weinstein, M.P., Scott, L., O'Niel, S.P., Siegfreid, R.C. & Szedlmayer, S.T. 1984. Population dynamics of spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River estuary, Virginia. Estuaries 7: 444-450.
- Weinstein, M.P. & Walters, M.F. 1981. Growth, survival and production in young-of-year populations of *Leiostomus xanthurus* Lacepede residing in tidal creeks. Estuaries 4: 185-197.
- Weinstein, M.P., Weiss, S.L. & Walters, M.F. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear estuary, North Carolina, USA. Marine Biology 58: 227-243.
- Weisberg, S.B. & Lotrich, V.A. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the Mummichog *Fundulus heteroclitus*: an experimental approach. Marine Biology 66: 307-310.

- Weisberg, S.B., Whalen, R. & Lotrich, V.A. 1981. Tidal and diurnal influence on food consumption of a salt marsh killifish *Fundulus heteroclitus*. Marine Biology 61: 243-246.
- West, R.J. & King, R.J. 1996. Marine, brackish, and freshwater fish communities in the vegetated and bare shallows of an Australian coastal river. Estuaries 19: 31-41.
- White, P.N. & Bruton, M.N. 1983. Food and feeding mechanisms of *Gilchristella aestuarius* (Pisces: Clupeidae). South African Journal of Zoology 18: 31-36.
- Whitfield, A.K. 1980. Distribution of fishes in the Mhlanga estuary in relation to food resources. South African Journal of Zoology 15: 159-165.
- Whitfield, A.K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. Estuarine, Coastal and Shelf Science 18: 315-329.
- Whitfield, A.K. 1985. The role of zooplankton in the feeding ecology of fish fry from some southern African estuaries. South African Journal of Zoology 20: 166-171.
- Whitfield, A.K. 1988. The fish community of the Swartvlei Estuary and the influence of food availability on resource utilization. Estuaries 11: 160-170.
- Whitfield, A.K. 1989a. Ichthyoplankton interchange in the mouth region of a southern African estuary. Marine Ecology Progress Series 54: 25-33.
- Whitfield, A.K. 1989b. Fish larval composition, abundance and seasonality in a southern African estuarine lake. South African Journal of Zoology 24: 217-224.

- Whitfield, A.K. 1989c. Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? Estuarine, Coastal and Shelf Science 29: 533-547.
- Whitfield, A.K. 1990. Life-history styles of fishes in South African estuaries. Environmental Biology of Fishes 28: 295-308.
- Whitfield, A.K. 1992. A characterization of southern African estuarine systems. South African Journal of Aquatic Science 18: 89-103.
- Whitfield, A.K. 1993. Fish biomass estimates from the littoral zone of an estuarine coastal lake. Estuaries 16: 280-289.
- Whitfield, A.K. 1994a. An estuary-association classification for the fishes of southern Africa. South African Journal of Science 90: 411-417.
- Whitfield, A.K. 1994b. A review of ichthyofaunal biodiversity in southern African estuarine systems. In: Biological Diversity of African Fresh and Brackish Water Fishes (ed. G.G. Teugels, J.F. Guegan & J.J. Albaret). Annales du Musee Royal de l'Afrique Centrale 275: 149-163.
- Whitfield, A.K. 1994c. Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. Marine Ecology Progress Series 105: 257-267.
- Whitfield, A.K. 1994d. Fish species diversity in southern African estuarine systems: an evolutionary perspective. Environmental Biology of Fishes 40: 37-48.
- Whitfield, A.K. 1998. Biology and ecology of fishes in southern African estuaries. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology, No. 2, 223pp.

- Whitfield, A.K., Beckley, L.E., Bennett, B.A., Branch, G.M., Kok, H.M., Potter, J.C. & van der Elst, R.P. 1989. Composition, species richness and similarity of ichthyofaunas in eelgrass Zostera capensis beds of southern Africa. South African Journal of Marine Science 8: 251-259.
- Whitfield, A.K. & Blaber, S.J.M. 1979a. Feeding ecology of piscivorous birds at Lake St Lucia, Part 1: Diving birds. Ostrich 49: 185-198.
- Whitfield, A.K. & Blaber, S.J.M. 1979b. Feeding ecology of piscivorous birds at Lake St Lucia, Part 2: Wading birds. Ostrich 50: 1-9.
- Whitfield, A.K. & Blaber, S.J.M. 1979c. Feeding ecology of piscivorous birds at Lake St Lucia, Part 3: Swimming birds. Ostrich 50: 10-20.
- Whitfield, A.K. & Bruton, M.N. 1989. Some biological implications of reduced fresh water inflow into eastern Cape estuaries: a preliminary assessment. South African Journal of Science 85: 691-695.
- Whitfield, A.K. & Kok, H.M. 1992. Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology 57: 1-39.
- Whitfield, A.K., Paterson, A.W., Bok, A.H. & Kok, H.M. 1994. A comparison of the ichthyofaunas in two permanently open Eastern Cape estuaries. South African Journal of Zoology 29: 175-185.
- Winter, P.E.D., Schlacher, T.A. & Baird, D. 1996. Carbon flux between an estuary and the ocean: a case for outwelling. Hydrobiologia 337: 123-132.
- Wooldridge, T. & Bailey, C. 1982. Euryhaline zooplankton of the Sundays Estuary and notes on trophic relations. South African Journal of Zoology 17: 151-163.
Zimmerman, R.J. & Minello, T.J. 1984. Densities of *Penaeus aztecus*, *Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. Estuaries 7: 421-433.

