CLIMATE-GROWTH RELATIONSHIPS OF *ARGYROSOMUS SPP*. FOUND ALONG THE NAMIBIAN COAST

A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR

THE DEGREE OF

MASTER OF SCIENCE FISHERIES AND AQUATIC SCIENCES OF

THE UNIVERSITY OF NAMIBIA

BY

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APRIL 2024

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Abstract

Understanding how fish growth responds to changing environments is critical for monitoring and predicting the impacts of climate change on fish populations. The ocean warming hotspot in the northern part of the northern Benguela provides an excellent opportunity to examine the responses of fishes to rapid environmental change. This research focused on the congeneric *Argyrosomus inodorus* and *Argyrosomus coronus* as these are commercially and recreationally important fishery species in Namibia. Standard otolith age determination techniques were used to determine if the age and growth of *A. inodorus* had changed from the 1990s to 2019. The results showed that there was a significant difference (Likelihood-ratio chi-square test, $\chi^2 = 33.36$, df = 4, $p < 0.001$) for the historical (1994-1996) and contemporary (2018-2019) period, thus indicating that *A. inodorus* stock used to grow older and faster in the historical period when compared to the contemporary. Kruskal-Wallis test showed that there was a significant difference between *A. inodorus* and *A. coronus* lengths at age 4 (H (1) = 8.264, $p = 0.004 < 0.05$). The linear mixed-effects models fitted to the *A. inodorus* otolith biochronology indicated that a best linear unbiased predictor (BLUP) of growth was significantly positively correlated (r = 0.580, n = 25, $p < 0.05$) with mean SSTs (July, year of formation) and significantly negatively correlated (r = -0.473, n = 25, $p < 0.05$) with mean spring-summer SSTs (October y-1 to December y-1) in the area 20-24˚S, 12-14˚E. Thus, faster annual growth was observed during cooler periods (above 15°C) and slower growth was noted when exposed to warmer temperatures >17°C. These findings suggest that changes in *A. inodorus* growth was associated with a change in temperature and that its growth and productivity will be negatively affected with the increasing frequency of extreme climate events and ocean warming.

Keywords: Otoliths, ocean warming, *Argyrosomus*, Benguela, biochronology

List of Publication(s) / Conference proceedings

1. 5th Annual Research Conference of the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC), Henties Bay

   Title: Growth rate changes of *Argyrosomus* spp. along the Namibian coastline

   Authors: C.E. Jagger, M.R. Wilhelm, W.M. Potts

   Date: 06 November 2020

   Format: Oral presentation

2. 6th Annual Research Conference of the Sam Nujoma Marine and Coastal Resources Research Centre (SANUMARC), Henties Bay

   Title: Long-term changes in the growth of *Argyrosomus inodorus* along the rapidly warming Namibian coast

   Authors: C.E. Jagger, M.R. Wilhelm, W.M. Potts

   Date: 19-20 October 2021

   Format: Oral presentation

3. 2021 Benguela Current Convention (BCC) Science and Governance Forum

   Title: Comparison of the growth of *Argyrosomus* species and long-term changes in the growth of *Argyrosomus inodorus* along the rapidly warming Namibian coast

   Authors: C.E. Jagger, M.R. Wilhelm, W.M. Potts

   Date: 03-05 November 2021

   Format: Oral presentation

Table of Contents

List of Tables

List of Figures

List of Abbreviations and/or Acronyms

AAC - age-at-capture

AIC - Akaike’s Information Criterion

ABFZ – Angola-Benguela Frontal Zone

BCLME – Benguela Current Large Marine Ecosystem

BLUP - Best Linear Unbiased Predictor

BUS – Benguela Upwelling System

DNP – Dorob National Park

EBUS - Eastern Boundary Upwelling Systems

F1 - Filial 1

LRT - Likelihood ratio chi-square test

Mean LAA - Mean lengths at age

MFMR – Ministry of Fisheries and Marine Resources

MIA - Marginal Increment Analysis

MtDNA - mitochondrial DNA

nBUS - northern Benguela upwelling sub-system

NCEP - National Centre for Environmental System

NOAA - National Oceanic and Atmospheric Administration

REML - restricted maximum likelihood

RSS - Residual Sum of Squares

sBUS - southern Benguela upwelling sub-system

SCNP – Skeleton Coast National Park

SST - sea surface temperature

VBGF - Von Bertalanffy growth function

Acknowledgements

When I started this MSc journey I had no clue as to how an otolith is removed from a fish let alone how the ageing technique works, however, today I can proudly say that what I have learntthroughout this journey was indeed something I mastered.

"*It always seems impossible until it is done.*"– Nelson Mandela

I am extremely grateful to my supervisors, Dr Margit Wilhelm and Professor Warren Potts, for your invaluable mentorship, support and patience throughout this MSc thesis. Your timely advice, meticulous scrutiny and scientific approach have helped me to a very great extent to complete this task. Thank you so much.

Ministry of Fisheries and Marine Resources, thank you for granting me study permission and financial assistance. Thank you to our Director of Resource Management, Ms. Graca D'Almeida, Deputy Directors Mr. Titus Iilende and Mr. Chris Bartholomae and all my supervisors for your support. Ms. Sarah Paulus and Ms. Collette Simwanza, thank you for always having your office door open when I needed guidance on questions related to the age and growth concept. To my entire colleagues at the National Marine Information and Research Centre (NatMIRC), thank you all for your support.

A special thank you to my colleagues, Mr. Uatjavi Uanivi and Mr. Erich Maletzky. Uatjavi, I appreciate the time you took out of your busy schedule to help me understand most of the statistical concepts through asking questions that pushed me into reading more. I am grateful that I had the opportunity to learn from you and show my appreciation to you while you were still alive, may your soul rest in peace, Uatjavi (+ 22/07/2023). Erich, I don't know where to start or how to thank you enough; I am truly grateful to you for taking your time to assist with R. I mastered the basics of R with your help; I owe you a lot, thank you, Erich. I would also like to acknowledge and thank Dr. Dawit Yemane Ghebrehiwet (Department of Forestry, Fisheries and the Environment, South Africa) for his assistance and statistical guidance. To Dr. Niall McKeown (Prifysgol Aberystwyth University, Wales) and Dr. Romina Henriques (University of Pretoria, South Africa), thank you for conducting the genetic analysis. Niall, I am extremely grateful to you for the constant correspondence and support, hope to meet you in person one day.

I am immensely grateful to my former colleague and “field partner” Mr. Stephanus Voges; without you there would not have been any results for this study. I do not have any silver or gold to give you, Stephanus, but know that I appreciate all you have done to ensure that I have samples. You went out of your way to assist me. Every time I was on the verge of giving up you would always just show up energetically with a huge smile on your face with a new “fieldtrip” scheduled or an idea around what I should also look at. Our field trips to the Skeleton Coast National Park will always remain close to my heart. To Spyker and Marina Kruger, thank you for assisting me with the data collection and accompanying me on sampling trips. A special thank you to all the recreational anglers who accompanied me during my sampling trips.

To Mr. Brett Pringle (Rhodes University MSc graduate), thank you for your support throughout this journey. Thank you to Dr. Alexander Winkler and Dr. Duncan Murray for your support during the first stages of this MSc thesis. Ms. Faye Brinkman and Ms. Diina Mwaala and everyone from Dr. Margit Wilhelm’s ageing lab, your support through the paper reading discussions meant a lot; I learnt so much.

Thank you to the University of Namibia, Sam Nujoma Campus for all the academic support. Dr. Mafwila, thank you for the financial support that was made available through the joint SA-Namibia NRF-NCRST project fund. Thank you to the Office of the Governor Erongo Region and NSFAF for their financial assistance. Also special thanks to Mr. Hein Truter and Mr. Jimmy Marais from the Wild skeleton coast adventure tours for their financial assistance towards my tuition fees.

Faye Brinkman, Diina Mwaala, Saskia Kisting, Jessica Manual, Lessyn Kalwenya, La-Toya Shivute, Usutha Kakuuai Hiko, Theopolina Iita, Ester Shoopala, Ester Nangolo, Johanna Naidoo, Jophine Job, Girlsery //Awases, Brumilda Haslund and Miki Byrnes, thank you my super sisters. You kept me going with your words of encouragement.

Lastly, this journey had many tears, sweat and at times moments of despondency but I kept pushing because of my family. I wouldn’t be here today without your help and endless support,especially from you **Mamma** (Hon. Bernadette M. Jagger), **I love you**. Thanks so much to my siblings- Daphne Roman, Gregory Jagger, Britney Jagger & Jan Roman, I appreciate your support. To my beautiful daughter, and best cheerleader, MiCha, I love you.

Praise the Lord. Give thanks to the Lord, for he is good; his love endures forever (Psalm 106:1)

Dedication

To my dad, Mr. Bernhard “Ou Barry’s” Jagger (+19 June 2021), I know you would have been so proud. I dedicate this MSc thesis to you.

Declarations

I, Charmaine Eleonora Jagger, hereby declare that this study is my own work and is a true reflection of my research, and that this work, or any part thereof has not been submitted for a degree at any other institution.

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Charmaine Eleonora Jagger Jagger April 2024

Research ethics

The study was based on research information collected from recreational shore and ski-boat anglers along the Dorob National Park of Namibia’s coastline, who operate under permit conditions regulated by the Ministry of Fisheries and Marine Resources (MFMR). Where targeted fishing was carried out in the Skeleton Coast National Park (SCNP), fish were sacrificed through the percussive stunning method. The percussive stunning method is believed to be a humane method of sacrificing the fish (OIE, 2021). ‘Stunning’ means any intentionally induced process which causes loss of consciousness and sensibility without pain, including any process resulting in instantaneous death (Grist et al., 2018; van de Vis et al., 2014). Fishing was done under Ethical Clearance Certificate Reference Number: SNC0002 (Appendix A1); under a Research Permission letter (Appendix A2) that was obtained from the University of Namibia. All experimental procedures and fish handling were approved and conducted in accordance with the University of Namibia, Research Ethics Guidelines.

