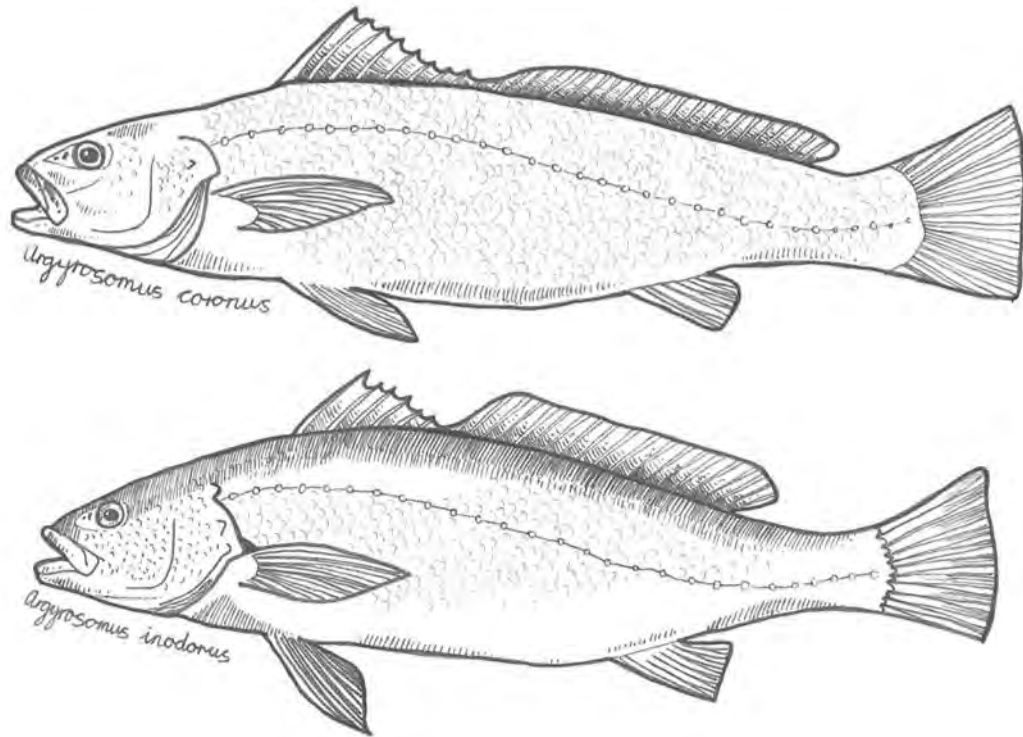


PHYSIOLOGICAL WINNERS AND LOSERS IN AN OCEAN WARMING HOTSPOT: A CASE STUDY ON *ARGYROSONOMUS* OFF THE NAMIBIAN COAST, WITH IMPLICATIONS FOR THEIR FUTURE MANAGEMENT



Thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

In Ichthyology and Fisheries Science

of

RHODES UNIVERSITY

By

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Supervisors: Professor WM Potts, Dr MI Duncan and Dr AC Winkler

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Preface

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All research activities were conducted under the Rhodes University Animal Research Ethics Committee (RU-AREC), reference number: 2019-0174-271, the Namibian Ministry of Environment and Tourism, and the National Commission on Research Science and Technology, authorisation number: 20190204

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Lastly, I would like to express my gratitude to my dad, Will, and mom, Gail, for their unwavering support throughout my studies and for always pushing me to pursue my dreams. To Graham and Shan, you have been so supportive and encouraging and for that I am thankful. To all my friends over the years, thanks for the support, the beers, weekends away and everything in between.



Declaration

I, Brett Andrew Pringle, hereby declare that the work described in this thesis was carried out at the Department of Ichthyology and Fisheries Science, Rhodes University, and at the University of Namibia's SANUMARC research centre in Hentiesbaai, Namibia, under the supervision of Professor WM Potts, Dr MI Duncan and Dr AC Winkler. I have not included ideas, phrases, passages or illustrations from another person's work without acknowledging their authorship and declare that all the work presented here is my own. The components of this thesis comprise original work by the author and have not been submitted to any other university.

Signed: 

Date: 11th December 2020

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Abstract

Anthropogenic-induced climate change is having a profound impact on aquatic ecosystems, and the resilience of fish populations will be determined by how they respond to these impacts. Changes in ocean water temperature is regarded as the most pervasive change, and affects the biological, physiological and distribution response of species, particularly ectotherms. The increasingly variable biological responses to a changing environment suggest that some species and populations will likely prove to be more tolerant than others.

The northern Namibian coast is an ocean warming hotspot, with temperatures rising at approximately ten times the global average. These rapid changes are predicted to have a considerable impact on the marine fauna. One recently documented change in distribution is a southern extension of the sciaenid, *Argyrosomus coronus*, from southern Angola into northern Namibian waters, where it now overlaps with the closely related Namibian species, *Argyrosomus inodorus*. Understanding how these species perform at current and future temperatures and where they overlap is vital to optimise any adaptive management for the *Argyrosomus* species, which forms a large component of Namibia's coastal commercial, recreational and subsistence fisheries. The aim of this study was to quantify the aerobic scope of both species (*A. coronus* and *A. inodorus*), to determine which *Argyrosomus* species will be a winner at the current and future climate predictions and to provide recommendations for the sustainable management of the Namibian *Argyrosomus* fishery.

Intermittent flow-through respirometry was used to quantify standard and maximum metabolic rates for both species across a range of temperatures. Results showed that metabolic rates scaled positively with temperature. It appears that the aerobic scope

of *A. inodorus* was notably higher at most temperatures (12, 15, 18 and 21°C), while that of *A. coronus* was only higher at the warmest test temperature of 24°C. This corresponded with the contemporary biogeographic patterns of each species. Based on these findings, it is likely that the warming ocean conditions in northern Namibia and the cold Lüderitz upwelling cell south of Walvis Bay will constrain these fish to central Namibia. While both species demonstrated signs of resilience to high temperatures, it is likely that the warming conditions will increasingly favour *A. coronus*, and that the leading edge of their distribution will shift southward in Namibia. The distribution of *A. inodorus* is likely to contract, as the energy budget of those on the northern trailing edge will be compromised. To promote the sustainable utilisation of the complex *Argyrosomus* fishery, adaptive management strategies need to be implemented. This will only be possible with a comprehensive monitoring program, including the collection of genetic data to inform the changing proportions of the two species. To maintain the *A. coronus* population, the current regulations need to be reassessed, and harvest slots should be introduced to protect juvenile *A. coronus* and the fecund large females of both species.



Word cloud representing most used words scaled by size.

Chapter 1. Introduction



Dr Murray Duncan with a silver kob *Argyrosomus inodorus* caught at the Toscanini old diamond mine in the Skeleton Coast National Park (image credit: Brett Pringle).

1.1 Climate change and fisheries

The persistence of fish populations in the Anthropocene will be determined by how they respond to the interacting effects of climate change and exploitation (Brander, 2010). It is now accepted that anthropogenic-induced climate change is causing a pervasive impact on aquatic ecosystems globally (Antão *et al.*, 2020; Little *et al.*, 2020). The ocean is undergoing accelerated changes in its physical properties (Bindoff *et al.*, 2019) including warming sea temperatures, increased eutrophication of coastal waters and decreases in oxygen availability (Friedrich *et al.*, 2014). Predicting ‘winners’ and ‘losers’ at current and future environmental conditions is challenging as species’ responses to this changing environment are variable (Somero, 2010; Fulton, 2011), but critically important in order to promote appropriate management strategies.

Marine organisms are particularly vulnerable to climate-related disturbances (Pinsky *et al.*, 2019) as many live close to their environmental limits (Howes *et al.*, 2015; Oliver *et al.*, 2018). Without many environmental refuges, marine fish populations are directly challenged with increasing levels of variability, including temperature (Bates *et al.*, 2018; Duncan *et al.*, 2019b), ocean acidification (Edworthy *et al.*, 2018), low oxygen zones (Crear *et al.*, 2020a) and extreme weather events (Boeke and Taylor, 2018; Pörtner *et al.*, 2019).

Because most fish are ectotherms, their internal physiology is governed by their external environment (Brown *et al.*, 2004), of which temperature is the primary driver (Schulte, 2015; Bozinovic and Pörtner, 2015; Horodysky *et al.*, 2015; Pinsky *et al.*, 2019). However, the response of fishes to increasing temperatures has been variable, with studies suggesting that they increase the cost of growth (Barneche *et al.*, 2019),

cause reductions in growth when combined with elevated CO₂ (Gräns *et al.*, 2014) or result in an increase in the growth of juveniles and adults (Audzijonyte *et al.*, 2016).

Changes in temperature regimes not only affect the physiological function of fish, but can also influence a variety of characteristics associated with the reproductive success of fish populations (Alix *et al.*, 2020). These include changes in fecundity and egg size (Brown *et al.*, 2006), synchronisation of reproductive events (Sheaves, 2006; Wang *et al.*, 2010), reproductive scope (Potts *et al.*, 2014a) and gametogenesis, which is significant because gamete quality is a primary determinant of developmental success (Bobe and Labbé, 2010).

Changes that affect the physiological processes of fish can also alter their behaviour and distribution (Somero, 2002; Ling *et al.*, 2009; Brander, 2010; Pörtner, 2010) and these changes may have negative population effects. For example, increasing levels of hypoxia in bottom waters may force fish to the surface as they seek oxygen-rich water (temperature-oxygen squeeze, Coutant, 1985). However, the warmer conditions near the surface may be physiologically stressful and increase vulnerability to disease or predation (Arend *et al.*, 2011; Lapointe *et al.*, 2014).

In addition to the direct effects, changes in ocean temperature may have indirect effects on fish populations by altering ecosystem structure and productivity. For example, warming waters have caused a regime shift of copepod species in the Baltic Sea, and this has directly impacted predator-prey relationships in favour of the early survival of larval European sprat *Sprattus sprattus* over Atlantic cod *Gadus morhua* (Möllmann *et al.*, 2009).

Climate change research has typically focused on ocean warming trends in global mean sea surface temperature (SST) (Ponte and Piecuch, 2018) highlighting the

pervasive effects of temperature on ecological processes (Farrell, 2016; Bates *et al.*, 2018). While physical changes in the ocean often act synergistically on fish populations (Munday *et al.*, 2009), temperature is regarded as the primary driver effecting fish physiological processes (Holt and Jørgensen, 2014; Potts *et al.*, 2015; Hoey *et al.*, 2016). Anthropogenic-induced-temperature extremes found towards the boundaries of fish distribution limits will cause physiological stress (Wiens, 2016), possibly resulting in extirpation in that area (Pinsky *et al.*, 2019). However, findings from Fredston-Hermann *et al.* (2020) suggest that warming at the cold edge of marine systems may result in widespread increases in the distribution of fish populations, through the provision of new habitats for marine organisms.

A typical consequence of ocean warming is the shift of species to more favourable climatic conditions (Stebbing *et al.*, 2002; Perry *et al.*, 2005; Last *et al.*, 2011). Range shifts across latitudes or depths (Pech *et al.*, 2017) may result in alterations to migration patterns, home ranges and geographic distributions of fish populations. In addition, range shifts create opportunities for new distributional overlaps between related species, and may even lead to hybridisation or extirpation (Garraway *et al.*, 2010; Potts *et al.*, 2014b).

Hybridisation, defined as the interbreeding of two distinguishable populations (Harrison and Harrison, 1993), is one of the greatest threats to native species (Rhymer and Simberloff, 1996), contributing to the extinction of a variety of plants and animals. The negative impacts of hybridisation have been exacerbated by habitat modification (Allendorf *et al.*, 2001), which will continue to increase in the Anthropocene. As climate change forces species to shift their distributions, the number of hybrid zones, areas where genetically distinct populations can successfully interbreed (Harrison and Harrison, 1993), will increase. Hybridisation is often regarded as a negative

occurrence, due to diversity and fitness loss after admixture (Muhlfeld *et al.*, 2009). However, hybridisation can also be considered beneficial in the face of climate change, by introducing genetic variation to a population, which may increase the evolutionary potential of a population to a changing environment (Grant and Grant, 2010; Hoffmann and Sgró, 2011).

1.2 Climate change hotspots and their value for empirical research

As mean increases in SST are recorded globally, researchers have identified hotspots where ocean surface temperatures have increased rapidly in the last 50 years (Hobday and Pecl, 2014) and are expected to continue changing and accelerating into the future (Hobday and Pecl, 2014). The southern Angolan and northern Namibian coastal area is an ocean-warming hotspot with temperatures rising at approximately ten times the global average (Hobday and Pecl, 2014; Potts *et al.*, 2014b), providing a window into the future and acting as a natural laboratory. By conducting research in these ocean warming hotspots, we can better understand the likely responses of fishes to rapidly changing ocean temperatures in a similar manner to the way biodiversity hotspots have been used to focus conservation on specific areas (Worm *et al.*, 2003).

Several important climate-driven changes on marine fauna have been observed in the area mentioned above. For example, a southward distributional shift of an important fishery species, *Argyrosomus coronus*, from southern Angola into Namibia has occurred (Potts *et al.*, 2014b). As a result, *A. coronus*' distribution has increasingly overlapped with its closely related congener, *Argyrosomus inodorus*, an important Namibian fishery species. This increasing distributional overlap has resulted in these species hybridising and producing viable offspring, with unknown consequences for

the two species (Potts *et al.*, 2014b). A central tenet of adapting to the impacts of climate change is to identify and rapidly adjust fisheries regulations as appropriate to maintain the sustainability of newly colonised species (Pech *et al.*, 2017; Maxwell *et al.*, 2015; Frusher *et al.*, 2014). Therefore, it is vital to predict the future distributions of these *Argyrosomus* species to develop adaptive, appropriate management strategies for the fisheries which target these species and their hybrids. This is critical in the Namibian fishing, as current fisheries regulations in Namibia are developed for *A. inodorus*, and as the two species have contrasting life histories, this allows for the exploitation of immature *A. coronus* individuals. The management regulations for the *Argyrosomus* fishery in Namibia therefore require attention to ensure that catches in the inshore fisheries are maintained.

1.3 Physiology to predict climate change winners

Predicting the potential impacts of climate change on fish has typically been assessed by correlating environmental variables with historical population responses (Horodysky *et al.*, 2015). While it is important to assess historical patterns to better anticipate future responses to climate change, understanding the physiological mechanisms underpinning responses can be used as a predictive tool (Deutsch *et al.*, 2015; Horodysky *et al.*, 2015; McKenzie *et al.*, 2016). By taking a mechanistic approach, one can examine the drivers of an individual's response to an environmental stressor and translate this into a population response (Helmuth, 2009; Somero, 2010; Cooke *et al.*, 2013; Ward *et al.*, 2016). Because the responses of fish populations to climate change may be variable, metabolic physiology experiments can be used to identify environmental limits/bottlenecks that may not have been discernible from past climate responses and apply these to improve future predictions (Wikelski and Cooke,

2006; Urban *et al.*, 2016). When considering predictive information for a range of populations or species, it may be possible to quantify future ‘winners’ (resilient characteristics) or ‘losers’ (vulnerable characteristics) (Horodysky *et al.*, 2015; Crear *et al.*, 2020a) in a particular region and to implement adaptive management strategies to mitigate these responses (Huey *et al.*, 2012; Cooke *et al.*, 2013; McKenzie *et al.*, 2016).

Metabolism constitutes a suite of chemical processes that organisms use to transfer stored energy into energy available for energetic processes (Nelson, 2016; Little *et al.*, 2020) and it is acutely sensitive to changes in temperature (Causey *et al.*, 2019). Changes in temperature can affect rates of physiological processes, and may elicit a physiological response which influences the energy available for maintaining equilibrium and metabolic rates (Clark *et al.*, 2013; Little *et al.*, 2020). For example, increases in temperature can disproportionately elevate the use of ATP (adenosine triphosphate) resulting in a decrease of energy available for activity over and above maintenance of basic function (McKenzie, 2011; Clark *et al.*, 2013; Norin and Metcalfe, 2019). It is therefore vital to quantify metabolic rates over a range of temperatures because these determine how well individuals, and when considered together, populations, perform in a changing environment.