Chapter 1: INTRODUCTION

1.1 Background of study

1.1.1 Understanding an organism's response to climate change in the marine ecosystem

The ocean is earth's life support, as it accommodates a large portion of biodiversity and provides most of the life-supporting environment on the planet and it is also responsible for 50% of the oxygen found in the atmosphere (Gattuso et al., 2018; Kleypas, 2019). The ocean is also earth's buffer to climate change as it absorbs up to 80 % of the heat and 50 % of the atmospheric carbon emitted (Hobday & Pecl, 2014). The substantial rise in ocean temperatures in the recent decades and further increases predicted are of great concern in terms of the negative impacts it might have on marine ecosystems (e.g. IPCC, 2014; Smoliński & Mirny, 2017; Denechaud et al., 2020). The impacts of climate change attributable to anthropogenic factors have caused a build-up of carbon dioxide in the atmosphere and driving ocean acidification and ocean warming, which also drives a decrease in oxygen concentration (Kleypas, 2019). Global ocean temperatures are predicted to increase by 3°C by the year 2100 (see Hoegh-Guldberg & Bruno, 2010; IPCC, 2014; Martino et al., 2019) and it is anticipated that this excessive and continuous warming of the ocean will lead to various changes, such as an increase in sea level height (an increase of 0.5 - 1.2 m by 2100), augmented ocean stratification, a decreased sea-ice extent, and altered patterns of ocean circulation, precipitation, and freshwater input (Doney et al., 2012; IPCC, 2014; Smoliński & Mirny, 2017; Denechaud et al., 2020).

Evaluating and understanding how fish populations adapt and respond to the anticipated climatic conditions is critical for the development of adaptation plans (Smoliński & Mirny, 2017; Denechaud et al., 2020). Broadly, fish populations are expected to respond to the range of expected changes in the ocean environment by altering their distributions, demography, behaviour and phenology (Campana et al., 2020; Shoji et al., 2011). One of the drivers of change in fish demography will be alterations to their growth (Ohlberger et al., 2022). Therefore, managing future fish populations will require an understanding of the drivers of growth rate, so that predictions of the demography of fish populations can be made.

As research evolves, different methods have emerged to help us understand growth rate changes of fish populations. For example, the crossdating technique of dendrochronology or sclerochronology has proven to be useful to examine how an organism responds to changes in climatic conditions (e.g. Black et al., 2005; Morrongiello et al., 2012; Smoliński & Mirny, 2017; Denechaud et al., 2020; Wilhelm et al., 2020). This technique is useful when exploring temporal and spatial variations in growth and can range in resolution from individuals to species by focusing on information found in an organism's hard structures (e.g., otoliths, vertebrae, scales, teeth) (Morrongiello & Thresher, 2015).

Namibia's marine waters are among one of the richest in the world and this is, in part, driven by the nutrient-rich Benguela Current, which is an eastern boundary upwelling system (EBUS) along the south eastern Atlantic Ocean which borders Angola, Namibia, and South Africa. The Benguela Current stretches from 5°S; 12°E off Cabinda in Angola to the south coast of South Africa at the Nelson Mandela Metropole (Port Elizabeth) at 34°S; 26° (Shannon, 1985; Sakko, 1998; Shillington et al., 2006; Hutchings et al., 2009; Iitembu et al., 2021) (Figure 1). Furthermore, the Benguela upwelling system is divided into two distinct regions by the Lüderitz Upwelling Cell;

namely the northern and southern Benguela regions (Shannon 1985; Duncombe Rae, 2005; Iitembu et al., 2021). The EBUS areas are believed to be susceptible to climate change (Lima et al. 2019) and this has been demonstrated over the past decades in the northern Benguela, where the rapid ocean warming and increased thermal variability, driven by the periodic intrusion of the warm Angola Current waters, has been recognised as a global marine hotspot (Hobday & Pecl, 2014; Yemane et al., 2014; Potts et al., 2014a).

Several studies have already shown the effects that increased climate variability has on marine organisms found in the northern Benguela, for example, Yemane et al. (2014) found that some of the observed changes in the range size and distribution of demersal fishes was correlated with the observed warming of ocean temperatures. Another observation linked to climate change was made by Potts et al. (2014b), who found that there was a change in the reproductive scope of blacktail seabream *Diplodus sargus capensis*, a resident species in the northern Benguela. They showed that the reproductive activity of the blacktail seabream was restricted to periods when the water temperature dropped below 20°C. Another example was from Potts et al. (2014a) who found evidence of hybridization between two coastal species from the genus *Argyrosomus* (*A. inodorus* and *A. coronus*), which was thought to be associated with a warming-driven poleward distributional shift of *A. coronus*.

1.1.2 The *Argyrosomus* spp. in Namibia

The *Argyrosomus* genus belongs to the Sciaenidae family (Griffiths & Heemstra, 1995) and occur in the eastern Atlantic and Indo-West Pacific regions and are usually found along continental shelves and adjacent waters (Horodysky, 2009). *Argyrosomus* spp. in Namibian waters locally referred to as “kob” or “kabeljou” have been exploited prior to Namibia’s independence in 1990, with the first land-based records of kob observed in 1964 (Kirchner, 1998; Kirchner et al., 2001). However, records from the “Sea Around Us” database (https://www.seaaroundus.org/data/) show catches were recorded as far back as 1950 (Heymans & Sumaila, 2007).

Namibia’s *Argyrosomus* spp. are mostly caught by the linefish sector. This sector has been described as a multi-species and multi-user fishery (Kirchner, 1998), which comprises commercial (ski-boat and linefish-boat) and a recreational (rock-and-surf angling and ski-boat) fishery (Holtzhausen & Kirchner, 2004) in which fish are captured with hook and line. The shore angling opportunities in Namibia have for decades attracted numerous anglers from all over the world (Holtzhausen & Kirchner, 2004). Recreational shore-based angling (rod and line fishing) only takes place along a small portion of the 1570 km coastline, including an approximately 325-km-long stretch in the Dorob National Park (21°11’S, 13°38’E to 23°19’S, 14°29’E), previously known as the West Coast Recreational Area (WCRA), and an approximately 25-km and 30-km stretch of coast near Torra Bay (20°19’S, 13°14’E) and Terrace Bay (19°59’S, 13°02’E), respectively, in the Skeleton Coast National Park (SCNP). Shore-based angling is allowed from 1 December to 31 January in Torra Bay and throughout the year in Terrace Bay (Kirchner, 1998; Kirchner, 2001; Kirchner et al., 2000; Kirchner & Stage, 2005; MET, 2013) (Figure 1).

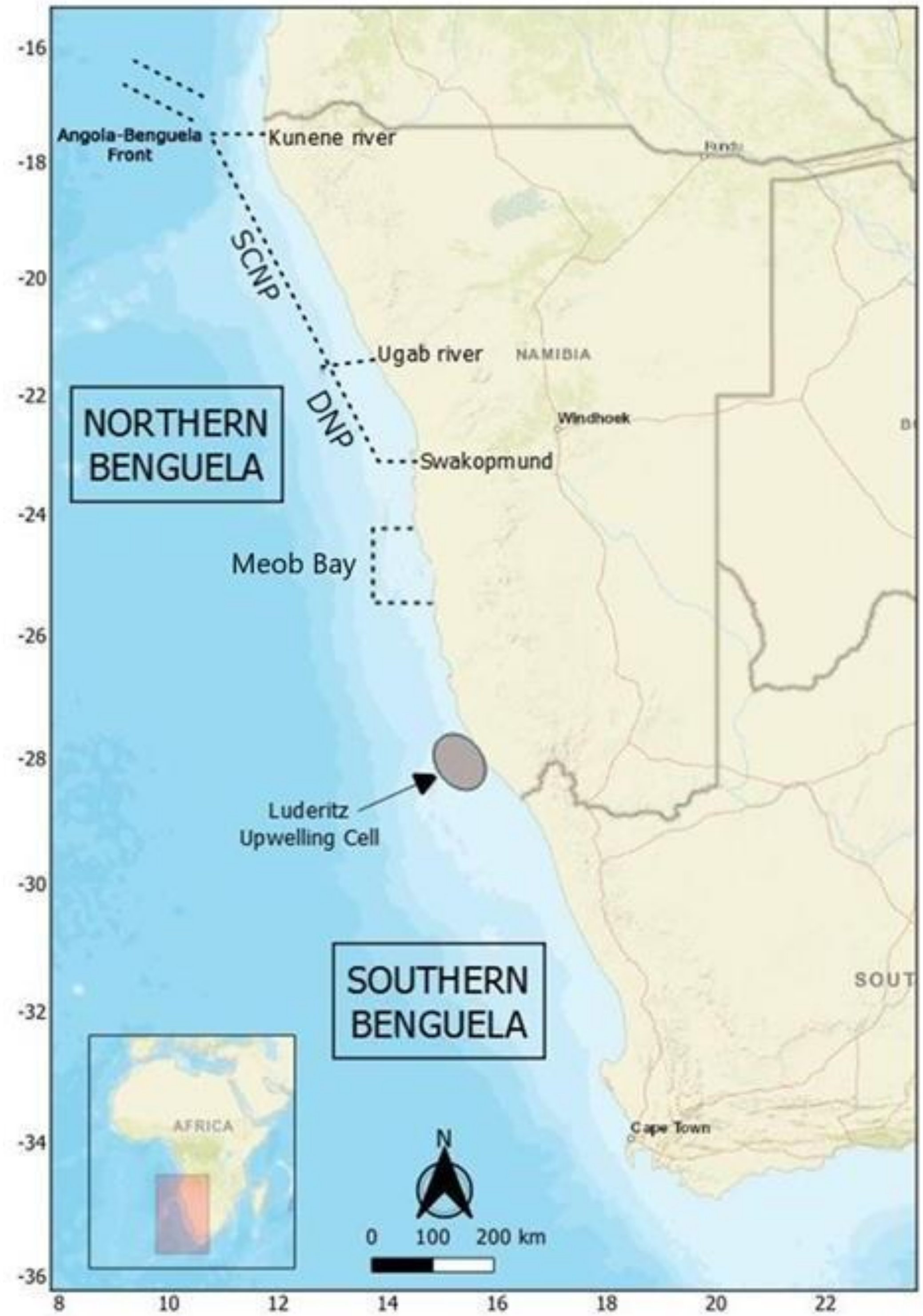

Figure 1: Map of the Namibian coast with Meob Bay, the Dorob National Park (DNP), and Skeleton Coast National Park (SCNP) indicated