A range of concepts have been developed to quantify metabolism and explain the link between an organism and its environment. For example, Brown *et al.* (2004) proposed the metabolic theory of ecology (MTE), Kooijman (2009) the dynamic energy budget (DEB) and Fry (1947, 1971) the concept of aerobic scope (AS) (Figure 1.1). One of the more pervasive concepts, which has been applied extensively in the context of climate change, although contentious (Jutfelt *et al.*, 2018), is the oxygen and capacity limiting thermal tolerance (OCLTT) theory (Pörtner and Knust, 2007). This theory

suggests that a mismatch between oxygen demand and oxygen supply is the first mechanism restricting the performance of an organism. Similar to the concept of aerobic scope (Fry, 1947, 1971) the OCLTT theory posits that the available energy budget for various energetic processes (such as growth and reproduction) varies across environmental gradients (such as temperature). The AS is defined as the difference between the maximum (MMR) and standard (SMR) metabolic rate, and represents the capacity for excess energetic tasks such as growth, reproduction and movement (Claireaux and Lefrançois, 2007; Clark *et al.*, 2013; Pörtner *et al.*, 2017). When the AS is plotted against temperature the resulting AS curve can be used to quantify the effects of temperature change on the 'free energy' of fish, and while there are limitations to the concept it is considered one of the most practical (Horodysky *et al.*, 2015).

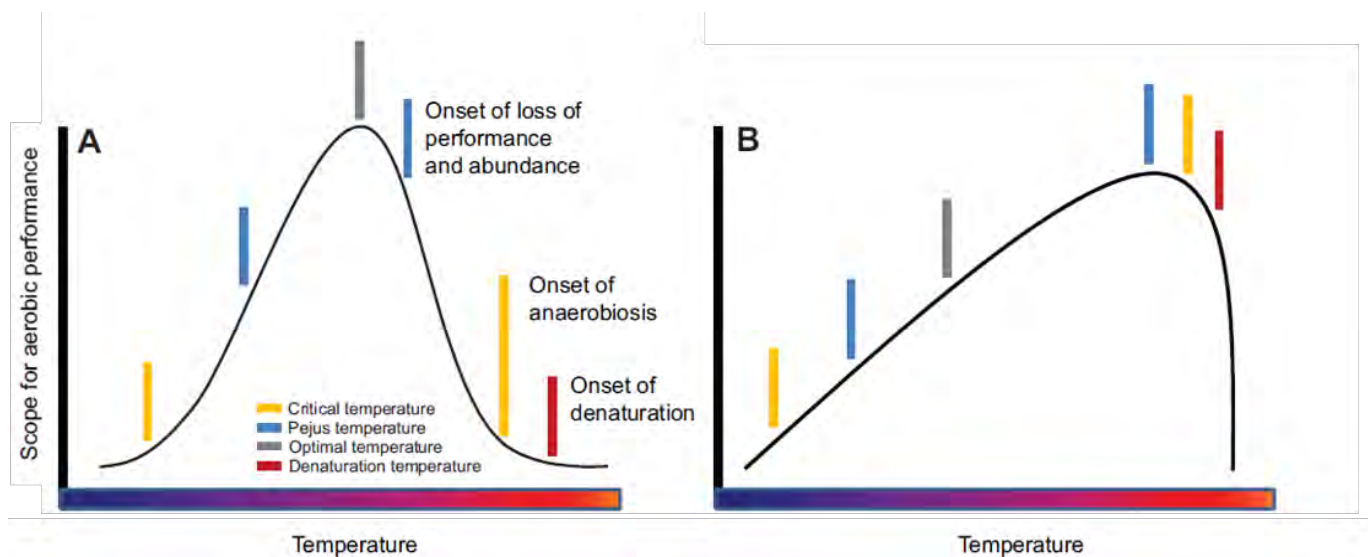


Figure 1.1: Extracted and reconfigured from Clark *et al.* (2013) Hypothetical curves depicting changes in aerobic performance (aerobic scope) of fishes with temperature, where A is redrawn from Pörtner and Farrell (Pörtner and Farrell, 2008) and B is an alternative explanation of how aerobic performance responds to temperature and interacts with animal performance (based on Clark *et al.* (Clark *et al.*, 2011)). Note the primary difference in that A assumes that the optimal (preferred) temperature of the species coincides with maximal aerobic scope, while B assumes the optimal temperature is below that which elicits maximal aerobic scope, and instead aerobic scope increases until close to the upper critical temperature.

Despite the broad use of the AS concept to predict population-level responses to climate change, it is well recognised that there may be considerable intrapopulation (Metcalfe *et al.*, 2016; Crear *et al.*, 2019) and interpopulation variability in AS. For example, Duncan *et al.* (2019a) showed interpopulation differences of AS variability when comparing exploited and unexploited populations of red roman *Chrysoblephus laticeps*. Additionally, AS thermal curves may be bell-shaped (Fry, 1971; Clark *et al.*, 2013; Duncan *et al.*, 2019a) or may steadily increase with temperature until a peak towards the upper lethal limit (Clark *et al.*, 2013; McKenzie *et al.*, 2016; Crear *et al.*, 2020a).

1.4 Overview and aims of this thesis

Understanding the impacts of this climate change-induced distributional shift of *A. coronus* will contribute to our understanding of the impacts of climate change on fishes. *Argyrosomus coronus* also has the potential to become an important fishery species in Namibia. The impact of the distributional shift of *A. coronus* on *A. inodorus*, which is Namibia's most important line-fish species, is currently unknown. It is possible that *A. inodorus* may be outcompeted due to its slower growth and smaller maximum size, however, the extent of potential overlap is not known. Therefore, understanding the thermal physiology to predict future distributions of both species is critical for the development of sustainable management strategies.

In this study, I took advantage of the unique climate change-induced distributional shift of *A. coronus* and the subsequent overlapping distribution with *A. inodorus* in Namibia to examine the impacts of rapid ocean warming on the metabolic physiology of the *Argyrosomus* species in Namibia. By simulating current and future temperature

scenarios, physiological indices were quantified between the two species to develop AS curves for the prediction of climate winners and/or losers.

To achieve this the study aimed to:

- 1) Compare the AS of *A. coronus* to *A. inodorus* across a thermal gradient, to predict what advantage one species may have over the other in a warmer future.
- 2) Use the AS information to discuss the likely future distribution of the two species.
- 3) Discuss the outcomes in the context of recreational, commercial and subsistence fisheries management in Namibia.

It was hypothesised that *A. coronus* may have a thermo-physiological advantage over its southern congener *A. inodorus* in the future, as its physiological performance is known to be optimised at higher temperatures. To test this hypothesis, intermittent flow-through respirometry was used to quantify metabolic rates, for both species across a range of temperatures.

Chapter 2. Study area and species profiles



Top: The skull and crossbones gate into the Skeleton Coast National Park (image credit: Brett Pringle), Bottom: The Toscanini old diamond mine, Skeleton Coast National Park (image credit: Marina Kruger).

2.1 Climate characteristics of the Northern Benguela

The west coast of southern Africa is home to one of the four major eastern boundary upwelling systems, the Benguela. This system supports a complex ecosystem and is divided into the southern and northern Benguela sub-systems (Duncombe Rae, 2005) by the Lüderitz upwelling cell (Figure 2.1). The Lüderitz upwelling cell is the most sustained, locally wind-driven, strongest coastal upwelling cell on the planet (Parrish *et al.*, 1983; Bakun, 1993) and is expected to intensify in the future (Rhein *et al.*, 2013). The cold, nutrient-rich northern Benguela system flows northwards until it meets the warm, southward flowing Angola current (Henriques *et al.*, 2014), forming the Angola-Benguela Frontal Zone (ABFZ) (Figure 2.1). The coastal waters of northern Namibia and southern Angola are dominated by the ABFZ which has no fixed boundaries, forming a seasonally fluctuating biogeographic transition zone within the Northern Benguela region. The front fluctuates seasonally in latitude, migrating southward from the Namibia/Angola border to central Namibia in summer and early autumn, and northward into northern Angola during winter and early spring (Boyd *et al.*, 1987; Lass *et al.*, 2000; Lass and Mohrholz, 2005; Veitch *et al.*, 2006; Anderson *et al.*, 2012).

The cyclical distribution pattern of the ABFZ causes distinct seasonal patterns. For example, the mean monthly temperature near the mouth at Flamingo Lodge (Figure 2.1) in southern Angola ranged between 16.0°C in September and 22.5°C (Figure 2.1) in April (Potts *et al.*, 2018). The temperature in central and northern Namibia is typically influenced by perennial upwelling and strong SST gradients (Bouali *et al.*, 2017) and a general increasing trend in SST has been reported for the region (Jarre *et al.*, 2015). Although less favourable upwelling winds have been documented (Lamont *et al.*, 2018), the strong thermal gradient between the cold Lüderitz upwelling cell and the warming ABFZ appears to be strengthening (Baumann and Doherty, 2013).

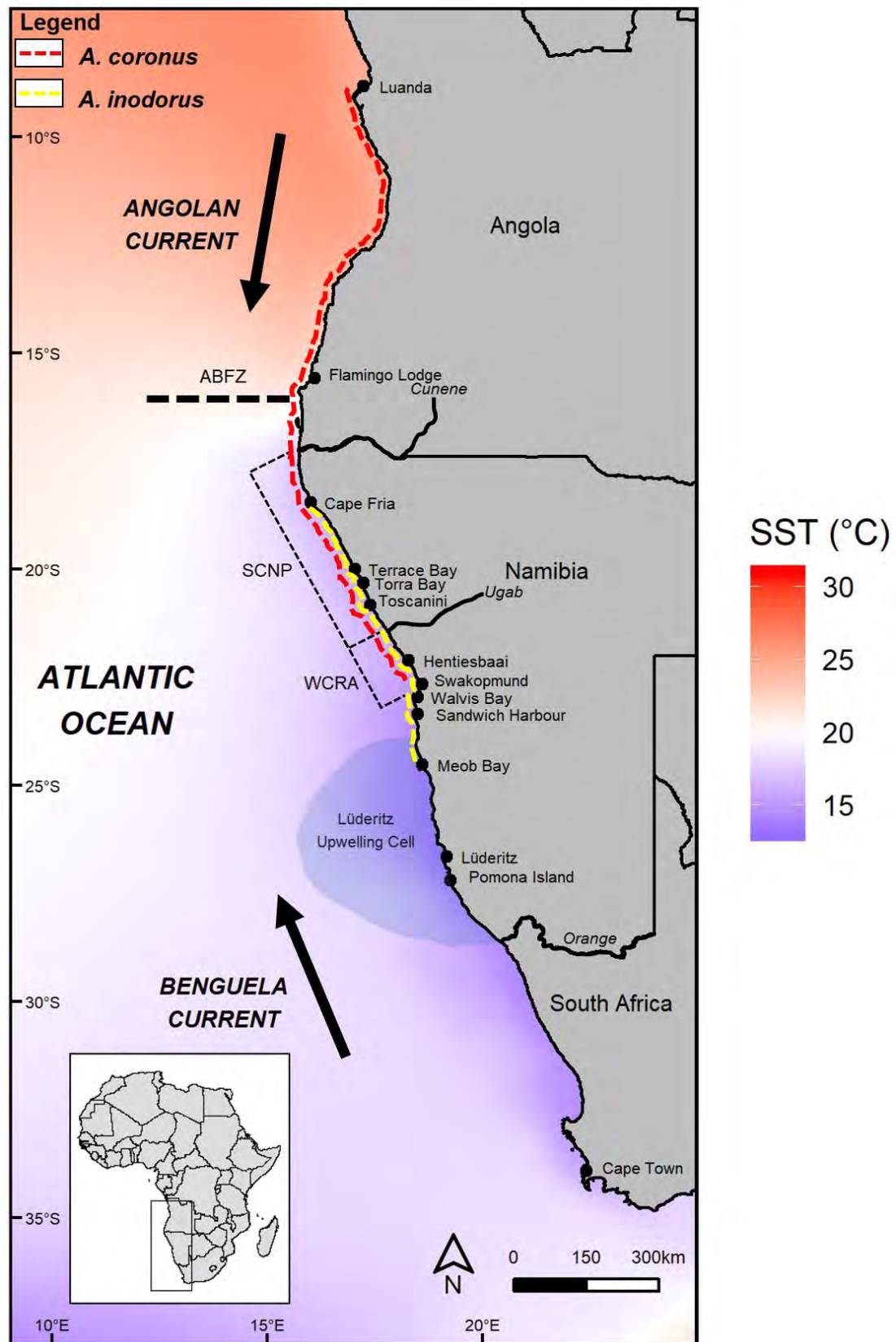


Figure 2.1: The west coast of southern Africa showing the known distribution of *Argyrosomus coronus* (red) and *Argyrosomus inodorus* (yellow), with the region's key oceanographic features, current mean sea surface temperature (SST) and features referred to throughout the text. SCNP = Skeleton Coast National Park, WCRA = West Coast Recreational Area, ABFZ = Angola Benguela Frontal Zone, SST = Sea Surface Temperature.

The southern Angolan and northern Namibian coastal region's SST has been rapidly rising (Hobday and Pecl, 2014; Potts *et al.*, 2014b) at 0.6°C/decade in the medium term (the last three decades) in the offshore zone (Monteiro *et al.*, 2008; Hutchings *et al.*, 2009). These predictions are far more rapid than the current global mean increase rate (1960-2009) of 0.07°C/decade (Burrows *et al.*, 2011) or the predicted future rates of change between 0.73°C (optimistic RCP 2.6, RCP: Representative Concentration Pathways) and 2.78°C (pessimistic 'business-as-usual' greenhouse gas scenario of RCP 8.5) by the end of the century (Pörtner *et al.*, 2019). The combination of warm events as a consequence of Benguela Niños and local wind anomalies (Richter *et al.*, 2010), the increased warming and southward movement of the ABFZ and the intensification of the cold Lüderitz upwelling cell, will likely increase SST variability and create a highly variable ocean environment off the coast of central and northern Namibia (Potts *et al.*, 2014b). Additionally, these events and the periodic intrusion of tropical hypoxic waters from the Angolan gyre into the Benguela system (Boyd *et al.*, 1987) are thought to contribute to environmental variability within the region. These hypoxic waters are possibly caused by decomposing organic matter (Mohrholz *et al.*, 2008) which may originate from the high freshwater outflow of the Congo River, affecting the productivity of the region (Thomas *et al.*, 2001). Once transported south by the Angolan Current, the oxygen-poor water settles on the Namibian shelf (Duncombe Rae, 2005), likely restricting the depth distribution of marine species, which may be linked to the apparent anoxic zone which extends deeper from 20 m (Griffiths, 1997). It is therefore important and more appropriate to assess the response of marine organisms to acute thermal variability, as opposed to long-term changes in temperature (Bates *et al.*, 2018).

2.2 Study location

The West Coast Recreational Area (WCRA) is a 260 km stretch of open access recreational and subsistence angling coastline (Barnes and Alberts, 2008) wedged between the northern border of the Namib-Naukluft Park south of Walvis Bay and the Ugab River at the southern border of the Skeleton Coast National Park (SCNP) on the Namibian coast (Figure 2.1). With the exception of the Cape Cross Seal Reserve (15 km) which is closed to fishing, the WCRA is open to recreational and subsistence/artisanal fishing. Three coastal towns, namely Walvis Bay, Swakopmund and Hentiesbaai, are situated in the WCRA. In addition to the WCRA, angling is also permitted from Pelican Point in Walvis Bay to Sandwich Harbour, from the northern limits of Lüderitz Bay to the southern limit at Grosse Bucht and from Pomona Island to the Orange River. In the north, limited seasonal angling is allowed around two settlements in the SCNP, Torra Bay and Terrace Bay (Stage and Kirchner, 2005).

The SCNP is a 500 km long protected stretch of coast between the Cunene River in the North and the Ugab River mouth in the South, and is closed to marine shore-based anglers. While the park is closed to angling, the open-access offshore waters of the SCNP are frequented by both recreational and commercial boat-based anglers. Torra Bay and Terrace Bay accommodate permitted marine shore-based anglers attracted by its productive *Argyrosomus* fishery during the open season between December and January (Stage and Kirchner, 2005). Additionally, there are a small number of local subsistence anglers and park employees who make use of these rich fishing grounds.

The Namib Naukluft Park is approximately 600 km long and stretches between Sandwich Harbour in Walvis Bay and Sperrgebiet, which is north of Lüderitz. The Namib Naukluft Park has highly productive *A. inodorus* fishing grounds at Sandwich

Harbour, south of Walvis Bay, and at Meob Bay. These embayments are thought to be important spawning grounds for *A. inodorus* (Kirchner and Holtzhausen, 2001) and although both are protected through limited access, the extremely high historical harvest, especially during the spawning season, appears to have placed *A. inodorus* under pressure (Kirchner *et al.*, 2001). To mitigate this, Sandwich Harbour is closed to fishing activity during the spawning season from the 25th of January to the 31st April (Kirchner and Beyer, 1999).

2.3 Study species

The sciaenid family consists of approximately 291 species (Fricke *et al.*, 2020) in about 70 genera (Nelson, 2006), most of which are exclusively marine. The marine species inhabit shallow temperate and tropical coastal waters of the eastern and western Atlantic and Indo-West Pacific regions (Griffiths and Heemstra, 1995). They are primarily demersal species, found over a variety of substrate types, but they generally prefer turbid waters and estuaries (Chao, 1986). The unique ability of this family to produce sound via the contraction of specialised drumming muscles alongside their often-enlarged swim bladder has led to them being referred to as drums or croakers, a reference to the type of sound typically produced by these fishes. According to the IUCN Red List (2020), there are currently 4 critically endangered, 4 endangered and 7 vulnerable sciaenid species, primarily due to unsustainable fishing practises and habitat degradation. Sciaenids are targeted by near-shore commercial, artisanal and recreational fisheries (Griffiths and Heemstra, 1995; Silberschneider and Gray, 2008) and are a frequent bycatch species by inshore trawl and purse seine fisheries (Gray *et al.*, 1990; Gray *et al.*, 2003). More recently the swim bladders of larger sciaenid species such as the critically endangered *Totoaba macdonaldi* in the Sea of Cortez

have become a highly prized Chinese delicacy, adding further pressure to their already threatened status (Sadovy de Mitcheson *et al.*, 2019). Fishes from the genus *Argyrosomus*, support a variety of fisheries throughout their global distribution, being particularly important to inshore fisheries in the southern African coastal waters around Angola, Namibia and South Africa.

This study focussed on two sciaenid species, the west coast dusky kob *Argyrosomus coronus* (Griffiths and Heemstra, 1995) (Figure 2.2a) and the Namibian silver kob *Argyrosomus inodorus* (Griffiths and Heemstra, 1995) (Figure 2.2b). *Argyrosomus coronus* is a coastal predatory species and distributed from central Namibia to northern Angola (Potts *et al.*, 2014b) (red dotted line, Figure 2.1). *Argyrosomus inodorus* is a south-eastern Atlantic endemic and has several separate stocks, being those in the south Eastern Cape, southern Cape, and south Western Cape in South Africa and in Namibia (Griffiths and Heemstra, 1995). The Namibian population of *A. inodorus* occurs only in central (from Meob Bay) and northern Namibia (up to Cape Fria) (Kirchner and Holtzhausen, 2001) (yellow dotted line, Figure 2.1). The number of *A. inodorus* in southern Africa is declining and the species has been categorised as vulnerable to extinction by the IUCN Red List (Fennessy, 2020; Fennessy and Winker, 2020). In contrast, *A. coronus* is categorised as data deficient (Fennessy, 2020) despite similar suggestions of population decline and overexploitation (Beckensteiner *et al.*, 2016).

Argyrosomus inodorus and *A. coronus* are morphologically similar and are generally referred to as 'kabeljou' or 'kob'. Despite the morphological similarity, the habitat and life history characteristics of these two species are markedly different. *Argyrosomus coronus* prefers water temperatures between 16 and 19°C (Potts *et al.*, 2010). It is primarily an inshore species that rarely ventures deeper than 60 m and is commonly

found over shallow reefs (< 20 m), the inshore surf zone and in permanently open estuaries (Griffiths and Heemstra, 1995; Lamberth *et al.*, 2008). In contrast, *A. inodorus* has a cool water (13 to 16°C) predisposition and prefers different depths depending on its distribution. For example, *A. inodorus* are found at depths between 20 and 100 m along the Eastern Cape and southern Cape coasts of South Africa, (Heemstra and Heemstra, 2004), where they overlap with another coastal congener, *A. japonicus*, which has a similar life history to *A. coronus* (Potts *et al.*, 2010). *A. inodorus* is found in shallow waters (< 50 m) along the Namibian and Western Cape (South Africa) coasts, including the nearshore surf zone (Griffiths and Heemstra, 1995; Griffiths, 1997; Kirchner and Holtzhausen, 2001). The Namibian stock is primarily found in the nearshore and is likely restricted by an anoxic zone found at depths greater than 20 m (Griffiths, 1997). This anoxic zone appears to force both west coast *Argyrosomus* species together into the shallow water habitat. The Namibian *A. inodorus* is confined by the Lüderitz upwelling cell in the south (Henriques *et al.*, 2014) and warming water in northern Namibia (Figure 2.1). It is hypothesised that these barriers limit further distribution due to a reduced metabolic potential in the warmer water temperatures in the north and the cooler water temperatures in the south (Henriques *et al.*, 2014).

The diet of the Namibian *A. inodorus* and *A. coronus* are largely similar. They feed mostly on small teleosts, squid and crustaceans (Kirchner, 1999; Potts *et al.*, 2010). Potts *et al.* (2010) studied the feeding of *A. coronus* in southern Angola and found that small pelagic fishes, *Sardinella aurita* and *Trachurus trecae*, made up the vast majority of their diet, with benthic crustaceans, blacktail *Diplodus sargus* and snake eels Opichthidae dominating the remainder. Similarly, the diet of *A. inodorus* in northern Namibia was dominated by pelagic fishes (*T. trecae*, *Trachurus capensis* and

Sardinops ocellatus) and crustaceans, while crustaceans dominated the diet of this species in central and southern Namibia (Kirchner, 1999).



Figure 2.2: Photographs of (a) *Argyrosomus coronus*, 63 cm TL and (b) *Argyrosomus inodorus*, 42 cm TL, both caught at the Toscanini old diamond mine in the Skeleton Coast National Park (SCNP), Namibia.

In terms of life history (Table 2.1), *A. coronus* attains a larger maximum size, weighing up to 77 kg and measuring up to 1900 mm total length (TL). The oldest fish aged by Potts *et al.* (2010) was 13 years. This individual was somewhat smaller than the maximum size, suggesting that this species may get substantially older. In comparison, *A. inodorus* can attain weights of up to 36 kg and measure up to 1200 mm TL (Griffiths and Heemstra, 1995; Kirchner, 1999) while living as long as 28 years (Kirchner and Voges, 1999). Typically, *A. coronus* mature at an age of between 4 and 5 years and a size of 82 to 90 cm TL (Potts *et al.*, 2010), while *A. inodorus* matures at an age of about 1.5 years and a size of 35 cm TL (Kirchner *et al.*, 2001).

Table 2.1: Life-history characteristics of selected large southern African *Argyrosomus* species (Adapted from Potts *et al.*, 2010)

Species	Country	Max. TL (mm)	Max. weight (kg)	Max. age (y)	L_{50} (mm)	A_{50} (y)	Sex ratio M:F
<i>A. coronus</i>	Angola	1900 ₁	77 ₁	13 ₉	870 ₉	4–5 ₉	1:1.4 ₉
<i>A. inodorus</i>	Namibia	1200 ₆	36 ₁	28 ₇	350-360 ₈	1.5–1.6 ₈	-
<i>A. inodorus</i>	South Africa	1450 ₁	-	25 ₄	300-350 ₅	1.3–2.4 ₄	1:1.6–2.1 ₅
<i>A. japonicus</i>	South Africa	1810 ₁	75 ₁	42 ₂	±1000 ₄	6–8 ₃	1:1 ₃

₁Griffiths and Heemstra, 1995; ₂Griffiths and Hecht, 1995; ₃Griffiths, 1996a; ₄Griffiths, 1996b; ₅Griffiths, 1997; ₆Kirchner, 1999; ₇Kirchner and Voges, 1999; ₈Kirchner *et al.*, 2001; ₉Potts *et al.*, 2010

Argyrosomus inodorus are thought to undertake a spawning migration from the SCNP southwards through the WCRA into Sandwich Harbour and further into Meob Bay within the Namib Naukluft Park at the beginning of austral summer (Kirchner and Holtzhausen, 2001). Once spawning has been completed, it is likely that larvae drift north with the current and settle in the WCRA. After about two years, the late juvenile/early adults begin to move northwards into the SCNP and then begin annual spawning migrations to the Namib Naukluft Park before returning when the water temperatures in the SCNP decline to approximately 15°C (Kirchner and Holtzhausen, 2001).

While there is limited information on the migratory patterns and spawning habits of *A. coronus*, previous studies (Potts *et al.*, 2010) suggest that adults may undertake a northward longshore migration in early winter, which is dependent on the movement of the ABFZ. It is hypothesised that once water temperatures rise and the ABFZ moves south, the adults migrate southward towards their southern distribution edge where spawning may occur, typically during late spring. However, recent findings from Potts *et al.* (2018) show that although conventional tagging data may provide evidence for a southward migration in the austral summer, acoustic telemetry information suggests

that only a small proportion of the population may undertake this migration. Further evidence of ripe and running individuals spawning in northern Angola during the austral winter may suggest that spawning occurs on shallow (< 20 m), sub-tidal reef habitats in Angola (Potts *et al.*, 2018). While the spawning behaviour and migratory movements of this sciaenid are still largely unknown, it is suggested that the duration of the pelagic egg and larval stages are similar to its congener *A. japonicus*, at approximately 26 days (Edworthy *et al.*, 2018; Henriques *et al.*, 2018). As with other congeners, it is likely that juveniles recruit into the inshore zone after the completion of the pelagic egg and larval stages. In the case of *A. coronus*, juveniles are found predominantly in southern Angola, northern Namibia, and increasingly in central Namibia.

Van der Bank and Kirchner (1997) first distinguished between *A. coronus* and *A. inodorus* using biochemical genetic markers, but did not find evidence of hybridisation, which suggests that adult *A. inodorus* and *A. coronus* were not spawning in the same area at that time. However, it is likely that the abundance of *A. coronus* has increased further south as their reproductive scope has increased in Namibia (Potts *et al.*, 2014a), and this has placed adults of both species in the same area, thus facilitating successful hybridisation (Potts *et al.*, 2014b). Several important climate-driven changes on marine fauna have been observed, with the major change being a general south-ward distributional shift of a number of coastal species from southern Angola into Namibia (Potts *et al.*, 2014b). Potts *et al.* (2015), in their review on the likely impacts of climate change on coastal fishes and fisheries, predicted that warm water-sensitive fish may shift rapidly southward due to oxygen limitation, while resident species are likely to shift more slowly due to changes in reproductive success. This was based on two case studies. The first showed that *A. coronus* had shifted its

distribution from southern Angola into Namibia (Potts *et al.*, 2014b). The second showed that the reproductive scope of blacktail *Diplodus capensis*, a popular Namibian angling species, was increasing in Namibia and decreasing in Angola (Potts *et al.*, 2014a). Both findings suggest that the abundance of certain species would increase in Namibia. Potts *et al.* (2014b) also found that *A. coronus* has begun hybridising with the local Namibian silver kob, *A. inodorus*, most likely because reproductively active adults of both species were occupying the same habitat due to the southward distributional shift of *A. coronus*. It was also found that the hybrids had successfully reproduced with the original pure species (a phenomenon known as backcrossing).

Historical data (Table 2.2) suggests that *A. inodorus* was the dominant species ($\approx 90\%$) in the recreational *Argyrosomus* catch in the WCRA and the SCNP between 1993 and 1995 (Kirchner, 1999; Holtzhausen *et al.*, 2001). However, catch data from 2008 and 2009 suggests that *A. coronus* outnumbered *A. inodorus* in the WCRA (Potts *et al.*, 2014b) (Table 2.2), with the proportion of *A. coronus* in the fishery at 57%.

Table 2.2: Percentage of *Argyrosomus coronus* (numbers sampled in parentheses) in the catch composition of the *Argyrosomus* fishery in the West Coast Recreational Area (WCRA) and Skeleton Coast National Park (SCNP) in Namibia and in the Cunene River mouth (border between Angola and Namibia) (Extracted from Potts *et al.*, 2014b)

Period	Namibia		Namibia-Angola
	WCRA	SCNP	Cunene River Mouth
1993-1995	8 (237*)	15 (325*)	99 (258*)
2008-2009	57 (146† + 18‡)	-	100 (12‡)

*Electrophoresis validated otolith morphometry.

†Molecular Polymerase Chain Reaction-based Restriction Fragment Length Polymorphism.

‡MtDNA sequencing.

2.4 The Namibian *Argyrosomus* fishery

Argyrosomus inodorus and *A. coronus* support a large recreational shore-based and ski-boat fishery (Kirchner and Beyer, 1999), a small commercial boat-based hook and line fishery (Stage and Kirchner, 2005) and a small subsistence/artisanal fishery (Cardoso *et al.*, 2006) in Namibia. All of these fisheries target *Argyrosomus* species in the WCRA, however, the commercial linefish boat fishery also operates between Meob Bay and the Cunene River (Kirchner and Beyer, 1999). Approximately 90% of all recreational marine shore-based angling in Namibia takes place in the WCRA. The remaining 10% takes place around Lüderitz, the Orange River Mouth, Torra Bay and Terrace Bay (Stage and Kirchner, 2005). While marine shore-based anglers are only permitted to harvest fish within the WCRA, commercial line-fishing boats have access to approximately 900 km of coastline, with the most fishing taking place between the Cunene River and Ugab River, spanning approximately 515 km (Figure 2.1) (Kirchner and Beyer, 1999).

While there has been limited recent literature published on the Namibian linefishery, anecdotal information suggests that historic records are still relevant to the current situation. Both *Argyrosomus* species are highly palatable and are readily captured, accounting for approximately 70% of the historic catch in the recreational shore-based fishery (Kirchner *et al.*, 2000). While the harvest of *Argyrosomus* species takes place year-round in Namibia, the catch rate is highest during the summer months. The considerable increase in effort in December, which coincides with South Africa and Namibia's summer school holidays (Kirchner and Beyer, 1999) has a major impact on this fishery, particularly as migrating and spawning adult *A. inodorus* are susceptible to capture during this time. Both *Argyrosomus* species are heavily exploited, and the

spawning stocks are considered to be well below unexploited levels (Kirchner, 1999; Holtzhausen *et al.*, 2001; Beckensteiner *et al.*, 2016).

Considering the outdated literature available on the fisheries economics and *Argyrosomus* species population depletions in Namibia, historic and anecdotal information suggests that they continue to contribute substantially to the local Namibian economy (Barnes and Alberts, 2008). Historic records suggest a gross domestic product (GDP) contribution of N\$ 24–26 million and a consumer surplus of N\$35 million per annum from the recreational marine shore-based sector being reported (Stage and Kirchner, 2005; Barnes and Alberts, 2008). Although there are more Namibian anglers participating in the shore-based fishery, foreign anglers contribute 10% more than Namibian anglers to the national economy (Kirchner *et al.*, 2000). In addition, the contribution of the recreational fishery is worth approximately six times more than the commercial linefishery (Holtzhausen *et al.*, 2001).

Historic records indicate that while all three *Argyrosomus* commercial fisheries cumulatively harvested approximately 1200 tons or 525 000 individuals per annum (Kirchner and Beyer, 1999, Holtzhausen *et al.*, 2001), the recreational marine shore-based sector harvested only 360 tonnes, or 230 000 individuals per annum (Kirchner and Beyer, 1999). While the data is considered outdated, this disproportionate contribution between Namibia's *Argyrosomus* fishery GDP and the number of fish harvested is still prevalent during current times and can be attributed to the indirect costs of recreation (travel, bait, fishing tackle, food and accommodation) and the difference in the size of fish caught in the commercial linefish boat fishery (Stage and Kirchner, 2005). In addition to the three previously mentioned fisheries, Cardoso *et al.* (2006) suggest that approximately 150 subsistence/artisanal fishers operate from the shore and hence compete directly with the shore-based recreational fishery around

Swakopmund, Hentiesbaai and Terrace Bay. Most of the subsistence/artisanal fishery harvest is used for personal consumption, however a small proportion is either bartered or sold (Cardoso *et al.*, 2006). Local fishing associations have been developed to facilitate the distribution of their catch to local communities and restaurants (e.g., Hanganeni Artisanal Fishing Association (HAFA), situated in Hentiesbaai). The sector has likely expanded since the mid-2000s as poor residential areas have grown (Cardoso *et al.*, 2006; Barnes and Alberts, 2008).