The kob *Argyrosomus* spp., are important species caught by the commercial and recreational linefish sectors in Namibia. The genus *Argyrosomus* found off Namibia consists of the silver kob *Argyrosomus inodorus* and a congener, the west coast dusky kob *Argyrosomus coronus* (Griffiths and Heemstra, 1995; Kirchner, 1998), and now a hybrid of the two pure-bred species (Potts et al., 2010, 2014a; Henriques et al., 2018; Pringle, 2020). Prior to the findings of Potts et al. (2014a), it was thought that the Namibian kob fishery only comprised *A. inodorus* (most abundant) and *A. coronus* (Griffiths & Heemstra, 1995; van der Bank & Kirchner, 1997; Kirchner, 1998; Kirchner & Holtzhausen, 2001a). It was assumed that fishing pressure on the *A. inodorus* stock has always been higher than on the *A. coronus* stock in Namibia because of its vast distribution along the Namibian coast (Kirchner, 1998). Based on this assumption, research in Namibia has so far only focused on *A. inodorus,* and thus all management measures implemented for kob by the Ministry of Fisheries and Marine Resources (MFMR) have been designed based on the population dynamics of *A. inodorus*.

Argyrosomus inodorus occurs along the entire Namibian coastline but is most abundant from Meob Bay (24°31’S, 14°36’E) to Cape Frio (18°00’S, 11°48’E) (Figure 1) (Kirchner, 1998; Kirchner & Voges, 1999; Kirchner & Holtzhausen, 2001b; Holtzhausen & Kirchner, 2004). However, being endemic to southern Africa, their distribution occurs along the Namibian coast and along the southern part of the South African coast from Cape Point to East London (Griffiths & Heemstra, 1995; Griffiths, 1996b; Kirchner & Voges, 1999). Two separate stocks with significant population genetic differences was detected for Namibia and South Africa (Mirimin et al., 2016). Kirchner (1998) described a spawning migration which extended from the SCNP (17°14’S to 21°11’S) area to Sandwich Harbor (23°46’S) and Meob Bay (24°31’S) in austral summer (October to March) (Kirchner, 1998; Kirchner & Holtzhausen, 2001b; Holtzhausen & Kirchner, 2004). The *A. coronus* distribution is believed to range from Gabon (0.8037° S, 11.6094° E) to central Namibia in the Dorob National Park (21°11’S, 13°38’E to 23°19’S, 14°29’E) (Potts et al., 2010, 2014a; Beckensteiner et al., 2016; Henriques et al., 2018). The rapid warming rate of the offshore seas of southern Angola and northern Namibia (Monteiro et al., 2008; Hobday and Pecl, 2014) have been linked to a southward shift of *A. coronus* from Angola into Namibia (Potts et al., 2014a). This distributional shift placed the *A. inodorus* and *A. coronus* adult spawning stocks within the same vicinity and has resulted in the hybridization of these species along the Namibian coast (Potts et al., 2014a).

The two species, although morphologically similar, have different life history patterns, for example, the *A. inodorus* stock grows slower and matures earlier than the *A. coronus* stock (Griffiths & Hecht, 1995; Griffiths & Heemstra, 1995; Griffiths, 1996a, 1996b, Potts et al 2010). Based on the differences in the life history of the two species and their recent hybridization, there is an urgent need to revise the growth parameters for both *A. inodorus* and *A. coronus* and their hybrids to improve the management of the Namibian kob fishery. Moreover, the faster growth and larger size of the *A. coronus* presents an opportunity for increased fisheries yield with a potentially more lucrative recreational fishery and therefore, not incorporating information from *A. coronus* into management strategies may result in a missed opportunity for the country.

1.2 Statement of problem

Age information forms the basis for calculating growth rates, mortality rates and stock productivity which provide information on the biological state of the fisheries resources for stock assessment purposes. Since the study by Kirchner and Voges

(1999) there has been no age and growth studies done on the Namibian *A. inodorus*. Additionally, no studies have been done on the age and growth of *A. coronus* in Namibia and there are no biological descriptions of the hybrid. Therefore, the long-term growth response to warming temperatures of these species living in the warming hotspot of the northern Benguela region has not been studied.

1.3 Aims and objectives

The overall aim of this study was to determine the ages and compare the growth rates between *Argyrosomus inodorus*, *A. coronus* and their hybrids (F1 and backcrosses) and to describe climate-growth relationships of *A. inodorus* along the Namibian coast using otolith biochronologies. Specifically, the objectives were to:

1. Determine whether there are purebred *Argyrosomus inodorus*, *A. coronus* or a hybrid of the two purebred species in the sample.

2. Validate the periodicity of translucent zone formation on the otoliths of *A. inodorous* and *A. coronus.*

3. Compare the contemporary growth rates of *A. coronus*, *A. inodorus* and their hybrids (F1 and backcrosses).

4. Compare the historical (1994-1996) and contemporary (2018-2019) growth rates of *A. inodorus* along the Namibia coast.

5. Examine long-term (1980 to 2019) trends in the mean annual growth rate of *A. inodorus* using an otolith biochronology (sclerochronological approach).

6. Correlate the mean annual growth rates of *A. inodorus* with sea surface temperature(SST) to assess the impact of thermal variability on its growth.

1.4 Hypotheses of the study

1. H_0: There are purebred *Argyrosomus inodorus*, *A. coronus* and hybrids of the two purebred species in the sample.

2. H_0: *A. inodorus* and *A. coronus* form opaque and translucent zones on their otoliths equally in all seasons throughout the year.

3. H_0: There is no significant difference in the growth of *A. inodorus*, *A. coronus* and their hybrids.

4. H_0: There is no significant difference in the historical (1994-1996) and contemporary (2018-2019) growth rates of *A. inodorus*.

5. H_0: Mean annual growth rates of *A. inodorus* remained constant from the 1980s to 2019.

6. H_0: There is no correlation between the mean annual growth rate of *A. inodorus* and themonthly SST along the Namibian coast.

1.5 Significance of the study

Contrary to what was recommended by Kirchner (1998), the only age and growth study done on *Argyrosomus inodorus* in Namibia was done by Kirchner and Voges (1999) more than 20 years ago. As a result, to this, no measures of the *A. inodorus* growth rate changes in response to ocean warming or exploitation were available. The information collected in this present study can therefore be used to aim at updating these measures used in the current Namibian *Argyrosomus* spp. stock assessment. Different growth rates and by implication reproductive rates are believed to have an impact on yield per-recruit calculations and resulting management measures of the *Argyrosomus* spp.

fishery in Namibia (which currently consists of *A. inodorus*, *A. coronus* and their hybrids). In addition, this study also describes the relationship between climate change and the growth of *A. inodorus* along the Namibian coast, using otolith biochronologies as proxies, to allow the variation in the somatic growth of the *A. inodorus* to be compared to climate variability. By using otolith biochronologies, shifts in growth rates over time were viewed and were directly compared to sea surface temperatures, giving us a strong indication of how this species and similar species react to environmental shifts over time.

Chapter 2: LITERATURE REVIEW

2.1 The Benguela Current Large Marine Ecosystem

The Benguela Current Large Marine Ecosystem (BCLME) is situated along the coast of southwestern Africa (Shillington et al., 2006; Louw et al., 2016; Rozmaric et al., 2022). Characterized by strong southerly winds and nutrient-rich waters, the Benguela upwelling current is one of the four major eastern boundary current upwelling systems of the world (Shillington et al., 2006; Rozmaric et al., 2022). The BCLME exerts a wide range of high SST variability, with daily fluctuations in SSTs occurring along central Namibia (Bartholomae & Hagen, 2007), which may at times be extremely cold or hot (Koungue et al., 2021). These and other physical properties of the environment such as wind, water circulation and mixing are known extrinsic drivers when it comes to fish growth (Claireaux et al., 2022).

The BCLME is divided into the northern and southern Benguela upwelling sub-systems (nBUS and sBUS, respectively) by the Lüderitz Upwelling Cell (LUC), located approximately between 26°S and 27°S, (Duncombe Rae, 2005; Rozmaric et al., 2022). The LUC is a major, perennial cold-water boundary formed south of the ABFZ and is believed to limit the dispersal of warm-temperate species (Henriques et al., 2014; Potts et al., 2014a).

The nBUS is considered to be one of the most productive upwelling systems in the world when compared to other large major upwelling systems such as the Humboldt, California and Canary, and this is mostly because of the strong along-shore like southwesterly trade winds near Lüderitz and the subsequent upwelling of cold nutrient enriched sub-thermocline waters to the ocean surface (Louw et al., 2016). When upwelling events occur in the Eastern Boundary Upwelling Systems (EBUS), cold-nutrient-rich waters are brought to the surface from deeper waters below, making these areas quite productive and important for marine biodiversity (Fréon et al., 2009; Lima et al., 2019).

The Angola-Benguela Frontal Zone (ABFZ) is an ocean current convergence that dominates and forms the northern boundary of the nBUS (Potts et al., 2014a; Siegfried et al., 2019). It is a thermal front which separates warm, oligotrophic water from cold, nutrient-rich upwelled water (Rouault, 2012). A warm temperate biogeographic transition zone and distinct geographic boundaries that are recognizable are formed because of the temperature gradient that the ABFZ provides. However, these boundary locations are not fixed as they can migrate southwards during austral summer into central Namibia (Anderson et al., 2012; Potts et al., 2014a).