2.5 Management of the Namibian *Argyrosomus* fishery

Presently, there are no conceptual objectives, operational objectives, performance indicators or reference points for the Namibian linefishery (Potts *et al.*, 2020; Marine Resources Act, 2000 (Act No. 27 of 2000)). The fishery is managed based on rules and regulations that were developed by scientists from the Namibian Ministry of Fisheries and Marine Resources in the 1990s. These include input controls (licences), spatial (marine protected areas) and temporal (closed seasons) closures, and technical measures (species-specific size and bag limits) that were promulgated in the Marine Resources Act, 2000 (Act No. 27 of 2000). These regulations are enforced by the Namibian Ministry of Fisheries and Marine Resources, but currently minimal monitoring of the fisheries takes place. In terms of marine-shore-based recreational anglers, an angler must be in possession of a valid angling permit, and may harvest no more than 10 '*kabeljou*' or '*kob*' per day, with a minimum size limit of 40 cm TL. Additionally, no more than 2 large individuals, over 70 cm TL, may be harvested. This law also pertains to subsistence/artisanal fishers, as only two sectors are recognised in Namibian legislation. Commercial operations are not subject to any restrictions other than the permit requirement (Kirchner and Stage, 2005).

Chapter 3. Materials and methods



From top to bottom right: Entrance into the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC) Mariculture laboratory in Hentiesbaai. Holding facilities at the SANUMARC. The respirometry experiment set up. A small silver kob *Argyrosomus inodorus* individual in the small respirometer. A large west coast dusky kob *Argyrosomus coronus* in a large respirometer (image credits: Brett Pringle).

3.1 Fish collection and husbandry

Argyrosomus coronus and *A. inodorus* specimens were collected from the shore in the vicinity of the Toscanini old diamond mine in the Skeleton Coast National Park (SCNP), Namibia, between the 2nd of March and the 6th of June 2019 (Figure 2.1). Individuals were caught using conventional marine shore-based angling tackle (12–15 ft. graphite rods, fixed or revolving spool reels, nylon or braided lines with circle and J hooks). Individuals were transported in 1 000 L or 500 L tanks filled with oxygenated seawater to the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC) Mariculture laboratory in Hentiesbaai, Namibia. Fish were held in 13 800 L recirculating holding tanks (follow the link to view the fish in their holding tanks: <https://twitter.com/brettpringle12/status/1102169932136173568?s=20>), under natural light conditions, where mechanical and bio-filtration and routine water changes were used to maintain the water quality and ambient water temperature (Mean = 18.29°C, SD = 1.11°C). Holding tank temperature was measured daily and adjusted where necessary, while dissolved oxygen, pH and ammonia were measured twice a week. Fish were acclimated for a minimum of 4 weeks prior to experimentation and fed sardine *Sardinops ocellatus* and round sardinella *Sardinella aureti* 3–4 times per week. Occasionally, their diet was supplemented with Patagonian squid *Doryteuthis gahi*; Cape Hope squid *Loligo reynaudii*; southern mullet *Chelon richardsonii*; and Pacific saury *Cololabis saira*.

3.2 Respirometer design

Respirometers were custom-built in the NRF-SAIAB Aquatic Ecophysiology Research Platform (AERP) at the Department of Ichthyology and Fisheries Science (DIFS) at Rhodes University using thick-wall Perspex following the guidelines of Clark *et al.*

(2013), Svendsen *et al.* (2016) and Duncan *et al.* (2019a). To ensure a water-tight chamber, lids were fitted with silicone O-rings and bolted shut. Due to the varied size range of *A. coronus* and *A. inodorus* (31.5–72.5 cm TL in this study), three different sized respirometers with a range of internal diameters (ID) and lengths (L) (small: 14 cm ID and 50 cm L, medium: 19 cm ID and 75 cm L, large: 24 cm ID and 100 cm L) were built to accommodate different sized fish while allowing sufficient decreases in oxygen consumption within a reasonable time. A flush pump (DAB Nova Salt W M-A submersible pump) was connected to all respirometers to replenish chambers with fresh-aerated seawater and remove built-up waste products. A programmed on/off digital timer (Eliro VODDTS) was used to repeatedly replenish respirometers on a 15-minute flush (on) and 5-minute closed/measurement (off) cycle, ensuring suitable water replacement. Due to potential oxygen leakages caused by backwashing from the submersible pumps, overflow lines and flush pump lines were fitted with one-way check valves. Flush pump and recirculation lines were made from oxygen-impermeable clear thick-wall hose. Internally connected pumps (small: 600L/h 12w 1m AC SOBO water pump, medium: 880L/h 15w 1.2m AC SOBO water pump, large: 1200L/h 25w 1.5m AC SOBO water pump) mixed water within respirometers to minimise water stratification and were connected to a recirculation loop to provide water to a custom-built peristaltic pump (4 x Peristaltic Liquid Pump 12V DC, Adafruit Industries, New York, United States of America) and later on a four-channel peristaltic pump (S100-2B+DG-4 Microflow Peristaltic Pump, Ditron Technology Co., Ltd, Baoding City, China). The peristaltic pump fed water into flow-through cells with an optical oxygen sensor (OXFTC, Pyro Science GmbH). Flow-through cells were connected to a FireStingO2 fibre optic oxygen meter (FSO2-4, Pyro Science GmbH) with bare optical fibres (SPFIB-BARE, Pyro Science GmbH) to determine dissolved

oxygen concentrations (Mg. L^{-1}). Oxygen concentration levels were recorded using Pyro Oxygen Logger Software (Pyro Science GmbH).

3.3 Experimental protocol

Respirometers and tanks were flushed and washed with chlorine prior to each experiment to reduce microbial growth. Standard metabolic rate (SMR) and maximum metabolic rate (MMR) were measured using intermittent-flow respirometry for a single individual at one of the test temperatures, 12, 15, 18, 21 or 24°C. The experimental test temperatures in this study were chosen as they represent the current and predicted future thermal range along the central Namibian coast (Junker *et al.*, 2017). The lowest test temperature was set at 12°C because the Lüderitz upwelling cell at the southern edge of *A. inodorus*' distribution is typically 11–14°C (Griffiths and Heemstra, 1995; Griffiths, 1997; Kirchner and Holtzhausen, 2001; Henriques *et al.*, 2014; Potts *et al.*, 2014b), while the upper test temperature was set at 24°C as the region's water temperature is predicted to increase by ~2°C from its current average of 22°C in the summer months by 2050 (Hobday and Pecl, 2014; Potts *et al.*, 2014b; Potts *et al.*, 2018).

Fish were fasted for 36 hours prior to experimentation. After fasting, fish were netted and individually placed into respirometers at a temperature that matched the holding temperatures on the day and allowed a 12-hour acclimation period, during which water temperature was adjusted (0.5°C per 45 minutes) to one of the test temperatures (12, 15, 18, 21 or 24°C). After the 12-hour acclimation period, SMR measurements were recorded using intermittent-flow respirometry, for a minimum of 22 hours to account for any diel variability (Chabot *et al.*, 2016).

Following SMR measurements, fish were individually removed from the respirometers, placed in a cylindrical tank, and subjected to 3 minutes of chasing and tail grabbing, to induce burst swimming, and one-minute of air exposure (Roche *et al.*, 2013; Clark *et al.*, 2013; Norin and Clark, 2016) before being placed back into a sealed respirometer (within 20 s). The MMR was estimated from the single steepest decline in oxygen concentration during ten hours of intermittent-flow respirometry after this chasing protocol. Experimental fish were removed after this ten-hour period and a 3-hour blank was run to measure and account for background microbial respiration in the empty respirometers (Clark *et al.*, 2013; Svendsen *et al.*, 2016). Experimental fish were weighed (g, ADAM WS-30) and measured (cm, TL). Fin clip and muscle tissue samples were removed from individual fish and stored in 95% ethanol for later mtDNA sequencing to confirm the species of each individual.

3.4 Genetic data collection

The genetic analysis was conducted by Dr Niall McKeown and Professor Paul Shaw at the Aberystwyth University's Institute of Biological, Environmental and Rural Sciences in Wales. Total DNA was extracted using a standard CTAB-chloroform/isoamylalcohol method (Winnepeninckx *et al.*, 1993). Each individual was genotyped at a fragment of the mtDNA cytochrome oxidase I (COI) gene using the FF2d and FF1d primers described by Ivanova *et al.* (2007) and at five microsatellite loci (UBA5, UBA40, UBA91, UBA853, UBA854) developed by Archangi *et al.* (2009). Polymerase chain reactions were performed in 10 µl volumes using a thermoprofile comprising 95°C for 3 minutes followed by 35 cycles of 95°C for 30 s, 50°C for 30 s and 72°C for 30 s, after which there was a final extension (72°C for 180 s) and cool down (4°C for 60 s). Sequencing of mtDNA amplicons was performed using the FF2d

primer with Big Dye technology and an ABI 3500 DNA analyser. The ABI 3500 analyser was also used to separate microsatellite alleles with genotypes inferred using PEAKSCANNER software.

3.5 Genetic data analysis

The mtDNA sequences were edited and aligned using BIOEDIT (Hall, 1999) and all subsequent analyses were performed in ARLEQUIN 3.1 (Excoffier *et al.*, 2005) unless stated otherwise. Genetic variation was described using indices of haplotype and nucleotide diversity (h and π respectively). A minimum spanning network was constructed in NETWORK (www.fluxus-engineering.com/sharenet.htm).

For analysis of nuclear genotypes, the individual-based Bayesian clustering method implemented in STRUCTURE (Pritchard *et al.*, 2000) was used to first estimate the most probable number of genetic groups represented by the samples and next to estimate individual admixture proportions (Q values), constituting the estimated proportion of an individual genotype originating from a particular group. Q values range from 0–1, and hybrids would be expected to report intermediate Q (~0.5 in the case of two parental groups). For each Q value, the 90% posterior probabilities were calculated by assuming an admixture model. The analysis was run three times for models of $K = 1-3$ without any prior information, with each run comprising 10^6 MCMC repetitions following a burn in period of 10^6 steps.

To investigate the statistical power to identify hybrids, 50 hybrid individuals were simulated using the method implemented in the program HYBRIDLAB (Nielsen *et al.*, 2006) and the STRUCTURE analysis was repeated under the model of $K = 2$. Genetic differentiation between groups was quantified by F_{ST} , calculated in GENALEX 6.2 (Peakall and Smouse, 2006). GENALEX was also used to characterise genetic

variability within groups using number of alleles (N_A), allelic richness (A_R ; El Mousadik and Petit, 1996), observed heterozygosity (H_O), and expected heterozygosity (H_E) (Nei, 1978) and to test for conformance to Hardy Weinberg equilibrium (HWE) expectations. The analysis of simulated hybrids was used to rule out the possibility that any analysed individuals were first generation hybrids.

3.6 Data preparation

Oxygen consumption rates for each measurement period (Figure 3.1) were quantified as the slope of the linear decline in oxygen over time for each measurement period. Individuals with oxygen consumption rates with a coefficient of determination (R^2) of less than 0.9 were omitted. The first minute of the measurement period was considered a wait period and was not included in the regression.

Oxygen consumption rate (RO_2) was calculated using Equation 3.1 (adapted from Svendsen *et al.*, 2016).

$$RO_2 = \left(\left(\frac{V_{re} - M}{W} \right) \left(\frac{\Delta[O_{2a}]}{\Delta t} \times 60 \right) \right) - \left(\left(\frac{V_{re} - M}{W} \right) \left(\frac{\Delta[O_{2b}]}{\Delta t} \times 60 \right) \left(\frac{V_{re}}{V_{re} - M} \right) \right)$$

Equation 3.1

where V_{re} is the total volume of the respirometer in litres, M is the mass of the specimen in kg expressed as l, W is mass of the specimen in kg, $\Delta[O_{2a}]/\Delta t$ is the slope of the linear decrease in oxygen concentration during the measurement period and $\Delta[O_{2b}]/\Delta t$ is the slope of the linear decrease in oxygen concentration when no specimen was in the chamber (background respiration).

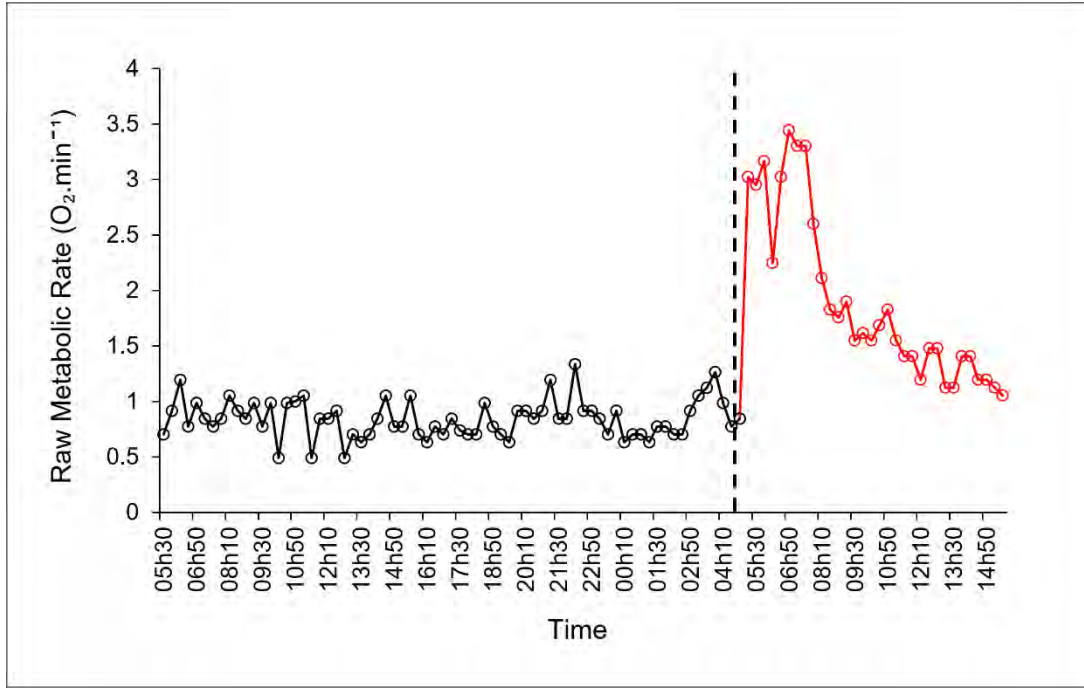


Figure 3.1: An example of a full metabolic rate trial at 18°C for a silver kob *Argyrosomus inodorus*. Each black point corresponds to a calculated raw metabolic rate (RO_2) before chasing (black dashed line). Each red point corresponds to a calculated raw metabolic rate (MO_2) post exhaustive protocol and the subsequent recovery.

The SMR was estimated as the quantile assigned to the bottom 20% of the RO_2 data, as the coefficient of variation between readings was above the suggested 5.4% threshold, following the guidelines of Chabot *et al.* (2016). Maximum metabolic rate was estimated as the single highest rate of oxygen consumption following the exhaustive protocol (Killen *et al.*, 2017).

To estimate the mass-scaling exponent for the metabolic rate of *Argyrosomus* species, the data were first temperature corrected by dividing metabolic rate data by the Arrhenius function (Brown *et al.*, 2004) (Equation 3.2):

$$RO_{2(temp\ corrected)} = RO_2 \times \frac{-E}{e kT}$$

Equation 3.2

where E is the average activation energy of ectotherms ~ 0.63 eV (Gillooly *et al.*, 2001), k is the Boltzmann constant 8.617×10^{-5} eV.K⁻¹ and T is the absolute temperature in kelvin.

The slope of the linear regression between the natural logarithm of RO_2 (temperature corrected) and the natural logarithm of mass was taken as the allometric exponent (α) of the mass scaling relationship for either SMR or MMR data. RO_2 data was then mass corrected (MO_2) using the mass scaling relationship in Equation 3.3:

$$MO_2 = \frac{RO_2}{M^\alpha}$$

Equation 3.3

where MO_2 is the mass corrected SMR or MMR, RO_2 is the standard or maximum oxygen consumption rate, M is the mass of the organism (g) and α is the allometric mass scaling exponent.

Absolute aerobic scope (AS) was calculated using mass corrected metabolic rates using Equation 3.4:

$$AS = MMR - SMR$$

Equation 3.4

where MMR is the mass corrected maximum metabolic rate and SMR is the mass corrected standard metabolic rate.

3.7 Statistical analysis

A generalised least squares (GLS) modelling approach was implemented using the nlme package (Pinheiro *et al.*, 2017) to account for data heteroscedasticity in R version 3.6.1 (R Core Team 2019). Differences in mass-corrected metabolic rate data between

species were tested by modelling a second order polynomial relationship between metabolic data and temperature, including species as an interaction term, and a variance structure weighted by temperature and species. Orthogonal polynomials were used for statistical inference to reduce the effect of collinearity among explanatory polynomial terms (Rawlings *et al.*, 1998).

Chapter 4. Results



**A typical scene in the West Coast Recreational Area, off-road vehicles and rods
– Dr Alex Winkler baits up multiple rods with the murky water in background
(image credit: Brett Pringle).**

4.1 Genetic results

A total of 263 base pairs (bp) were aligned across all individuals, which revealed 18 haplotypes ($h = 0.618$). The network phylogeny partitioned these haplotypes into two groups (Figure 4.1). The separation of haplotypes into these groups readily aligned with the prior morphological identification of individuals in that sequences from all individuals, with the *A. inodorus* phenotype clustered into one group (*A. inodorus* clade; Haplotypes 1, 3, 6, 9, 10, 12, 14, 15, 18) while those from individuals with the *A. coronus* phenotype were clustered into the other group (*A. coronus* clade; Haplotypes 2, 4, 5, 7, 8, 11, 13, 16, 17) (Figure 4.1). Among the sequences from the *A. inodorus* clade h were 0.37 (SD = 0.08) and π was 0.0018. Among the sequences from the *A. coronus* clade h were 0.73 (SD = 0.12) and π was 0.004.

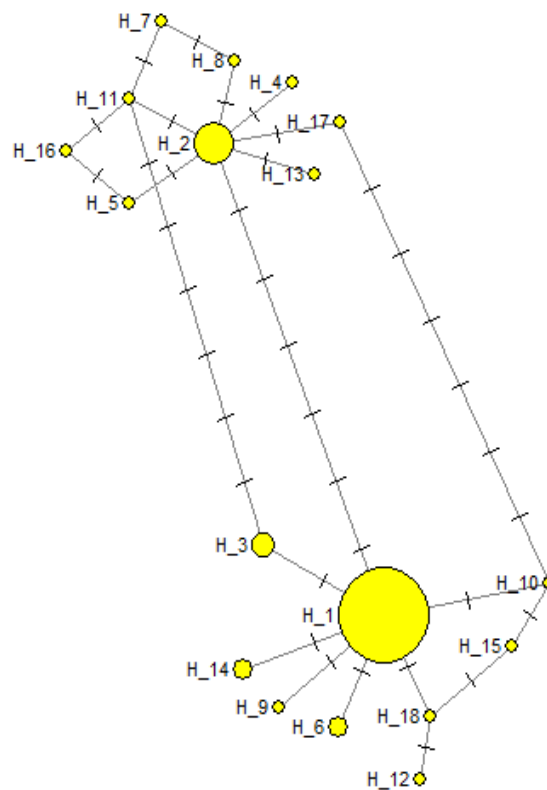


Figure 4.1: Haplotype network for two *Argyrosomus* species sampled in this study. *Argyrosomus inodorus* clade; Haplotypes 1, 3, 6, 9, 10, 12, 14, 15, 18 and *Argyrosomus coronus* clade; Haplotypes 2, 4, 5, 7, 8, 11, 13, 16, 17.

For the microsatellite loci, the total number of alleles per locus ranged from six to 17 (mean = 12.8). STRUCTURE analysis unanimously supported a model of $K = 2$ wherein individuals were robustly partitioned into two groups concordant with the morphological and mtDNA species designation (Figure 4.2). Q values reported individuals to be robustly assigned to their respective species.

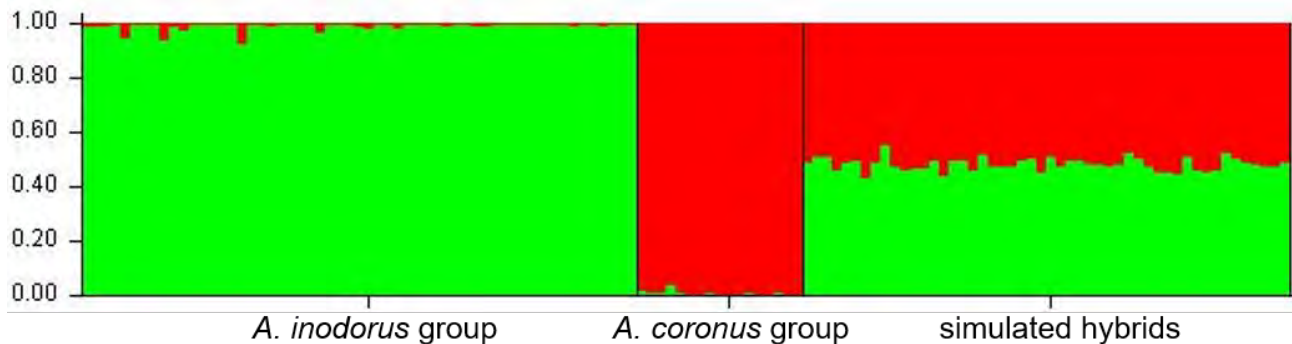


Figure 4.2: Multilocus genetic tests performed on 74 *Argyrosomus* species individuals sampled in the study and the simulated hybrids on the far right of the figure, using STRUCTURE. Green vertical bars indicate *Argyrosomus inodorus* type individuals while the red bars indicate *Argyrosomus coronus* types.

Of the 57 individuals with *A. inodorus* phenotypes and mtDNA haplotypes, all but three had Q values > 0.9 , identifying them as belonging to one genetic cluster (hereafter *A. inodorus* group). These lower Q values were still high (0.86, 0.85, and 0.78). Similarly, all 17 individuals reporting *A. coronus* morphotypes and haplotypes were identified as belonging to the other group (hereafter *A. coronus* group) with high probabilities. Only one individual (belonging to the *A. coronus* group) had a Q value < 0.9 , and this Q value was still high at 0.83. With the exception of the four individuals with Q values < 0.9 of assignment to one species, the confidence intervals on group membership Q values were non-overlapping. Rerunning the analysis with simulated hybrids indicated that all hybrids had intermediate Q values of ~ 0.5 , with the highest upper 95% confidence limit being 0.73 (Figure 4.2).

Summary indices of variability for the *A. inodorus* and *A. coronus* groups are reported in Table 4.1. The multilocus F_{ST} between both groups was 0.24. Genotype proportions conformed to HWE for each species group X locus combination, with the exception of UBA853 for the *A. inodorus* group ($P = 0.018$).

Table 4.1: Genetic variability for the resolved *Argyrosomus inodorus* and *Argyrosomus coronus* groups as summarised using allele number (N_A), allelic richness (A_R) and observed and expected heterozygosity (H_O and H_E , respectively)

Average across loci	Species	
	<i>Argyrosomus inodorus</i>	<i>Argyrosomus coronus</i>
N_A	11	6.8
A_R	7.9	6.8
H_O	0.63	0.66
H_E	0.69	0.72

4.2 Experimental fish

In total, 74 individuals were captured, of which 57 were genetically identified as *A. inodorus* and 17 as *A. coronus* (Appendix A). *Argyrosomus inodorus* individuals included in the study ranged in total length (TL) from 38.9 cm to 72.5 cm (Mean = 51 cm) with fish mass ranging from 454 g to 2875 g (Mean = 1130.5 g). *Argyrosomus coronus* individuals included in the study ranged in TL from 31.5 cm to 71.7 cm (Mean = 53 cm) with mass ranging from 291 g to 2878 g (Mean = 1589.4 g) (Table 4.2, Figure 4.3). There was no significant difference in total length between *A. coronus* and *A. inodorus* (one-tailed T-test, $p\text{-value} > 0.05 = 0.26$), however, there was a significant difference in mass between the two species (one-tailed T-test, $p\text{-value} < 0.05 = 0.04$).

Table 4.2: Mean mass (g), mass range, mean total length (cm) and total length range of number of specimens (n) per *Argyrosomus* species used in this study

Species	n	Mass (g)		Total length (cm)	
		Mean	Range	Mean	Range
<i>Argyrosomus coronus</i>	16	1589.4	291–3878	53.0	31.5–71.7
<i>Argyrosomus inodorus</i>	40	1130.5	454–2875	51.0	38.9–72.5

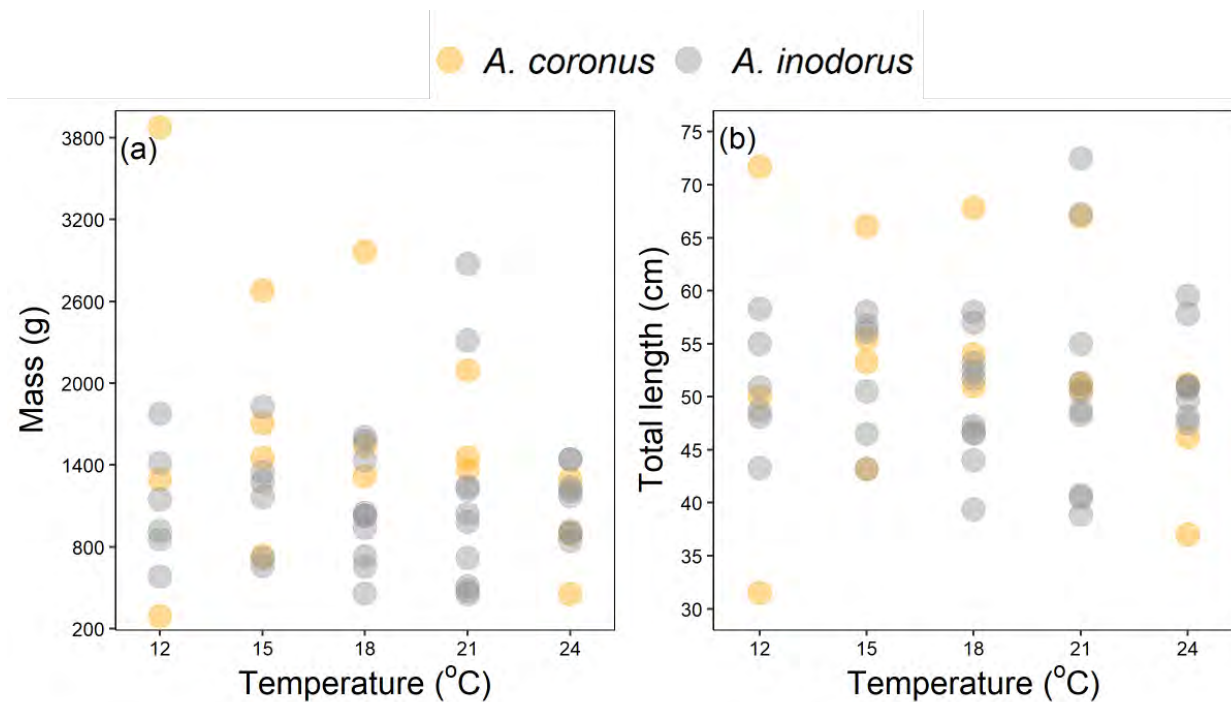


Figure 4.3: Individual mass (g) (a) and total length (cm) (b) of specimens for *Argyrosomus coronus* (orange) and *Argyrosomus inodorus* (silver) per test temperature used in this study.

4.3 Mass corrected metabolic data

There was considerable variation in the raw SMR data, which showed no clear trend with temperature (Figure 4.4a). The mass scaling exponent was estimated as 0.68 for *A. coronus* and 1.05 for *A. inodorus* (Figure 4.4b). Mass-corrected SMR reduced the variability of the data for both species, but showed conditional heteroscedasticity, as variances increased with temperature (Figure 4.4c).

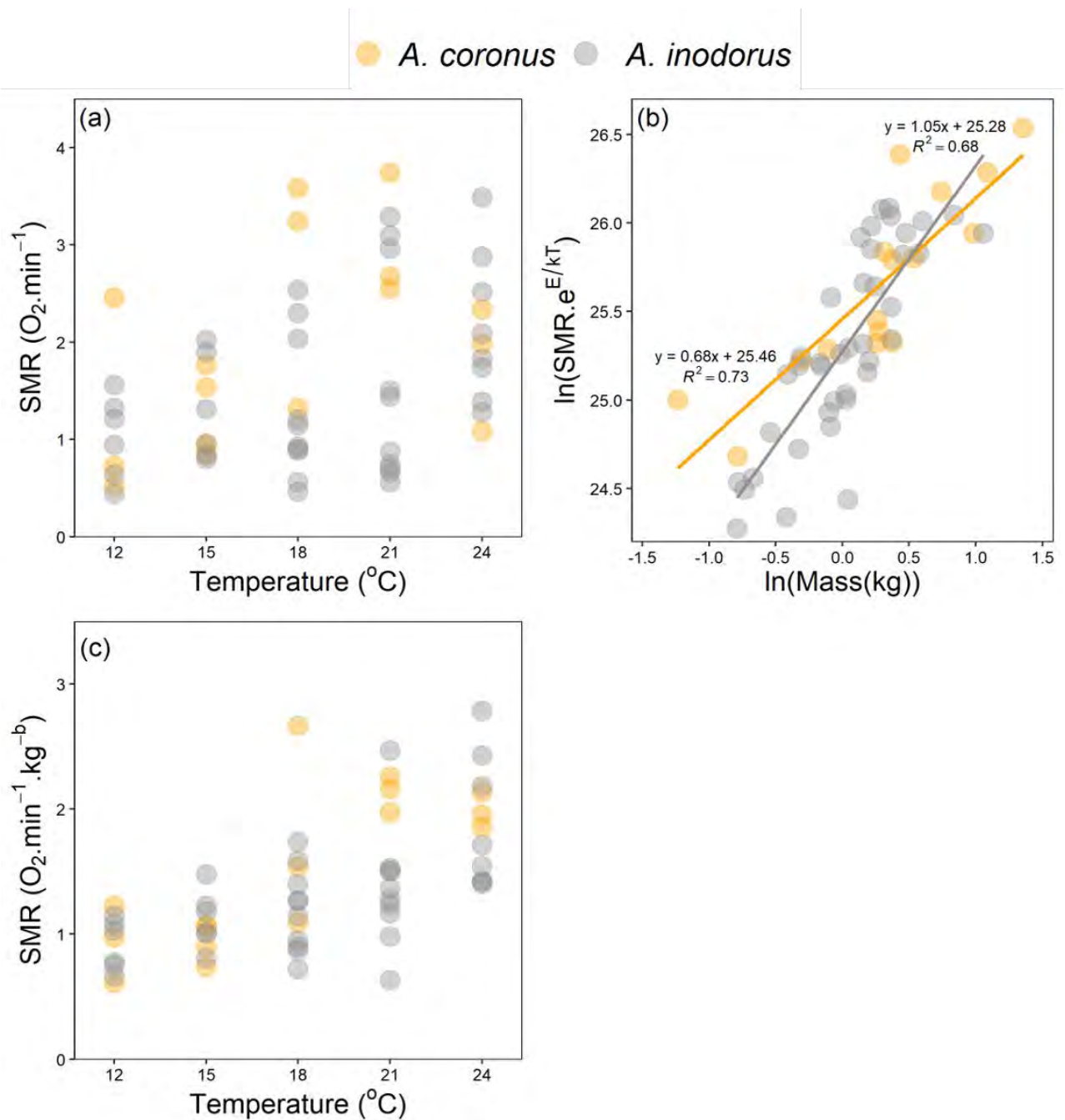


Figure 4.4: Mass correcting SMR for *Argyrosomus coronus* (orange) and *Argyrosomus inodorus* (silver). (a) Raw SMR values ($\text{O}_2 \cdot \text{min}^{-1}$) per temperature, (b) regression of the natural logarithm of temperature-corrected SMR ($\ln(\text{SMR} \cdot e^{E/kT})$) against the natural logarithm of mass ($\ln(\text{Mass}(\text{kg}))$) and (c) mass-corrected SMR values ($\text{SMR} (\text{O}_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-b})$) per temperature.

Raw MMR data showed similar variability, with no clear temperature trend evident (Figure 4.5a). The allometric mass scaling exponent was estimated as 0.82 for both species, taken as the slope of the linear relationship between the log of temperature

corrected MMR and mass (Figure 4.5b). Mass corrected MMR increased with temperature and showed conditional heterogeneity as variances increased with temperature (Figure 4.5c).