The nBUS is described as an ocean warming hotspot due to its rapid increase in sea surface temperature (SST) (Hobday & Pecl, 2014; Potts et al., 2014 a; Beckensteiner et al., 2016; Henriques et al., 2018). A rapid warming of 0.8℃ per decade was described in the coastal waters of the Angola-Benguela Frontal Zone (Potts et al., 2014a). The warming of SST is believed to cause a faultily strong Angola Current and weak Benguela Current and in doing so it is also affecting the seasonality and displacing the ABFZ southwards (Potts et al., 2014a; Koseki et al., 2018).

The steadily warming waters due to strengthening of the Angola Current and the subsequent shift in the position of the ABFZ has an influence on the distribution of species as observed by Potts et al. (2014a), reproduction of species (e.g. Potts et al., 2014b; Sims et al., 2004; Pankhurst & Munday, 2011) and their productivity. These changes in species distribution are facilitated by differential responses in the growth, survival, and reproduction of coastal species, and to changes at other trophic levels because of warming temperatures (Perry et al., 2005).

2.2 *Argyrosomus inodorus* and *A. coronus*

During the period from 1994 to 1996, Namibia's MFMR had a fish tagging programme for linefish, where routine biological sampling of linefish took place. Kirchner and Voges (1999) investigated the age structure and growth patterns from the otoliths of the Namibian *A. inodorus* stock collected through this period (1994-1996) using two methods: 1. Age determination through otolith analysis and 2. Mark-recapture data to validate the age estimates. They sampled 357 *A. inodorus* from the Meob Bay (24°31'S) area which was classified as the southern distribution of the *A. inodorus*; 160 *A. inodorus* from the SCNP (17°14'S to 21°11'S) classified as the northern distribution and 33 *A. inodorus* from WCRA, now Dorob National Park (21°11'S to 23°19'S) which was classified as the central region (Figure 1). They only used recaptured fish from the southern and central regions for validating the age estimates because of the distributional overlap of *A. inodorus* and *A. coronus* in the northern region (see Kirchner & Voges, 1999). However, for growth comparisons they combined the northern and central regions because of the annual migration *A. inodorus* takes between the northern and central regions during the onset of the spawning season. Findings from Kirchner and Voges (1999) showed that there was a significant difference between the growth rates of *A. inodorus* sampled in northern Namibia and those samples in southern Namibia. For example, the maximum age of *A. inodorus* sampled in the southern region was 19 years, considerably younger than those sampled in the northern region (28 years). Kirchner (1998) found evidence of size segregation with smaller fish observed in the Meob Bay Sandwich harbor, Dorob National Park area and larger fish observed in the SCNP. Differences in size was attributed to the

SST, which was believed to be driven by the northwesterly surface currents and the ABFZ (Kirchner, 1998).

During the summer (October-March, which is also the spawning season for *A. inodorus*) the temperature of the coastal waters in northern Namibia increases due to the intrusion of the ABFZ southwards into central Namibia during austral summer (Lass et al., 2000; Lass & Mohrholz, 2005; Potts et al., 2014a). This has been attributed to increased solar radiation and the intrusion of the warm, saline waters off Angola into northern Namibia (Kirchner, 1998). This temperature change is thought to drive a southward migration of adult *A. inodorus* into central and southern Namibia, where they are thought to spawn between Sandwich Harbour to Meob Bay (see Figure 1) (Kirchner, 1998; Kirchner & Holtzhausen, 2001b).

The *A. coronus* occurring along the Namibian coast represents the most southern distribution of the stock that is most abundant in Angola (Griffiths & Heemstra, 1995). The life history of *A. coronus* was described by Potts et al. (2010). They found that when compared with other sciaenid species, *A. coronus* had a similar growth rate (L_∞ = 188.3 cm total length (TL), K value = 0.11 year^{-1}), maximum size (190 cm TL), and size- and age-at-maturity (87 cm and 4– 5 years, respectively) to their congeneric *A. japonicus* (Griffiths, 1996a) which is found off the South African coast (Griffiths & Heemstra, 1995; Potts et al., 2010). Other Sciaenids which were believed to have similar life history traits to *A. coronus* were *A. regius* and *Totoaba macdonaldi* which occur off the coasts of Mauritania and Mexico, respectively (Potts et al., 2010).

Potts et al. (2010) used mark-recapture data and showed that *A. coronus* southward migratory patterns seemed to coincide with increasing SST and the southerly movement of the Angola- Benguela Front (Potts et al., 2010; Potts et al., 2014a).

However, a more recent telemetry study showed that most of the individuals in the southern Angolan population remained resident to a small area (30 km) during a two-year period (Parkinson, 2023). While there seems to be no specific spawning habitat yet identified for *A. coronus* (Potts et al. 2010), recent evidence (Potts, unpublished data) suggests that they spawn in several coastal sites along the length of their distribution.

When compared with *A. japonicus* and *A. coronus*, the life history of *A. inodorus* is different i.e., maturation age, maximum total length, longevity, growth, spawning season. Firstly, *A. inodorus* matures at an earlier age than *A. coronus*, with the age at 50% maturity (A_{50}) being 1.5 years for females and 1.6 years for males, while the A_{50} for *A. coronus* is 4.3 years and 4.4 years for females and males, respectively. Secondly, *A. inodorus* is believed to be a slower growing species that matures earlier than *A. coronus* (Griffiths and Heemstra, 1995; Griffiths and Hecht, 1995; Kirchner, 1998; Potts et al., 2010; Pringle, 2020). Thirdly, *A. inodorus* has a southward spawning migration in summer while *A. coronus*' spawning migration is noted to be northward from the southern region of their distribution in Angola at the onset of winter and a return migration in late winter and early spring (Kirchner & Voges, 1999; Kirchner & Holtzhausen, 2001b; Potts et al., 2010). Lastly, a considerable difference between the maximum ages of the two species was observed: 28 years and 13 years for *A. inodorus* and *A.coronus*, respectively (Kirchner & Voges, 1999; Potts et al., 2010).

Pringle (2020) used metabolic physiology experiments to compare the aerobic scope (energy available for anything beyond basic function) of *A. inodorus* and *A. coronus* captured in Namibia at different temperatures (12, 15, 18, 21, 24°C). His experiments showed that the aerobic scope for *A. inodorus* increased up until 21°C, after which it declined up to the maximum temperature measured (24℃). In contrast, the aerobic scope for *A. coronus* was lower than that of *A. inodorus* up until 21℃, after which it increased to greater levels than *A. inodorus*. These findings suggest that warming sea temperatures will increasingly favour *A. coronus* and limit the distribution of *A. inodorus* into central Namibia. Pringle (2020) further showed that the distribution of *A. inodorus* might be restricted to temperatures between 15℃ and 18℃. He concluded that if the SSTs in the northern part of the northern Benguela region continue to increase the *A. inodorus* will most likely be the "loser" (species showing vulnerable characteristics to climate change) with the *A. coronus* being the "winner" (species showing resilient characteristics to climate change) (Potts et al., 2014a; Pringle, 2020).

With different physiological and life history traits, it is likely that the rapidly changing environment in Namibia will impact *A. inodorus* and *A. coronus* differently. It is likely that warming will potentially have negative consequences for the distribution and productivity of *A. inodorus* in Namibia while conditions are likely to favour *A. coronus*. The current Namibian fisheries management measures in place for the *Argyrosomus* spp. are based on the life history traits and population dynamics of *A. inodorus.* Therefore, failing to adapt new measures which incorporate information from *A. coronus* may negatively influence the *A. coronus* population found along the Namibian coast. Both Potts et al. (2014a) and Pringle (2020) highlighted the need for Namibia's fisheries to incorporate life history information from *A. coronus* into their management measures to ensure that they are sustainably managed. Also, with the introduction of hybrids of the two species, it is not clear whether the hybrid's life history traits will be similar to that of the *A. coronus* or *A. inodorus* and how these species would compete with the purebred *A. coronus* and *A. inodorus* and how they would adapt in the predicted future climate change scenarios in the nBUS.

2.3 Hybridization

Barton and Hewitt (1985) described the term hybridization as the reproduction between members of genetically distinct populations. According to Tea et al. (2020) the concept of hybridization is not uncommon in the marine environment and is a widespread occurrence in the plant and animal kingdoms (Montanari, 2018). Hybridization has both negative (Allendorf et al., 2001; Muhlfeld et al., 2009) and positive (Hoffmann & Sgro, 2011) effects on marine ecosystems. For instance, it could lead to the extinction of fish populations, especially when rare species encounter other species that are more in abundance as this could introduce competitive interactions among species (Allendorf et al., 2001; Chunco, 2014; Potts et al., 2014a; Pringle, 2020). On the other hand, the positive side of hybridization could be that it may stimulate the formation of novel phenotypes that can speed adaptation to novel climates (Chunco, 2014).

Research on hybridization in marine environments has increased, but several aspects are still poorly understood. For example, not much is known on the pervasiveness of hybridization between sympatric species and the degree of genetic discrepancy when looking at the ability by the heterospecific parents to produce viable hybrid offspring (Tea et al., 2020). Also, it is imperative that hybrid zones (where genetically distinct organisms occur, interbreed, and produce hybrids) are studied for us to understand the nature and occurrence of this phenomenon (Barton & Hewitt, 1985). As the coastal waters of Namibia (northern Benguela) can be classified as a hybrid zone, based on the definition by Barton and Hewitt (1985), enhancing our understanding of how these pure-bred *A. inodorus*, *A. coronus* and their hybrids interact is critical to improve our understanding of fish hybrid zones and to predict likely outcomes to improve the management of the *Argyrosomus* fishery.

2.4 Age determination and validation: Marginal Increment Analysis

Knowing the age of individuals helps us understand the variability in the structure and abundance of fish populations (Panfili & de Pontual, 2002). Calcified structures such as otoliths or teeth, provide useful periodic information because they have the potential to grow throughout an individual's life (Vitale et al., 2019). The information in these hard parts (calcified structures) helps us determine the age of individuals (Campana, 2001). Hard structures also permanently record episodic patterns of growth at different timescales (Vitale et al., 2019). The age of fish is one of the most important and relevant data as it is used to estimate growth, maximum age and mortality rates, which are the cornerstone of stock assessment models (Carbonara & Follesa, 2019).

Accuracy of age determination is critical for the estimation of growth rates (Campana, 2001). To ensure accuracy, it is critical that the periodicity of the deposition of growth zones on the calcified structure is validated (Beamish & McFarlane, 1983). Several methods have been used for age validation in fishes, including bomb radiocarbon, mark-recapture of chemically-tagged fish, radiochemical dating, progression of discrete length modes sampled for age structures, capture of wild fish with natural, date-specific markers, marginal increment analysis, release of known-age and marked fish and captive rearing from hatch (Campana, 2001). Each of these methods have their advantages, limitations and costs (See Table I, Campana 2001). Marginal increment analysis (MIA) is, however one of the most commonly used techniques from these methods, primarily because of its conceptual simplicity and low cost (Campana, 2001; Vitale et al., 2019) and was therefore used for the purpose of this study. Campana (2001) stated that the marginal increment is commonly calculated as a proportional state of completion of an otolith increment, which ranges from near zero (just when an increment is beginning to form) to one (when a complete increment has formed). The assumption is that an annual opaque/translucent zone pair is laid down once per year and this validation method therefore generally aids in the verification of this hypothesis (Kimura et al., 2007). A sinusoidal cycle with a frequency of one year in true annuli (a zone pair forming once per year) should be described by the mean marginal increment plotted as a function of month or season (Campana, 2001).

2.5 The use of otolith chronologies for tracking long-term shifts in somatic growth

Climate change is placing immense pressure on exploited fish stocks (Fincham et al., 2013). It is therefore important to understand the relationship between organisms and the environment around them, as this contributes toward improved fisheries management, especially in a constantly changing environment (Lopez et al., 2017). The drivers of change in biological indicators can be difficult to detect because of the multitude of possible natural stressors and anthropological activities and the varying responses of organisms at individual, population, species, and group levels (Morrongiello & Thresher, 2015). Despite this, the somatic growth of fish can be a suitable indicator of a response to environmental change. Understanding how somatic growth changes in response to environmental changes is vital as it can be used to predict their response to future changes. However, it is difficult to obtain a meaningful understanding of the relationship between environmental conditions and somatic growth just by looking at short-term patterns. Thus, researchers in this field are using the dendrochronology approach to investigate at long-term pattern in fish growth.

Dendrochronology (or tree-ring dating) is a scientific method that provides an opportunity to collect long-term growth data from once off sampling events. The increments in the hard parts of marine organisms (otoliths, skeletons, shells) can provide long-term chronologies of growth analogous to tree rings (e.g. Dean 1997; Gillanders et al., 2012). In fishes, the dendrochronology technique uses the width between annulus rings of fish otoliths as a proxy for somatic growth. This approach delivers long-term data on a fish's response to environmental factors because annual otolith growth can reflect the condition of a fish's physical environment during its growth period (e.g., Black et al., 2005, Matta et al., 2010; Gillanders et al., 2012; Black et al., 2013; Wilhelm et al., 2020).

The otolith chronologies are used to show temperature or other environmental effects on fish growth (e.g. Morrongiello et al., 2012). When combined with other techniques (e.g. stable isotope analysis), biochronology can also provide information on the movements of fish (between either marine or freshwater habitats), spawning frequency and the onset of sexual maturity (e.g. Morrongiello et al., 2012).

Morrongiello et al. (2012) summarized a suite of papers showing the use of biochronologies on hard parts of aquatic organisms (either otoliths, fin rays, corals, or shells) in ecology, and this showed that biochronology procedures allow the temporal reconstruction of environmental histories that can be directly correlated to an individual's life history. For example, the width of the growth-increments in the otoliths of Atlantic cod *Gadus morhua* were related to oceanographic conditions and suggested that ocean cooling reduced growth and this in turn, played a role in the collapse of the Eastern Scotian Shelf fishery for the species (Jones & Campana, 2009; Morrongiello et al., 2012). In addition, Woodbury (1999) identified the strong El Niño events in 1983 as a driver for poor growth of the yellowtail rockfish (*Sebastes entomelas*) and widow rockfish (*S. flavidus*) in the coastal waters off central and northern California. Also, the otolith increment widths of Pacific whiting (*Merluccius productus*), splitnose rockfish (*Sebastes diploproa*), and canary rockfish (*Sebastes* *pinniger*) were substantially influenced by a variety of physical variables, including SST and upwelling (Blacket al., 2005). In another example, Smoliński and Mirny (2017) developed a 74-year biochronology of European flounder *Platichthys flesus* growth using otoliths. Their results showed that regime shifts in otolith growth which occurred in 1988, 1992 and 2006 were linked to the sea surface temperatures and the Baltic Sea index, which highlighted the potential for applying biochronological techniques to identify rapid regime shifts in marine ecosystems. Another example by Neuheimer et al. (2011) used otoliths from the banded morwong (*Cheilodactylus spectabilis*) to see whether there was a correlation between sea surface temperature and growth for the species (Morrongiello et al., 2012). They found that an increasing sea surface temperature trend at five sites in the Tasman Sea off Australia and New Zealand coincided with increasing growth for mid-range populations, but reduced growth for population at the warm northern range limit.

High-latitude regions such as the Arctic are believed to be more prone to be affected by climate change and this led to a study by Denechaud et al. (2020) on the Northeast Arctic cod (*Gadusmorhua*). They developed a century-scale biochronology from the year 1924-2014. Results showed that the growth of cod was negatively correlated to its population abundance but showed that it was positively correlated to the capelin (*Mallotus villosus*) population size structure. In addition, the growth of cod was also positively correlated with temperature although there was a negative correlation between growth and the Atlantic Multidecadal Oscillation (AMO) index (Denechaud et al., 2020). They further observed that fishing pressure had a significant, but negative impact on the growth of cod. All in all, Denechaud et al. (2020) showed how different interacting factors had an impact on cod growth either directly or indirectly.

As a last example on the use of otolith chronologies as indicators of fish growth responses to environmental changes, and as a first of its kind in the northern Benguela, a study was done on Namibia’s commercially important deep-water hake *Merluccius paradoxus* (Wilhelm et al., 2020). They constructed a 32-year otolith biochronology (1982–2013) and found that an increase in winter-spring coastal upwelling index in the area 30°S led to an increase in the growth of *M. paradoxus*, possibly influenced by the prey abundance associated with the primary productivity induced by upwelling.

In view of the warming in the ABFZ, and the short-term respiratory responses of *A. inodorus* to changes in temperature as described by Pringle (2020), an understanding of the long-term responses of the growth of *Argyrosomus inodorus* to changes in water temperature are necessary and are investigated in this study.

Chapter 3: MATERIALS AND METHODS

3.1 Study area and sample collection

Fish otoliths were obtained for historical (1994 – 1996) and contemporary periods (2018 - 2019). A historical otolith collection was made available by the Ministry of Fisheries and Marine Resources (MFMR), Namibia. These otoliths were obtained from fish collected from the northern (SCNP, 17°14’S to 21°11’S), central (Dorob National Park, 21°11’S to 23°19’S) and southern (Meob Bay, around 24°30’S) regions (Figure 1). Meob Bay is situated in the Namib-Naukluft National Park between Walvis Bay and Lüderitz and is a closed fishing area. The historical (1994-1996) data collected from Meob Bay was only permitted for research purposes and were collected by the Ministry of Fisheries and Marine Resources. Kirchner and Voges (1999) divided the region into three areas to compare growth rates between the areas, namely northern (SCNP), central (WCRA now Dorob National Park) and southern (Meob Bay) Namibia. The division of the three areas when comparing growth rates was based on tagging studies done on *A. inodorus* which indicated clear seasonal migratory patterns along the distribution range of *A. inodorus* (Kirchner & Holtzhausen, 2001b). Kirchner and Voges (1999) conducted routine biological sampling at the same time tagging took place in the different areas and thus used recapture data to validate the growth of *A. inodorus*. They concluded that growth rates of fish collected from northern (N) and central (C) areas were similar and differed from the growth rates of fish collected in the southern (S) area. This present study re-affirmed that the growth rates of fish collected between the N and C area were still similar to each other (see Appendix A3). It is based on this confirmation that the same divisions by area as described by Kirchner and Voges (1999) were used in this present study: N and C were pooled and separated from S in the analysis (Table 1).

The contemporary (2018-2019) *Argyrosomus* spp. otoliths were collected randomly and opportunistically from fish catches of recreational and commercial fishers between January 2018 and July 2019 between latitude positions 17-21°S (N) and 21-23°S (C) (Table 1). No fish were collected from the southern region (Meob Bay) during the contemporary (2018-2019) period because of sampling permit restrictions. Thus, the contemporary samples only represented the central and northern regions as defined by Kirchner and Voges (1999) and were categorized as such (Table 1). For Von Bertalanffy comparisons, therefore only northern and central samples from the historical period were used (historical n = 63; contemporary n = 146). A total of 264 samples were used in the otolith chronology, *A. inodorus* (historical, n = 89, contemporary, n = 149), *A. coronus* (n = 20) and hybrids (n = 6) (Table 1).