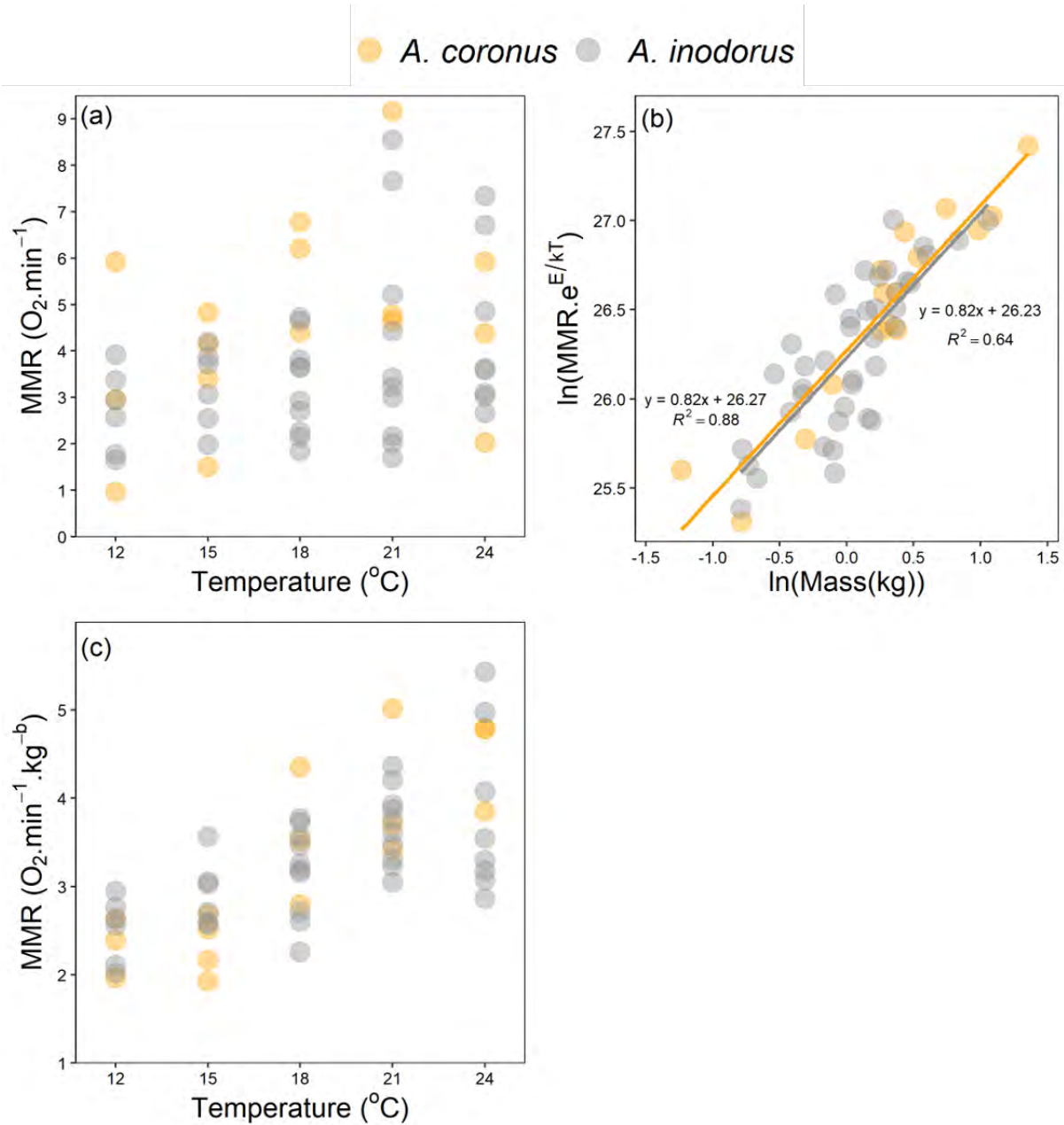


Figure 4.5: Mass correcting MMR for *Argyrosomus coronus* (orange) and *Argyrosomus inodorus* (silver). (a) Raw MMR values ($\text{O}_2 \cdot \text{min}^{-1}$) per temperature, (b) regression of the natural logarithm of temperature-corrected MMR ($\ln(\text{MMR} \cdot e^{E/kT})$) against the natural logarithm of mass ($\ln(\text{Mass}(\text{kg}))$) and (c) mass-corrected MMR values ($\text{MMR} (\text{O}_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-b})$). per temperature.

4.4 Standard and Maximum Metabolic Rates (SMR and MMR)

Standard and maximum metabolic rates increased with temperature (Figure 4.6a, b). The rate of change for SMR increased with temperature for both *A. coronus* and *A. inodorus*. The rate of change in MMR for *A. coronus* also increased with temperature but remained relatively constant for *A. inodorus*. There was no significant effect of species (*A. coronus*/*A. inodorus*) on the relationship between SMR and temperature (p-value = 0.484, Table 4.3) or between MMR and temperature (p-value = 0.783, Table 4.4) but there was a significant interaction between the first temperature polynomial term and MMR (p-value = 0.038, Table 4.4).

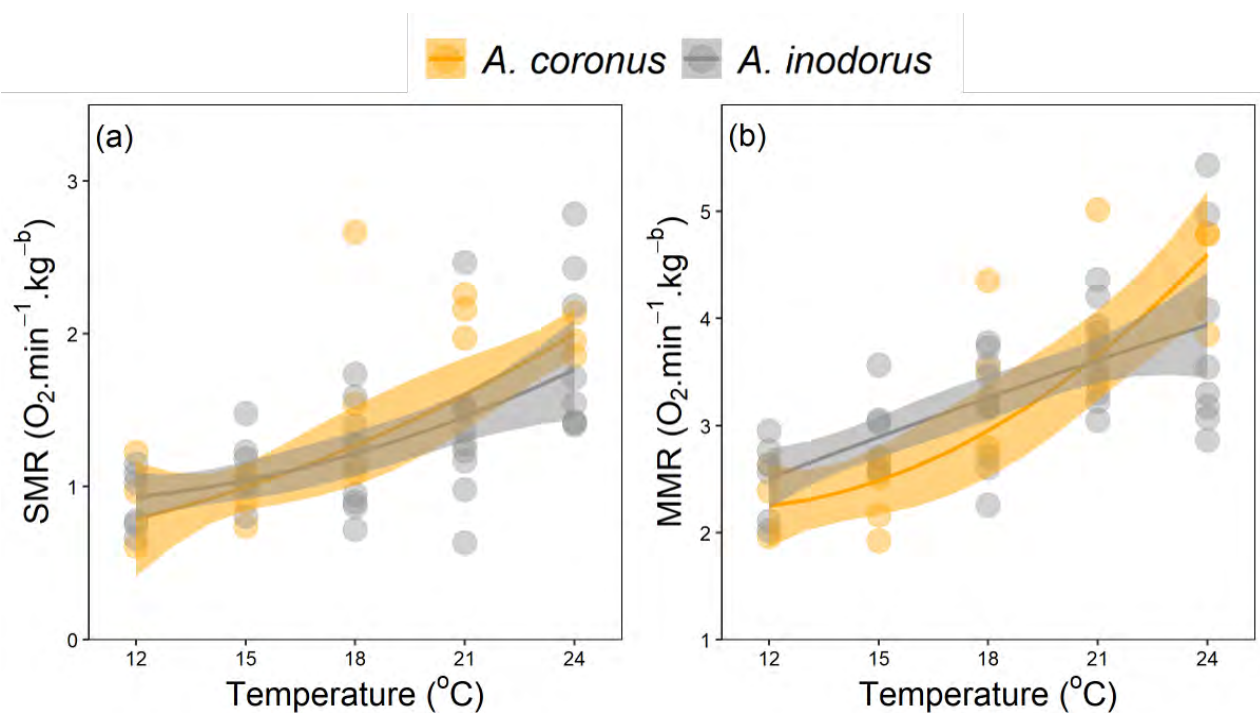


Figure 4.6: GLS model fit for *Argyrosomus coronus* (orange) and *Argyrosomus inodorus* (silver). (a) Standard metabolic rate (SMR) and (b) maximum metabolic rate (MMR) across test temperatures with shaded areas representing 95% confidence intervals.

Table 4.3: Generalised least squares modelling results for the standard metabolic rate (SMR) of *Argyrosomus coronus* and *Argyrosomus inodorus* presented as a quadratic function of temperature (Temp), with *A. coronus/A. inodorus* (species) as an interaction term, SE = standard error, AIC = Akaike information criterion, and significant p-values are highlighted in bold

Effect	Estimate	SE	t-value	p-value
Intercept	1.366	0.063	21.751	0.000
Species	-0.061	0.087	-0.706	0.484
Temp	3.086	0.494	6.248	0.000
Temp ²	0.389	0.649	0.597	0.553
Species: temp	-0.959	0.674	-1.423	0.161
Species: temp ²	0.025	0.760	0.034	0.973
AIC	70.937			
Residual SE	0.349			

Table 4.4: Generalised least squares modelling results for maximum metabolic rate (MMR) of *Argyrosomus coronus* and *Argyrosomus inodorus* presented as a quadratic function of temperature (Temp), with *A. coronus/A. inodorus* (species) as an interaction term, SE = standard error, AIC = Akaike information criterion, and significant p-values are highlighted in bold

Effect	Estimate	SE	t-value	p-value
Intercept	3.244	0.146	22.230	0.000
Species	0.046	0.166	0.277	0.783
Temp	6.010	0.891	6.748	0.000
Temp ²	1.458	0.941	1.549	0.128
Species: temp	-2.386	1.121	-2.129	0.038
Species: temp ²	-1.578	1.151	-1.371	0.177
AIC	109.655			
Residual SE	0.348			

4.5 Aerobic Scope (AS)

The modelled AS of *A. inodorus* was notably higher at cooler temperatures (12, 15, 18 and 21°C) compared to that of *A. coronus*, but this pattern reversed at higher temperatures (24°C) (Figure 4.7). Differences in AS were most pronounced in the middle temperatures (15, 18 and 21°C). Despite these differences, species (*A. coronus/A. inodorus*) did not have a significant effect on the relationship between AS and temperature (p-value = 0.145, Table 4.5).

Table 4.5: Generalised least squares modelling results for aerobic scope (AS) of *Argyrosomus coronus* and *Argyrosomus inodorus* presented as a quadratic function of temperature (Temp), with *A. coronus*/*A. inodorus* (species) as an interaction term, SE = standard error, AIC = Akaike information criterion, and significant p-values are highlighted in bold

Effect	Estimate	SE	t-value	p-value
Intercept	1.808	0.120	15.106	0.000
Species	0.217	0.147	1.481	0.145
Temp	2.886	0.774	3.728	0.001
Temp2	0.902	0.842	1.071	0.290
Species: temp	-1.095	1.070	-1.023	0.311
Species: temp2	-1.254	1.076	-1.165	0.250
AIC	107.450			
Residual SE	0.387			

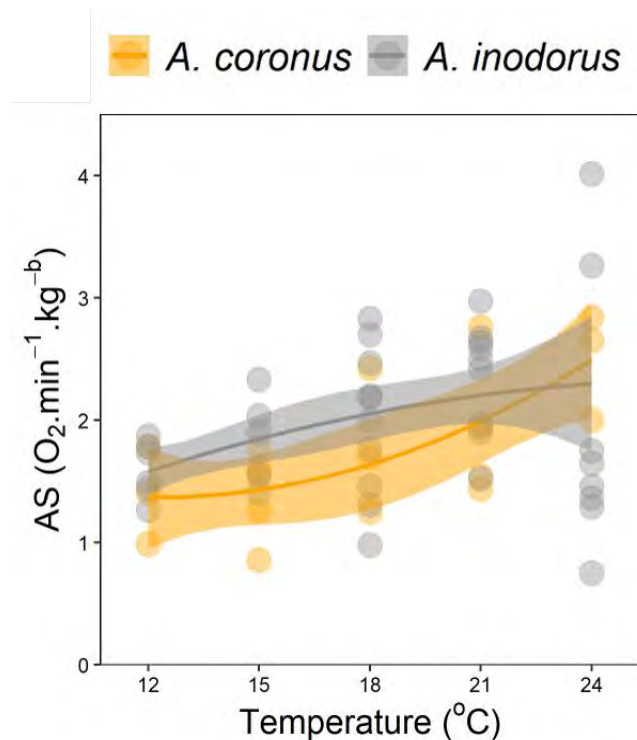


Figure 4.7: Modelled relationship between AS and temperature. Individual absolute aerobic scope (AS) (solid points) for *Argyrosomus coronus* (orange) and *Argyrosomus inodorus* (silver) and their modelled (GLS quadratic polynomial) relationship with temperature (solid lines) with 95% confidence intervals shaded.

Chapter 5. Discussion



Top: Dr Murray Duncan deep in thought about our ‘fisheries research’ while overlooking the vast Namib desert, Skeleton Coast National Park (image credit: Brett Pringle), Bottom: Brett Pringle explains the project and what the experiments entail to the Vice President of Namibia and Chancellor of the UNAM and his delegates (image credit: Kauna Tomas Namupala).

5.1 Metabolism and climate resilience

Overall, this study revealed that *A. inodorus* had a comparatively higher AS at the cooler temperatures compared to *A. coronus*, which had a higher AS at the warmest temperature. While the AS of *A. inodorus* plateaued at around 21°C, the AS for *A. coronus* remained on an upward trajectory as temperature increased to 24°C (Figure 4.7). At the lower temperatures, the steepest decline in the AS of *A. inodorus* occurred below 15°C, while the steepest decline in AS for *A. coronus* occurred between 24°C and 18°C. These findings explain the current distributions of the two species, with *A. inodorus* predominantly found in central Namibia and *A. coronus* predominantly found in the warmer waters of northern Namibia and Angola. These findings also suggest that both species will be energetically limited in the cold water associated with the Lüderitz upwelling cell (Figure 2.1) as hypothesised by Henriques *et al.* (2014). However, with future climate conditions in the area warming rapidly, it is expected that conditions in Namibia will increasingly favour *A. coronus* over *A. inodorus*, whose energy budget may be compromised.

The higher AS for *A. inodorus* at temperatures between 12 and 21°C suggests that if the metabolic requirements between these congeneric species are similar, then *A. inodorus* will be more competitive in the current ocean conditions around the WCRA and southern SCNP. The sensitivity to climate change of the South African population of *A. inodorus* was categorised as low–medium by Ortega-Cisneros *et al.* (2018) and the study predicted that the species may show signs of resilience to ocean warming. However, the increase in variability and decline in AS at 24°C for *A. inodorus* in our study suggests that only certain individuals will perform optimally as temperatures warm in central and northern Namibia. In contrast, the higher AS for *A. coronus* at 24°C suggests that this may be the tipping point where the species could outcompete

A. inodorus. As SSTs in this region are predicted to increase beyond this temperature range (Hobday and Pecl, 2014), it is likely that *A. coronus* may begin to dominate the species composition in northern Namibia.

While the mean temperature in central and northern Namibian coastal waters is increasing (Burrows *et al.*, 2011; Hobday and Pecl, 2014; Potts *et al.*, 2014b), it is likely that the high variability (seasonal and short-term) around this mean may trigger rapid species shifts as temperature surpasses the critical temperature for the species (Bates *et al.*, 2018). In addition to the large seasonal thermal fluctuations associated with the ABFZ, the frequency of marine heatwaves and upwelling events are increasing in the northern Benguela (Richter *et al.*, 2010; Oliver *et al.*, 2018). It is therefore possible that these short-term events (ocean weather) could be the ultimate driver of range shifts for *Argyrosomus* species in Namibia.

Based on the findings in this study, we can predict that the distribution of *A. inodorus* is likely to contract in the northern Benguela while *A. coronus* will likely extend its range further south, increasing the abundance of *Argyrosomus* species in central Namibia. However, while the predicted increase in temperature in northern Namibia will drive a southward shift in the *A. coronus* population, *A. inodorus* and *A. coronus* will most likely be restricted from further southward movement by the cold water (<12°C) associated with the intensifying perennial Lüderitz Upwelling cell (Rhein *et al.*, 2013; Henriques *et al.*, 2014). Further cooling in this area will most likely exceed the critical lower limits of these species as two of the four *A. inodorus* lost equilibrium during SMR measurements and none were able to recover from the exhaustive protocol to elicit MMR at 10°C during a pilot study in this project. While some fishes have been observed to respond to warming by shifting to deeper waters (Fredston-Hermann *et al.*, 2020) this is unlikely to be the case in Namibia, primarily due to the anoxic zone

which extends from 20 m (Griffiths, 1997). Therefore, it is most likely that the distribution of *A. inodorus* will contract in a coastal squeeze while *A. coronus* will extend its range further south into central Namibia.