The species, total fish length (to the nearest cm), sex and approximate catch location was recorded for each fish. A small piece of the pectoral fin was removed immediately and preserved in 96%-100% ethanol for later genetic analysis. Otoliths were removed for age and growth analysis and stored in labelled envelopes after they were cleaned of any residual material. Most of the otoliths selected from the historical (1994-1996) and contemporary (2018-2019) samples were collected during the austral summer months, from November to April (Table 1), which is characterized by the highest catch rate in the fisheries (Kirchner, 1998) and the spawning season for *A. inodorus* (Kirchner & Holtzhausen, 2001b) (Table 1).

3.2 Genetic analysis

Genetic analysis was done by Dr Niall McKeown at the Aberystwyth University's Institute of Biological, Environmental and Rural Sciences in Wales and Dr Romina

Henriques at the University of Pretoria, South Africa. Dr Niall McKeown did the data collection (extraction and mtDNA and microsatellite genotyping) and Dr Romina Henriques did the analysis. To ensure that the individuals were identified correctly, the pectoral fin sample was subjected to a mitochondrial DNA (mtDNA) analysis. Putative hybrids were identified through mtDNA morphology mismatches i.e., where an individual had an mtDNA type of one species and a morphotype characteristic of a different species (Potts et al., 2014a; Pringle, 2020). A subset of individuals were genotyped for mtDNA and nuclear microsatellite loci to permit identification of hybrid or potential backcrosses between the species and separation from putative ‘pure’ members of both species in the analysis of physiological data. Genetic ancestry was also compared with phenotype inferred at time of sampling. Total DNA was extracted using a standard CTAB-chloroform/isoamyl alcohol method (Winnepenninckx et al., 1993). For mtDNA analysis, a fragment of the cytochrome oxidase I (COI) gene was amplified by PCR using the FF2d and FF1d primers described by Ivanova et al. (2007). PCRs were performed in 10 µl volumes using a thermoprofile comprising 95˚C for 3 minutes followed by 35 cycles of 95℃ for 30 s, 50℃ for 30 s and 72℃ for 30 s, after which there was a final extension (72℃ for 180 s) and cool down (4℃ for 60 s). Sequencing of mtDNA amplicons was performed using the FF2d primer with Big Dye technology and an ABI 3500 DNA analyser. The mtDNA sequences were edited and aligned using BIOEDIT (Hall, 1999). A minimum spanning network was constructed in NETWORK (www.fluxus-engineering.com/sharenet.htm) and used to classify each individual mtDNA as belonging to either *A. inodorus* or *A. coronus*.

For nuclear analysis, individuals were genotyped at five microsatellite loci (UBA5, UBA40, UBA91, UBA853, UBA854) developed by Archangi et al. (2009) and shown to be useful for hybrid identification in *Argyrosomus* (Potts et al., 2014a). The ABI

3500 analyser was also used to separate microsatellite alleles with genotypes inferred using PEAKSCANNER software. Following Potts et al. (2014a) individual admixture proportion were investigated using both the STRUCTURE (Pritchard et al., 2000) and NewHybrids (Anderson and Thompson, 2002) programs. For the STRUCTURE analysis the admixture with correlated allele frequencies model was used. Five independent analysis were run for a model assuming two clusters (k = 2), for 500 000 MCMC steps for burn-in, followed by 2 000 000 MCMC steps. A threshold of q = 0.15 was chosen to separate parental individuals and putative hybrids (Potts et al., 2014a). For the NewHybrids analysis the threshold of posterior probability was set to q = 0.75 (Potts et al., 2014a), using a Jeffrey's prior for mixing and allele frequencies, and ran for 2 000 000 MCMC iterations. Individuals were only considered hybrids if identified as such by both STRUCTURE and NewHybrids. The power of the data to detect hybrids and potential backcrosses was assessed by running the STRUCTURE and NewHybrids analysis on simulated genotypes (F1, F2, backcross to *A. coronus* and backcross to *A. inodorus*) generated with HYBRIDLAB (Nielsen et al., 2006).

3.3 Otolith preparation

The otoliths were embedded in clear casting Polyester resin and longitudinally sectioned at approximately 0.5 mm thick through the primordium (otolith core) with a low-speed double-bladed, diamond-edged saw (Griffiths & Hecht, 1995; Kirchner & Voges, 1999). The thin sections were mounted onto glass slides with DPX mountant for microscopy and then photographed using reflected light against a black background (Kirchner & Voges, 1999). Two camera-attached stereo microscopes, a Zeiss Stemi DV4 microscope with an AxioCam ERc 5s at up to 160x magnification or an Olympus SZ61 microscope with an Olympus SC30 camera were used to photograph the otoliths at up to 200x magnification. Two different microscopes and cameras were used due to their availability at different times during Covid- 19 lockdown restrictions.

3.4 Otolith measurements and age determination

Sectioned otoliths from the *Argyrosomus* spp. caught during the study comprised of broad opaque zones and narrow translucent zones and showed clear, visible growth rings, particularly in older fish (Figure 2). *A. inodorus* ranged in size from 33.5-99.9 cm TL and 34.2-91.0 cm TL (historical and contemporary, respectively), while the *A. coronus* and hybrids ranged from 46.0-76.0 cm TL and 49.5-67. 0 cm TL, respectively.

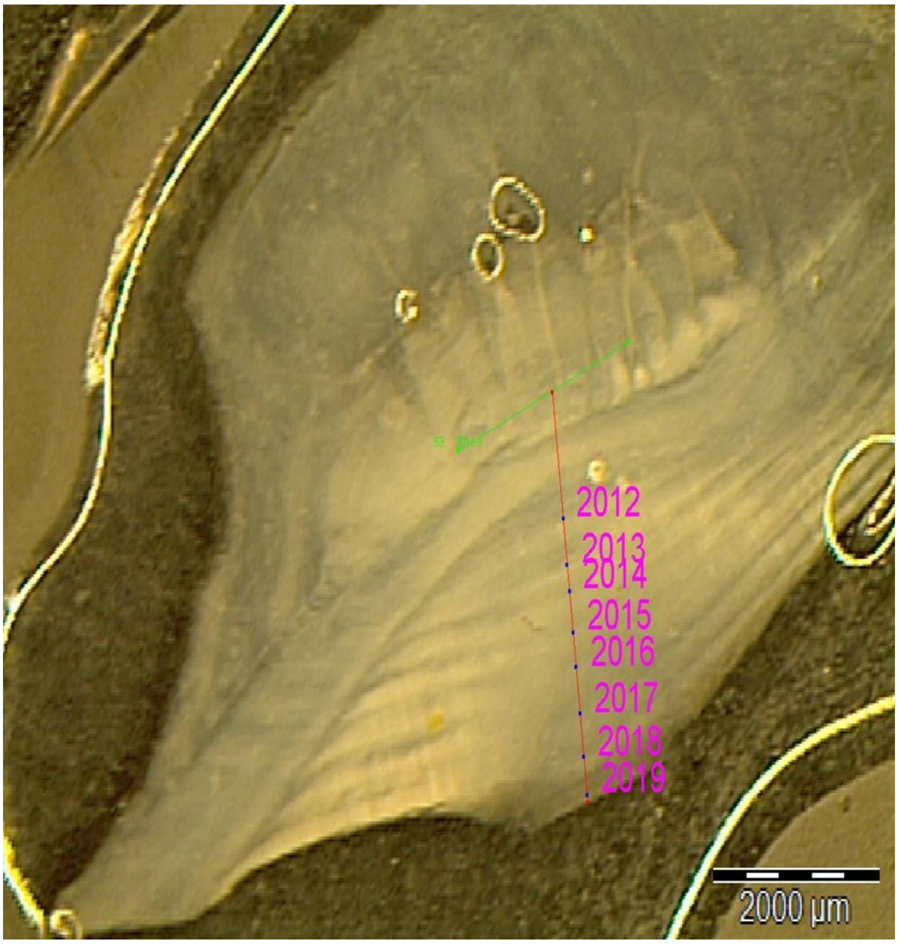

Figure 2: Thin section of an otolith of an 8-year-old *Argyrosomus inodorus* caught in central Namibia in 2019 with indicated annual growth increments (blue points) and their calendar years assigned

To do the otolith biochronologies, an image processing package ImageJ version 1.53a (http://imagej.nih.gov/ij/) was used to measure the otolith increments and estimate age of the fish (Abràmoff et al., 2004). This was done using the automated age-reading plug-in from the ImageJ macro ObjectJ version 1.05e (https://sils.fnwi.uva.nl/bcb/objectj/index.html) which allowed for the counting and measuring of annual growth increments on the otolith. A similar method to Kirchner and Voges (1999) (for *A. inodorus* age determination) and Wilhelm et al. (2020) (for increment measurements) was used, and each increment was defined as the distance from the end of the translucent zone (beginning of the opaque zone) to the end of the next translucent zone so that each annual increment contained an opaque and a translucent zone. Each complete growth increment as well as the last incomplete growth increment (marginal increment) for each individual fish was then measured from the nucleus to the dorsal edge perpendicular to the annual growth zone along the longitudinal section of the otolith (Figure 2). The measurements were converted to mm by a different pixel-to-mm ratio for each microscope and each magnification.

Every individual fish was then assigned a final age-at-capture (AAC) (number of complete growth increments) and Cohort (Year of birth of the fish = Year of Capture – AAC – 1) after increments were marked and measured. Otolith increment width measurements in mm (Inc) were assigned an age and calendar year at the time of increment formation (Year) (Morrongiello & Thresher, 2015). When increments were measured, they were assigned grades from 1 to 3, with 1 being the best (highest confidence) and 3 poor (low confidence). Only the clearly visible increments were measured and the otoliths that were assigned with the grades 1 and 2 were retained to be used in the final statistical analysis (e.g., Roe, 2012). This meant that from an initial 427 prepared otoliths for *A. inodorus*, only 337 otoliths (historical n = 89 and contemporary n = 248) were clear enough to take accurate measurements and thus 21% of the *A. inodorus* otoliths were rejected from the analysis. Of the 248 contemporary samples, a genetic sample was only collected from 149 individuals and thus only 60% of the otoliths with clearly visible increment widths were used for the final analysis of the otolith biochronology (Table 1). The measurement of the increments took place three times and were validated by a second reader.

3.1 Data analysis

3.1.1 Marginal Increment Analysis

Similar to Ferguson et al. (2014), the marginal increment was defined as the distance between the last complete increment and the outer edge of the otolith. The mean marginal increment and standard deviations by month were plotted and visually inspected for an annual peak.

3.1.2 Estimation of growth parameters

The Von Bertalanffy growth model was fitted to the age-length data for *A. inodorus* for the historical (1994-1996) and contemporary (2018-2019) period after individual ages (AAC) were determined. The Von Bertalanffy Growth (VBG) model was determined by the equation:

$$Lt\ = (L\infty\ (1 - e\ -K^{(t-t0)})\quad 1,$$

where L_∞ is the theoretical asymptotic length of the fish, K is the Brody (growth) coefficient and t_0 is the theoretical age at zero length, L_t is length at age (t) and t is the age in years.

In order to determine whether the growth rates from the *A. inodorus* historical and contemporary periods differed, a number of separate models were fitted to the age-length datasets. The models were classified as follows: the model that had two Von Bertalanffy parameters between the historical and contemporary period in common; the model that consisted of one common Von Bertalanffy parameter between the two periods; the model that consisted of all the three Von Bertalanffy parameters (L_∞, t_0, and K) (growth rates equal) and lastly the model that had all different L_∞, t_0, and K for each period. These growth parameters then were compared using a Likelihood-ratio chi-square test, χ^2 (LRT) (Kimura, 1980). The growth curves for *A. inodorus* historical (1994-1996) and contemporary (2018-2019) were furthermore visually compared to the growth curve of Kirchner and Voges (1999). All analysis were performed using the nlstools package (Baty et al., 2015) in R Version 4.0.5 (R Core Team, 2021).

It was not possible to compare growth curves between *A. inodorus, A. coronus* and hybrids in this study using the LRT because of the low number of samples available per age group. Statistical comparisons were done on mean length at each age between all three species for ages that had a sample size of $N > 1$ available. Since the sample sizes were uneven and < 10 in most instances for *A. coronus* and the hybrids, the lengths at each age were compared using a non-parametric test. This was done using the SPSS Statistical software (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp).

3.1.3 Mixed Effects modelling to calculate annual otolith growth

The mean annual otolith growth (from increment width measurements) was only calculated for *A. inodorus* because only *A. inodorus* samples were available from the historical period. Prior to the modelling, otolith increment width in mm (Inc), Age (at increment formation) and Age- at-capture (AAC) were log-transformed (Morrongiello

& Thresher, 2015). This was done to satisfy the model assumptions. All continuous variables were mean centered afterwards (Morrongiello & Thresher, 2015). To relate the increment width (Inc), which is also the response variable, the data were used in a linear mixed effects model to test for potential intrinsic (ontogenetic or individual-specific) and extrinsic (environmental or intra- or interspecific interactions) sources of variation for the *Argyrosomus* spp. annual growth rates (e.g. Morrongiello & Thresher, 2015; Martino et al., 2019; Wilhelm et al., 2020). Intrinsic factors included Age, AAC, Sex (either male or female or unsexed), allowing for the interaction between Age and Sex, and FishID (each specific fish had a unique identification). The Age, AAC and Sex were treated as fixed effects. The extrinsic effects were Cohort, Area (North-Central or South) and Year (of increment formation). The effects of Year, Cohort, Area and FishID were treated as random effects (allowing for intercepts and slope log(Age) | or just intercept 1|). The full model is shown in Equation 2.

$$log\ (Inc) \sim \log(Age) + Age * Sex + \log(AAC) + \log(Age)\ |\text{FishID} + \log(Age)\ |\text{Year} + \log(Age)\ |\text{Cohort} + \log(Age)\ |Area \qquad 2.$$

A method modified from Morrongiello and Thresher (2015) was used to test for the best possible combination of the explanatory variables, testing all possible combinations of fixed effects and random effects, and intercept or slope for random effects (Morrongiello & Thresher, 2015). This modelling approach considers the hierarchical structure of the biochronological data (repeated measurements of otolith annual increments from one individual, year, or cohort) and allows for robust assessment of different sources of variation (Morrongiello & Thresher, 2015). The lowest Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) was used to select the most parsimonious model – fitted with maximum likelihood

(Akaike, 1973; Burnham & Anderson, 2002; Johnson & Omland, 2004; Zuur et al., 2009).

To produce the best linear unbiased predictor of annual otolith growth (BLUP) 1982–2018, the optimal selected model was refitted with restricted maximum likelihood (REML) to produce unbiased parameter estimates (Zuur et al., 2009), using the random effects of year. All analysis were performed in RVersion 4.0.5 (R Core Team, 2021), with libraries lme4 (Bates et al., 2015), AICcmodavg (Mazerolle, 2020), effects (Fox & Weisberg, 2021) and lattice (Sarkar, 2021) for plotting.

3.1.4 The effects of sea surface temperature on *A. inodorus* growth

The best linear unbiased predictor of otolith growth (BLUP) time series was correlated using Pearson's correlation coefficient with independently calculated environmental indices that represent local forcing. The Pearson's correlation coefficient was used to measure the strength of the relationship between two variables (BLUP and SST). Mean monthly sea surface temperatures (SST) were used as an environmental indicator (e.g., Morrongiello & Thresher, 2015; Smoliński & Mirny, 2017; Wilhelm et al., 2020).

Average monthly SSTs values were extracted from the NOAA National Centre for Environmental System (NCEP) database (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/. Reyn_S mithOIv2/.monthly/.sst/) (Reynolds et al., 2002). Monthly averages from January 1982 to December 2018 were calculated for the two areas: 17-20°S, 10-12°E and 20-24°S, 12-14°E.

The BLUP time series (estimate of year effect) obtained from the best-fit mixed effect model was correlated with monthly mean SSTs of the growth year they overlapped with (lag 0) and 3-monthly means lagged 1 for summer (October to December of year-1) in each of the two areas using Pearson's Product Moment Correlation.

It was assumed that the translucent zone (of both species and their hybrids) is formed at the same time in October, at the beginning of the austral summer, and the beginning of the *A. inodorus* spawning migration period (Kirchner & Holtzhausen, 2001b).

Chapter 4: RESULTS

4.1 Genetic analysis

A 230 base pair fragment was aligned across all individuals for mtDNA. Phylogenetic inference from this alignment reported each sequence to cluster into one of two highly distinct groups corresponding to *A. coronus* and *A. inodorus*. Accordingly, the genotyped individuals could be identified as having an *A. coronus* or *A. inodorus* mitotype. The simulation analysis of the microsatellite data indicated two things, namely, (i) high power to distinguish pure individuals of both species from F1 and F2 hybrids and (ii) reduced power to distinguish backcrosses from pure individuals. To account for this resolution threshold, a conservative approach was adopted and only considered individuals as F1/F2 hybrids if identified as such by both the STRUCTURE and NewHybrids analysis. This consensus approach identified six individuals as hybrids which were sampled during the contemporary period (Table 1, Table 2). In all cases the individuals exhibited *A. inodorus* phenotypes. Five out of the six reported an *A. inodorus* mitotype (i.e. *A. inodorus* female mated with *A. coronus* male) with the remaining reporting an *A. coronus* mitotype (i.e. *A. coronus* female mating with an *A. inodorus* male).

Table 1: Number of *Argyrosomus inodorus, Argyrosomus coronus* and hybrids used for final analysis per month during the historical (1994-1996) and contemporary (2018-2019) periods in the different sampling regions (Northern, 17-21°S, (N), Central, 21-23°S, (C) and Southern,around 24°30’S, (S))

Months	***A. inodorus***		***A. inodorus***	***A. coronus***	**Hybrids**
	1994-1996		**2018-2019**		
	N&C	S	N&C		
Jan	2	1	18	0	1
Feb	8	8	26	0	1
Mar	3	3	22	9	1
Apr	3	9	34	4	2
May	4	2	11	1	1
Jun	0	0	5	0	0
Jul	0	2	6	2	0
Aug	0	0	0	0	0
Sep	0	0	0	0	0
Oct	12	0	6	3	0
Nov	19	1	21	1	0
Dec	12	0	0	0	0
Total	**63**	**26**	**149**	**20**	**6**

*Note: The historical samples were otoliths collected by MFMR during the 1994-1996 data collection period

Table 2: Area of capture, age, length, and sex data for individuals identified as hybrids by both STRUCTURE and NewHybrids analysis. The FishID refers to ID tag of individual fish. Area captured was divided into two regions: Northern (SCNP, 17°14’S to 21°11’S) and central (Dorob National Park, 21°11’S to 23°19’S) regions. Sex was identified as either female (F), male (M) or juvenile (J)

FishID	Area captured	Age (years)	Length (cm)	Sex
A220	Central	8	67.0	M
A264	North	5	53.5	F
A588	North	8	49.5	F
Kob476	North	5	60.1	F
Kob545	North	4	51.2	J
Kob549	North	5	51.7	M

4.2 Marginal Increment Analysis

Clear opaque and translucent zones were visible on the otoliths, which allowed for the age determination of *Argyrosomus* spp. (Figure 3). Zone pair widths varied among fish, ranging from a continuous narrow band, starting from the core to the edge of the otoliths for some individual sectioned otoliths while others had wider bands from the core. The wider bands were much easier to read as opposed to the narrower ones. The core in this study was described as the nucleus or centre of the otolith where it was sectioned assuming the otoliths were sectioned through the nucleus. The core had an opaque zone and was also regarded as the first growth increment (age-0 to -1 growth), which was excluded from the biochronology analysis.

There were exceptionally large standard deviations of mean marginal increments (mm) in most months, with a peak marginal increment (MI) and standard deviation in October for *A. inodorus*. For *A. coronus* no large standard deviations or notable peaks were observed since only five months of the year were sampled (Figure 3).