Historical data indicate that *A. inodorus* was the dominant species ($\approx 90\%$) in the recreational *Argyrosomus* catch in the WCRA and the SCNP between 1993 and 1995 (Kirchner, 1999; Holtzhausen *et al.*, 2001). However, more recent catch data shows that *A. coronus* has outnumbered *A. inodorus* in the WCRA (Potts *et al.*, 2014b), with the proportion of *A. coronus* in the fishery comprising 57% between 2008 and 2009. Interestingly, the proportion of *A. coronus* from this study in the SCNP was 23%. This contrast could be explained by the cold Benguela Niña event which occurred in 1991 and 1992 (Imbol Kounoue *et al.*, 2019) which may have temporarily pushed *A. coronus* individuals further north, reducing the composition of *A. coronus* in the WCRA during the 1993–1995 period. In addition, it is likely that these fish follow the temperature gradient more frequently than previously anticipated. An alternative theory is that an early movement of *A. coronus* further south may have been triggered by the warm Benguela Niño events in 1995 (Gammelsrød *et al.*, 1998), 2010 and 2011 (Imbol Kounoue *et al.*, 2019) further skewing the catch composition of the 2008–2009 period. Therefore, the previous 1993–1995 period is likely a closer reflection of the current catch composition as it shows a more realistic change in the catch composition.

The physiological response exhibited by fish in our study suggests that these warm water intrusions, such as the Benguela Niño events in 1995 (Gammelsrød *et al.*, 1998), can facilitate the movement of *A. coronus* south into Namibia, which concurs with previous research information regarding spawning of adults, maturity of hybrids and the spawning of hybrids and pure species (Potts *et al.*, 2014b). This suggests that these Benguela Niño events may be significant factors in determining the species

composition in Namibia and for species shifts globally. In addition, areas with intermittent warming conditions where spawning adult *Argyrosomus* species overlap may facilitate sporadic hybridisation events (Potts *et al.*, 2014).

The AS of *A. coronus* continued to increase with temperature. Interestingly, although increases in the AS of *A. inodorus* are less pronounced, they also continue to rise with temperature. These AS curves contradict the bell-shaped curve purported for aquatic ectotherms under the oxygen-and capacity-limited thermal tolerance (OCLTT) theory (Frederich and Pörtner, 2000; Pörtner and Farrell, 2008; Pörtner, 2010; Pörtner, 2012). This is not uncommon in AS studies; for example, the Crear *et al.* (2020a) study on cobia *Rachycentron canadum* and the Norin *et al.* (2014) study on barramundi *Lates calcarifer*, revealed AS shapes which continued to increase without depicting optimal temperature. In these instances, AS may not have been a suitable predictor of optimal temperature range. This being acknowledged, the two *Argyrosomus* species likely have similar energetic requirements, and therefore, the AS can be utilised as a comparative indicator between the two species. In addition, oxygen limits on MMR were not considered in our study and the warm test temperature may not have been high enough to elicit a sharp drop in AS.

While it is possible that the AS of *A. inodorus* may have increased further at temperatures above 24°C, it appears that the relatively high mean AS at this temperature was influenced by two outliers (Figure 4.7). If these were excluded from the analysis, it is likely that there would have been a bell-shaped AS curve for this species. If this is the case, then it is likely that a similar bell-shaped curve would have been observed for *A. coronus* as this species can tolerate much higher temperatures than the 24°C used in the study (Potts *et al.*, 2010).

The occurrence of physiological outliers at 24°C deserves some discussion. Duncan *et al.* (2019a) provided evidence that an unexploited population of an important linefish species, *Chrysoblephus laticeps*, had a comparatively higher phenotypic diversity compared to an exploited population. The difference in phenotypic diversity was attributed to the selective removal of individuals with broad thermal tolerance by angling. While our study did not compare the phenotypic diversity between *Argyrosomus* species in the SCNP and WCRA, it is likely that the heavy angling pressure in the WCRA may have removed individuals with broad thermal tolerance. The remaining individuals may therefore not exhibit tolerance to the warming temperatures expected in the region.

Climate change is negatively impacting most marine species (Little *et al.*, 2020) and some ectotherms are showing signs of persistence and physiological acclimation (Morley *et al.*, 2019), particularly those in protected areas. Additionally, this is evident for species with adult mobility and with broad distributions, such as the *Argyrosomus* species, which can facilitate the colonisation of newly available thermal habitats (Sunday *et al.*, 2015). For this to occur, it is critical that physiological diversity is maintained and even promoted to ensure that individuals with broad thermal tolerance are present in the population. As the SCNP, in particular, is at the warm edge of the distribution of *A. inodorus*, and appears to host the high-performance phenotypes, it is critical that the integrity of this protected area is maintained to promote the resilience and adaptation of this species in Namibia.

These *Argyrosomus* congeners appear to have evolved to tolerate a broad range of thermal conditions. This may be due to the longshore southward summer migrations that are undertaken across a broad thermal gradient by *A. inodorus* (Griffiths and Heemstra, 1995), and the resident nature of most of the *A. coronus* in their seasonally

variable thermal environment (Potts *et al.*, 2010; Potts *et al.*, 2014b; Potts *et al.*, 2018). It appears that these species experience a wide range of temperatures in the wild, as adult *A. inodorus* undergo spawning migrations (Griffiths and Heemstra, 1995) and *A. coronus* have a broad distribution. This may confer some resilience to thermal change, particularly when compared to resident species that live in a thermally stable environment (such as many tropical coral reef species).

While our study did not explicitly consider oxygen, the known factor of reduced lower oxygen at higher water temperatures may play an increasingly important role in the susceptibility of fishes to future climate conditions (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; McBryan *et al.*, 2013). Ectotherms are affected by the synergistic combination of increasing temperatures and lower oxygen levels due to the higher oxygen demand relative to oxygen supply at extreme temperatures, and reduced oxygen supply in hypoxic zones (Pörtner and Knust, 2007; Pörtner, 2010). In addition to this relationship, increases in microbial respiration associated with warmer temperatures are likely to further reduce oxygen levels (Brown *et al.*, 2004). Sunday (2020) describes this situation that fish face as “It simply gets too cold or hot to breathe”. The effects of hypoxia on fish changes with temperature (Rogers *et al.*, 2016) and ranges from behavioural changes (reduced activity and avoiding hypoxic areas) to physiological changes (changes in ventilation and cardiac activity) (Richards, 2009). More recently, ocean warming and hypoxia have also been shown to negatively affect the embryonic growth and fitness of small-spotted catsharks *Scyliorhinus canicula* (Musa *et al.*, 2020), and has been shown to negatively impact the immune function and increase susceptibility to disease in largemouth bass, *Micropterus salmoides* (Sun *et al.*, 2020). Future research should therefore aim to quantify the tolerance of

Argyrosomus species to hypoxia to further understand the physiological tolerance of these species.

Environmental stress or change can also create thermal bottlenecks in larval populations (Edworthy *et al.*, 2018). While Dahlke *et al.* (2020) suggest that spawning adults and embryos are the most susceptible to temperature change, the work of Edworthy *et al.* (2018) on the larval stage of *A. japonicus* suggests that the larvae may be extremely susceptible to environmental perturbations. Therefore, it is recommended that the response of larval *A. coronus* and *A. inodorus* to temperature changes should be explored to better understand their resilience to climate change.

A number of potential caveats may have influenced the findings of this study. Our study encountered difficulties in maintaining temperature during holding acclimation. Subsequently, some fish may have been acclimated a degree above or below other fish. However, it is likely that our experimental acclimation period was long enough to counteract any major influence on the results and was a realistic representation of what the fish experience in the wild. Thermal acclimation has been exhibited for intertidal fish in a rapidly fluctuating environment (da Silva *et al.*, 2019), and for a range of ectotherms under extreme heat events (Morley *et al.*, 2019). It was also apparent in our study that background respiration was increasingly evident within respirometers due to the build-up of microalgae. However, this was mitigated by routinely cleaning tanks, respirometers and tubing with chlorine before each experiment. Due to the similar morphology of *A. coronus* and *A. inodorus*, it was difficult to guarantee equal sample sizes in the study, because the sampling site in the southern region of the SCNP is in the middle of the core distribution of *A. inodorus* and at the edge of the core distribution of *A. coronus*. As a result, the AS of *A. inodorus* presented here may provide a better representation of the population's physiology of *A. inodorus* than of *A.*

coronus, which likely represents individuals living at their lower thermal limits. In addition, the exceptionally fast acclimation to holding facilities by *A. coronus*, compared to the poorer acclimation of *A. inodorus*, further suggests that exposure to a changing environment will favour the northern species. As the collection site was at the edge of the warming conditions, it is likely that these experimental fish, which were captured on the leading edge of the distributional shift, have provided information on individuals with a lower upper tolerance. However, this will not alter the likely outcome of the distributional shift of this species.

Individual MMR may have been underestimated for larger fish, as larger individuals were more difficult to chase than the smaller fish. As a result, some fish may have been less exhausted than others. However, the chase protocol used in the study is presumed to be the most appropriate method to induce MMR in body caudal swimmers (Roche *et al.*, 2013; Clark *et al.*, 2013; Norin and Clark, 2016). Norin *et al.* (2014) argued that if this caused an underestimation of MMR, it should be independent of temperature (Brett, 1964; Beamish, 1978) or considered to be greatest at the higher temperatures (Farrell, 2007). Therefore, if MMR and thus AS were underestimated, it would be equal at all temperatures, or greater at the higher temperatures and would not change the results of a continual increase in MMR up to 24°C.

5.2 Genetic confirmation

We found no hybrids, but rather two distinct populations of *A. inodorus* and *A. coronus*. In a previous study, Potts *et al.* (2014b) employed a critical Q value threshold of 0.9 to classify individuals as pure or introgressed (i.e. < 0.9) to some extent. In our study, upon application of similar arbitrary thresholds, all but four individuals would be unambiguously identified as pure *A. inodorus* or *A. coronus* on account of their nuclear

genotypes. An important consideration here, as well as in Potts *et al.* (2014b), is that individuals could exhibit Q values below 0.9 for reasons other than post-speciation introgression, such as retained genetic similarity and/or marker resolution. Potts *et al.* (2014b) reported two individuals in their study with *A. inodorus* phenotypes and haplotypes but with *A. coronus* nuclear genotypes. However, no such discordance was detected in our study, as the morphological, mtDNA and microsatellite data were in alignment and were able to distinguish individuals as *A. inodorus* or *A. coronus*.

5.3 Ecological consequences of the distributional shift

While most physiology research to predict the response of species to climate change has focused on single species and population differences in physiological rates (Duncan *et al.*, 2019a; Crear *et al.*, 2020a), this study was novel as it compared the AS between two congeners that overlap in terms of distribution, ecology and economic value. While there are differences in life-history and similarities in economic and ecological relevance between these congeners (Griffiths and Heemstra, 1995; Kirchner, 1999; Kirchner and Voges, 1999; Kirchner *et al.*, 2001; Potts *et al.*, 2010), this study showed that these species will have different responses to thermal change in terms of OCLTT predictions.

There is also a lack of recent research to predict the response of species which share similar ecological roles, to climate change. Norin *et al.* (2019) provided an important comparative study on Atlantic cod *Gadus morhus* and haddock *Melanogrammus aeglefinus*, two important commercial species with similar ecological roles, and like both *Argyrosomus* species, are affected by overfishing (Cardinale *et al.*, 2012) and climate warming (Rogers *et al.*, 2011). Norin *et al.* (2019) found similar and expected trends in that the haddock tolerated warmer temperatures than the Atlantic cod, a

finding which corresponds with their natural temperature ranges. The study also suggests that Atlantic cod will face physiological trade-offs more frequently, and would exhibit reduced swimming efficiency compared to the haddock. Norin *et al.* (2019) concluded that this metabolic trade-off may result in an increase in the numbers of cod caught compared to haddock, because the haddock would likely be better at escaping fishing gear (Norin *et al.*, 2019). In our study, both species face pressure from the fisheries operating in the area, however, the *A. inodorus* population will face further competition from its northern congener if waters continue to warm and disproportionately favour the metabolic physiology of *A. coronus* in the WCRA. As previously mentioned, *A. coronus* attains larger sizes and grows faster than its southern counterpart. As a result, *A. inodorus* may be outcompeted for habitat and resource use. The response of prey items to climate change in this area is unclear and may result in a change in diet for both *Argyrosomus* species. The combination of fisheries exploitation, climate change and interspecies competition does not bode well for the future of *A. inodorus* in Namibia.

5.4 Implications for the Namibian *Argyrosomus* fishery

As coastal waters in the WCRA continue to warm and favour *A. coronus*, the sustainability of the Namibian *Argyrosomus* fishery is questionable, particularly as the fisheries policy and management will become increasingly inadequate. The recent catch composition of the *Argyrosomus* fishery in the WCRA conforms to the global pattern of species shifting poleward (Potts *et al.*, 2014b; Sunday *et al.*, 2015; Kleisner *et al.*, 2017; Crear *et al.*, 2020b) and it is likely that the shift of *A. coronus* (which attains larger sizes) may result in an increase in the number of large fish in the Namibian linefishery. The anticipated coastal squeeze will likely concentrate fishes in the WCRA,

and potentially improve the fishing opportunities. As a result, this distributional shift may be advantageous for all linefishery sectors (recreational, subsistence and commercial) in the WCRA. The recreational fishery in particular may benefit due to an increase in trophy specimens, and this may have positive consequences for the local economy due to the economic impact associated with this sector. However, it is likely that an increase in recreational fishing will have negative consequences for the population of *A. coronus*, as anglers are not readily able to differentiate between the *Argyrosomus* species, and the regulatory framework was designed to manage *A. inodorus*. With a minimum legal-size limit of 40 cm, it is likely that *A. coronus*, which only matures at a size of 82 to 90 cm, will be susceptible to growth overfishing (this means, heavily harvesting a cohort before it reaches maximum biomass or socially optimal size, Beverton and Holt, 1957; Diekert, 2012). This will lead to a truncated age-distribution and potential stock collapse of an establishing *A. coronus* population in Namibia.

In their global review on effective recreational fisheries governance, Potts *et al.* (2020) examined Namibia's recreational fisheries policy and the efficacy of its governance. They found that Namibia does not have any contingency plans to respond to a potential stock collapse. While there is currently no monitoring of the recreational fishery, an increase in catch rate and catch in the Namibian linefishery should not necessarily be interpreted as an increase in the size of the *Argyrosomus* populations.

While it is unlikely that these species can be successfully managed separately due to their morphological similarities, it is feasible to reconsider the current catch-regulations. Because *A. coronus* matures at such large sizes (~87 cm, Potts *et al.*, 2010), an increase in the minimum size limit could benefit the species. However, a very large minimum size for *A. inodorus* would substantially decrease the harvest, and

this will dramatically reduce the catch and most likely the popularity of this fishery. This may have substantial socio-economic consequences for a region that relies heavily on angling tourism. Gwinn *et al.* (2015) found that harvest slots consistently increase the number of trophy fish while conserving reproductive biomass, providing a valuable option for fisheries managers to meet both conservation and recreational, commercial and subsistence needs. Harvest slots (such as keeping fish between 40–70 cm) in the Namibian *Argyrosomus* recreational and subsistence fisheries, would still allow the harvest of some juvenile *A. coronus*, but it would also protect maturing and large adult *A. coronus*. Further amendments could include a change from the current limit of two fish over 70 cm to one fish over 90 cm (all fish between 70 and 90 cm must be released). This would limit the harvest of large breeding fish and maintain an abundance of trophy specimens. The introduction of the harvest slot limit would create a favourable compromise between conservation and the goals of the fishery. Similar harvest slots have been successfully implemented for sciaenids such as the red drum *Sciaenops ocellatus* and the black drum *Pogonias cromis* in the United States.

Although our study limited the upper experimental temperature to 24°C, several fish (four *A. inodorus* and one *A. coronus*) exhibited signs of impairment (loss of equilibrium) post exhaustive exercise. At the upper test temperature, one *A. inodorus* mortality was observed. This finding suggests that *A. inodorus* may be more vulnerable to excessive stress at high temperatures than *A. coronus*. This is concerning in a recreational fishery most productive in summer, with warm water temperatures, and could place *A. inodorus* under additional pressure post-release. However, the majority of fish caught above the minimum legal size in the Namibian recreational fishery are not released. However, promoting catch-and-release in the Namibian recreational fishery is essential. While the practise of catch-and-release is

assumed to be associated with low mortality rates (Raby *et al.*, 2014; Bower *et al.*, 2016), there is a great deal of potential for physiological and physical impairment (Arkert *et al.*, 2020; Butler *et al.*, 2020; Pringle *et al.*, 2020) and mortality (Bartholomew and Bohnsack, 2005; Moxham *et al.*, 2019), particularly in high-energy, predator-rich surf zones (Mannheim *et al.*, 2018). With this in mind, anglers who practice catch-and-release should employ best practices such as those outlined in Brownscombe *et al.* (2017). To facilitate this, educational drives and incentives, particularly those associated with the catch-and-release, Namibian Rock and Surf Super Pro League (RASSPL) are needed to promote best practice (Mannheim *et al.*, 2018). Strategies to limit effort, such as postponing angling competitions during warm water events, may also be necessary to reduce post-release mortality. Crear *et al.* (2020a) reported a 30% mortality of the cobia *Rachycentron canadum* at warm temperatures, and suggested that further research on the effect of temperature on blood oxygen binding, gill gas exchange rates and heart function is necessary; this applies equally to the *Argyrosomus* species.

According to Arlinghaus *et al.* (2019), recreational fisheries should be managed on an equal footing to other fisheries sectors to achieve sustainability. To equitably manage the *Argyrosomus* fishery in Namibia it may be necessary to develop separate policies for the recreational, subsistence and commercial linefish sectors. When developing these policies, it will be critical to develop and articulate the overall objectives of the *Argyrosomus* fishery. This will ultimately govern the allocation of resources and the management objectives for each of these sectors. The development of policy is considered to be critical, particularly as the number of people that are reliant on the *Argyrosomus* resource as a source of food is on the rise (Cardoso *et al.*, 2006; Barnes and Alberts, 2008).

The participants in the subsistence sector are an extremely vulnerable group and may be most impacted by reductions in the *Argyrosomus* catch. Fishers in this sector compete directly with the far better resourced recreational shore-based fishery, and due to their limited mobility will likely deplete local stocks and suffer reduced catch rates. While local fishing associations have been developed to facilitate the distribution of their catch (such as the Hanganeni Artisanal Fishing Association, or HAFA, situated in Hentiesbaai) it is recommended that the subsistence anglers are permitted to continue harvesting according to the current regulations, as any reduction in legal take will likely push the local communities further into poverty and increase the amount of illegal fishing activities. Barnes and Alberts (2008) recommended that the subsistence sector should be prioritised and managed using a simple licensing system. This will avoid confusion in the recognition of subsistence and recreational fishers and will provide fishers with food for their livelihoods during force majeure such as those imposed during the 2020 COVID-19 lockdown, where recreational fishing was banned but not commercial fishing.

While the fishery is dominated by the shore-based sector, regulations for the boat-based fishery should also be introduced. The commercial boat-based fishery which has no set catch limits, is comprised of a few vessels due to poor economic incentives. The lack of economic incentive is further strained because many recreational ski-boat anglers sell their catch to local restaurants and fishmongers. The ski-boat fishery can access most of the Namibian coast, increasing the potential for overfishing and post-release mortality. For example, studies on *A. inodorus* in South Africa (Kerwath *et al.*, 2013) and *A. japonicus* in Australia (Butcher *et al.*, 2013; Hughes *et al.*, 2019) indicated that barotrauma was experienced at relatively shallow depths, with significant post-release mortality. Further research on the effects of barotrauma and its potential for

delayed post-release mortality should be conducted as *A. coronus* and *A. inodorus* may not be suitable boat-based catch-and-release species. Fishing effort by this sector is also most likely occurring in protected areas. This may undermine the physiological diversity of *Argyrosomus* populations (see section 5.1 above).

To improve the long-term sustainability of the Namibian linefisheries, the recommendations highlighted in Potts *et al.* (2020) should be implemented. These recommendations include the amendment of policy to recognise all fishery sectors (recreational, commercial and subsistence) and to proactively improve planning and incorporate contingency plans to effectively secure the valuable resources on offer along the Namibian coast. While Namibia partly adopts a precautionary approach to fisheries management (Potts *et al.*, 2020) they have no emergency plans for stock collapse, which is problematic for a fishery that currently harvests immature *A. coronus*. To protect these fish, the Namibian Ministry of Fisheries and Marine Resources needs to enforce and control the harvest and selling of *Argyrosomus* species in the WCRA and beyond. The Namibian Ministry of Fisheries and Marine Resources should also promote more sustainable fishing practices such as catch-and-release by re-initiating their citizen science tagging program. This, along with routine genetic analysis and continually monitoring catch rates, can provide valuable information on the ratio of *A. coronus* to *A. inodorus*, and therefore their shifting distributions. In addition, to effectively manage this valuable fishery, routine stock assessments on both species will provide reliable information on the health and status of *Argyrosomus* populations along the west coast of southern Africa. This can only prove successful with cooperative management strategies which link government with anglers and scientists, who need to cooperate and agree on achievable conceptual and operational objectives (Potts *et al.*, 2020). To realise this, local government,

researchers and public stakeholders need to engage proactively sooner rather than later.

Non-compliance is synonymous with recreational fisheries (Potts *et al.*, 2020). Namibian recreational fishers are considered to be only partly compliant with regulations (Potts *et al.*, 2020). While this is unsurprising for a developing nation, it is concerning because of the high number of visiting recreational anglers, predominantly South Africans, who harvest substantial quantities of fish in the WCRA (Kirchner and Beyer, 1999). Strong monitoring and enforcement programs will be essential for adaptive management strategies to be implemented, and critical for sustainable fishery systems (Potts *et al.*, 2020). While monitoring recreational fisheries is difficult due to the broad distribution and high mobility of recreational fishers (Post *et al.*, 2002), the WCRA provides a unique opportunity for successful monitoring. This is because the WCRA has one major road that follows the surf zone running from the Ugab River through Hentiesbaai and Swakopmund and down to Walvis Bay, which could be monitored for illegal activities with routine vehicle surveillance and enforcement. This approach would be far less cost prohibitive than roving creel-type monitoring and compliance initiatives, which would require beach driving and the interception of anglers along a vast coastline.

The inclusion of an adaptive management strategy is considered to be beneficial in situations where fishes are shifting their ranges (Maxwell *et al.*, 2015). This would be appropriate for the highly dynamic *Argyrosomus* fishery, where the species composition in the WCRA may change over short time scales. Concurrent monitoring of the fishery and the coastal sea temperatures may, over time, provide predictive information on the composition of the *Argyrosomus* population, and will allow informed decisions on the appropriate regulations for the season/year. While this type of

adaptive strategy may have benefits, other components of management should not be adaptive. For example, the integrity of the current spatial protection (MPAs) must be retained and if possible, reinforced. This is particularly important for *Argyrosomus inodorus* as these areas protect the early life stages (in the SCNP) as well as adults during their spawning aggregations in Meob Bay and Sandwich Harbour (Kirchner and Holtzhausen, 2001).

5.5 Conclusions

Making reference to our study and the Potts *et al.* (2014b) study, it seems that *A. coronus* is better physiologically suited for future conditions along the Namibian coast. Based on the findings of this study, it is likely that the distribution of *A. inodorus* will contract in the northern Benguela, as they appear to be less resilient to the impacts of ocean warming than *A. coronus*. While a shift to deeper water may allow these fish to remain at their thermal optimum for AS, this is unlikely due to the anoxic zone which extends deeper from 20 m (Griffiths, 1997). As *A. inodorus* and *A. coronus* will compete for resources, the higher AS observed at the highest experimental temperature should make *A. coronus* the future winner in this rapidly changing climate. Fisheries are likely to benefit from the coastal squeeze of *A. inodorus* and the increase in abundance of *A. coronus*. This may result in increased catch rates and size of ‘*kabeljou*’ or ‘*kob*’ in central Namibia. However, these benefits may be negated by the current governance of the fishery, which has no clear objectives, target reference point or monitoring. In addition, the current regulatory framework was designed for *A. inodorus*, and this may reduce the potentially positive impacts that increasing numbers of *A. coronus* may bring to the fishery. This suggests that governance reform is

urgently required to respond to the unique challenges associated with Namibia's coastal fisheries in the Anthropocene.

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Appendices

Appendix A: Information for all *Argyrosomus* individuals caught at the Toscanini old diamond mine in the Skeleton Coast National Park (SCNP), Namibia. AP = Acclimation Period (days); Res. size = Respirometer size; ET = Experimental Temperature; M = Mass; TL = Total length; ID = Identification; mtDNA H = mitochondrial DNA Haplotype; Bold n = included in study.

n	Code	Capture date	Trial date	AP	Trial	Res. size	ET (°C)	M (g)	TL (cm)	Sex	Visual ID	Genetic ID	Multilocus Q value (0-1)	mtDNA H
1	T1C1	02/03/2019	11/04/2019	40	1	S	10	580	41.6	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.964	1
2	T1C2	02/03/2019	11/04/2019	40	1	M	10	890	49.9	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.982	1
3	T1C3	02/03/2019	11/04/2019	40	1	L	10	1291	54	Juvenile	<i>A. inodorus</i>	<i>A. inodorus</i>	0.98	1
4	T1C4	02/03/2019	11/04/2019	40	1	M	10	863	51.2	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.986	1
5	T2C1	02/03/2019	15/04/2019	44	2	S	24	521	40.7	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.865	1
6	T2C2	02/03/2019	15/04/2019	44	2	M	24	1296	51.2	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.113	2
7	T2C3	02/03/2019	15/04/2019	44	2	L	24	1445	59.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	1
8	T2C4	02/03/2019	15/04/2019	44	2	M	24	850	45.6	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.991	1
9	T3C1	02/03/2019	18/04/2019	47	3	S	18	459	39.4	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
10	T3C2	02/03/2019	18/04/2019	47	3	M	18	1028	51.7	Juvenile	<i>A. inodorus</i>	<i>A. inodorus</i>	0.848	3
11	T3C3	02/03/2019	18/04/2019	47	3	L	18	1542	54	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.015	4
12	T3C4	02/03/2019	18/04/2019	47	3	M	18	1029	52.4	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.984	1
13	T4C1	02/03/2019	21/04/2019	50	4	S	21	480	40.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.928	1
14	T4C3	02/03/2019	21/04/2019	50	4	L	21	2096	67	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.009	5
15	T5C2	02/03/2019	28/04/2019	57	5	M	15	1276	56.7	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
16	T5C4	02/03/2020	28/04/2019	57	5	M	15	917	47.3	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	6
17	T5C1	09/03/2019	28/04/2019	50	5	S	15	441	37.9	Juvenile	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
18	T5C3	09/03/2019	28/04/2019	50	5	L	15	2678	66.1	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.156	7
19	T6C1	09/03/2019	01/05/2019	53	6	S	21	512	40.7	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
20	T6C2	09/03/2019	01/05/2019	53	6	M	21	1040	51.3	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.988	1
21	T6C3	09/03/2019	01/05/2019	53	6	L	21	2875	72.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.761	1
22	T6C4	09/03/2019	01/05/2019	53	6	M	21	721	48.3	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
23	T7C2	09/03/2019	06/05/2019	58	7	M	12	854	48.7	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.989	1
24	T7C3	09/03/2019	06/05/2019	58	7	L	12	1001	55	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.977	1
25	T7C4	09/03/2019	06/05/2019	58	7	M	12	1611	53.4	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.014	8
26	T8C2	09/03/2019	10/05/2019	62	8	M	18	939	46.5	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
27	T8C3	09/03/2019	10/05/2019	62	8	L	18	1085	53	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	1

28	T8C4	09/03/2019	10/05/2019	62	8	M	18	732	46.7	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.991	1
29	T9C2	09/03/2019	17/05/2019	69	9	M	15	720	46.5	Juvenile	<i>A. inodorus</i>	<i>A. inodorus</i>	0.985	1
30	T9C3	09/03/2019	17/05/2019	69	9	L	15	1833	60.1	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.878	1
31	T9C4	09/03/2019	17/05/2019	69	9	M	15	735	45.3	Juvenile	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
32	T10C2	09/03/2019	20/05/2019	72	10	M	24	915	49.7	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	1
33	T10C3	09/03/2019	20/05/2019	72	10	L	24	1207	50.8	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	9
34	T10C4	09/03/2019	20/05/2019	72	10	M	24	902	48.1	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.985	1
35	T11C1	03/04/2019	24/05/2019	51	11	S	12	377	34.2	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.953	10
36	T11C2	09/03/2019	24/05/2019	76	11	M	12	918	48.1	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.988	6
37	T11C3	09/03/2019	24/05/2019	76	11	L	12	1418	55	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	1
38	T11C4	09/03/2019	24/05/2019	76	11	M	12	1146	50.9	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.942	3
39	T12C2	08-11/05/2019	8/06/2019	28	12	M	15	736	43.2	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.008	2
40	T12C3	11/05/2019	8/06/2019	28	12	L	15	1348	58	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.995	3
41	T12C4	11/05/2019	8/06/2019	28	12	M	15	1165	50.5	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
42	T13C1	08/05/2019	11/06/2019	34	13	S	12	291	31.5	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.008	11
43	T13C2	11/05/2019	11/06/2019	31	13	M	12	998	51	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.995	12
44	T13C4	11/05/2019	11/06/2019	31	13	M	12	1080	52.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
45	T14C1	16-18/05/2019	15/06/2019	28	14	S	24	455	37	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.028	2
46	T14C2	16-18/05/2019	15/06/2019	28	14	M	24	896	46.2	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.006	2
47	T14C3	16-18/05/2019	15/06/2019	28	14	L	24	1443	57.8	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.983	1
48	T14C4	16-18/05/2019	15/06/2019	28	14	M	24	1240	51	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.989	1
49	T15C1	16-18/05/2019	18/06/2019	31	15	S	21	454	38.9	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
50	T15C2	16-18/05/2019	18/06/2019	31	15	M	21	984	48.7	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.98	1
51	T15C3	16-18/05/2019	18/06/2019	31	15	L	21	1367	50.7	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.005	13
52	T15C4	16-18/05/2019	18/06/2019	31	15	M	21	1242	50.4	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.987	1
53	T16C1	16-18/05/2019	22/06/2019	35	16	S	18	656	44	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.991	1
54	T16C2	16-18/05/2019	22/06/2019	35	16	M	18	1317	51	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.006	2
55	T16C3	16-18/05/2019	22/06/2019	35	16	L	18	2968	67.8	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.009	2
56	T16C4	16-18/05/2019	22/06/2019	35	16	M	18	1050	47.3	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.99	14
57	T17C2	05-06/06/2019	19/07/2019	43	17	M	24	846	47.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	15
58	T17C3	05-06/06/2019	19/07/2019	43	17	L	24	1950	61.1	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.987	14
59	T17C4	05-06/06/2019	19/07/2019	43	17	M	24	1175	51	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.993	1
60	T18C1	05-06/06/2019	23/07/2019	47	18	S	12	583	43.3	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.988	1
61	T18C2	05-06/06/2019	23/07/2019	47	18	M	12	1297	50	Female	<i>A. coronus</i>	<i>A. coronus</i>	0.007	2

62	T18C3	05-06/06/2019	23/07/2019	47	18	L	12	3878	71.7	Female	<i>A. coronus</i>	<i>A. coronus</i>	0.006	16
63	T18C4	05-06/06/2019	23/07/2019	47	18	M	12	1777	58.3	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.99	1
64	T19C1	05-06/06/2019	26/07/2019	50	19	S	15	663	43.2	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.992	1
65	T19C2	05-06/06/2019	26/07/2019	50	19	M	15	1452	55.4	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.016	2
66	T19C3	05-06/06/2019	26/07/2019	50	19	L	15	1707	53.3	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.005	2
67	T19C4	05-06/06/2019	26/07/2019	50	19	M	15	1825	56.1	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.975	1
68	T20C1	05-06/06/2019	30/07/2019	54	20	S	21	770	44.5	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.99	1
69	T20C2	05-06/06/2019	30/07/2019	54	20	M	21	1455	51.2	Juvenile	<i>A. coronus</i>	<i>A. coronus</i>	0.005	17
70	T20C3	05-06/06/2019	30/07/2019	54	20	L	21	2313	67.2	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1
71	T20C4	05-06/06/2019	30/07/2019	54	20	M	21	1223	55	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.985	1
72	T21C2	05-06/06/2019	02/08/2019	57	21	M	18	1575	58	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.995	1
73	T21C3	05-06/06/2019	02/08/2019	57	21	L	18	1607	57	Male	<i>A. inodorus</i>	<i>A. inodorus</i>	0.99	1
74	T21C4	05-06/06/2019	02/08/2019	57	21	M	18	1436	53.2	Female	<i>A. inodorus</i>	<i>A. inodorus</i>	0.994	1