Data gaps (where no otoliths were available) were present for *A. inodorus* in August, September and December (Figure 3) and for *A. coronus* in over more than half of the year (January, February, May, June, August, September and December) (Figure 3). Overall, a peak of otolith MI was observed during austral spring for *A. inodorus* (October) (Figure 3). This confirmed the assumption that the translucent zone of *A. inodorus* was formed in October and warranted correlations of annual otolith growth with October to December of the previous calendar year (year y-1).

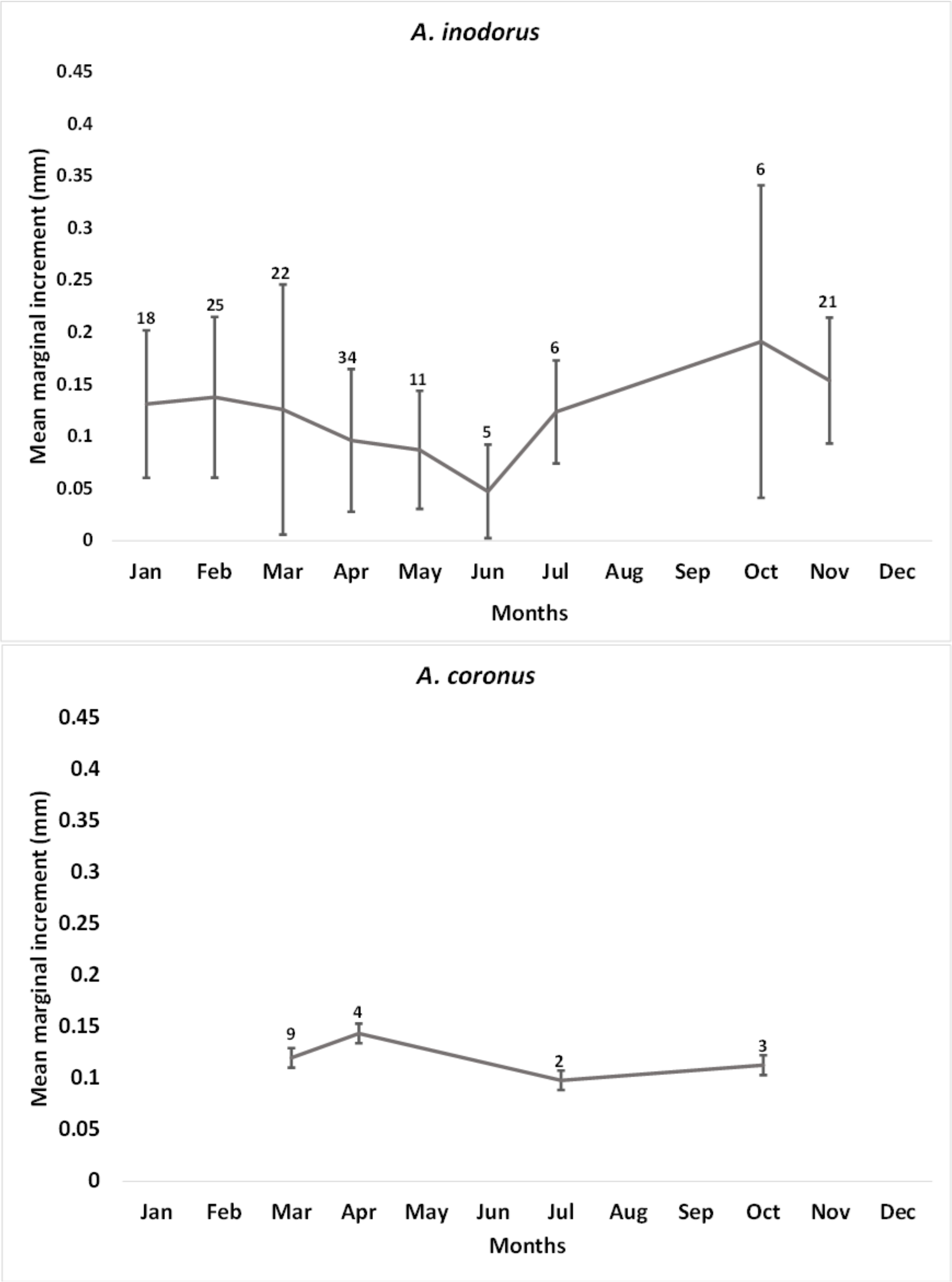

Figure 3: Mean marginal increment (± 1 standard deviation of *Argyrosomus inodorus* (top) and *Argyrosomus coronus* (bottom) caught in the Northern and Central regions of Namibia 2018-2019 by month. The numbers above the bars indicate the number of otoliths sampled per month

4.3 Age determination and growth

To confirm the validity of the growth model, model diagnostics were checked through fitted and residual plots (Appendix A4) and quantile-quantile plots (Appendix A5). The histogram of the residuals (Appendix A4) and the points on the quantile-quantile plots (Appendix A5) both showed that the datasets had a normal distribution.

A. inodorus ages ranged from 2-15 years and 3-12 years for historical (1994-1996) and contemporary (2018-2019) individuals, respectively. The ages of *A. coronus* and the hybrids ranged from 3-9 years and 4-8 years, respectively (Figure 4). The summary of the estimated parameters for *A. inodorus* (historical; 1994-1996) and (contemporary; 2018-2019) are presented in Table 3. The *A. inodorus* age-length data for both the contemporary and historical period had a substantial variation which was noted through wide confidence intervals which were obtained from the L_∞ for both periods (Table 3).

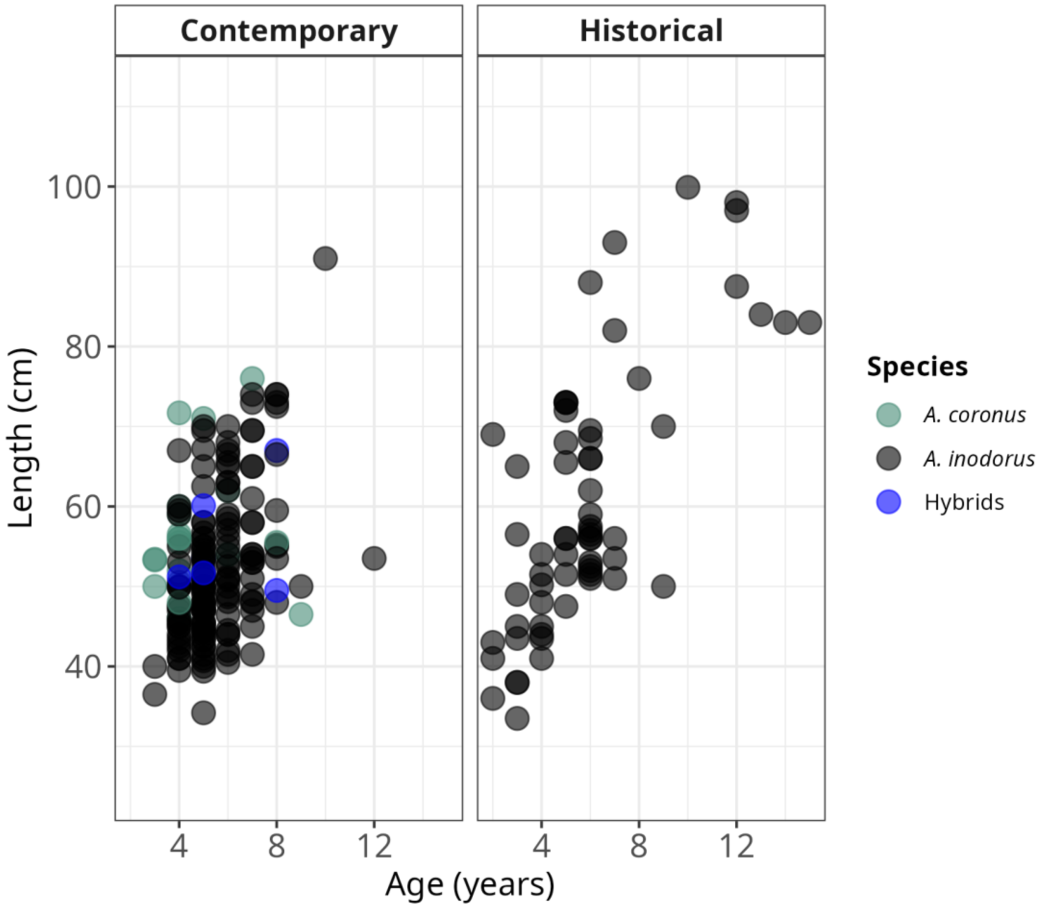

Figure 4: Visual summary of length (cm) at different ages (years) for individuals of *Argyrosomus inodorus* historical (right, grey), *Argyrosomus inodorus* contemporary (left, grey), *Argyrosomus coronus* (green) and hybrids (blue)

A comparison of the Von Bertalanffy growth parameters, using the likelihood ratio test showed that there was no significant difference in the Brody growth coefficient ($p = 0.77$), L_∞ ($p = 0.60$) or t_0 ($p = 0.92$) between the historical and contemporary growth rates of *A. inodorus*. However, there was a significant difference in the full model between the historical and contemporary population ($p < 0.01$) (Table 3 and 4). Both the historical and contemporary growth curves (parameters in Table 3) were visually compared to the Kirchner and Voges (1999) Von Bertalanffy growth curve (Figure 5), and showed that the Kirchner and Voges (1999) fitted growth curve was much closer to the historical growth curve. The visual comparisons: Age data of *A. coronus* and the hybrid population to the fits of the growth model for *A. inodorus* from the historical and contemporary age data are shown in Appendix A6.

Table 3: Von Bertalanffy growth parameter estimates and Mean lengths-at-age for Kirchner & Voges (1999), historical (1994-1996) – this study and contemporary (2018-2019) – this study and samples of *Argyrosomus inodorus* captured along the northern (SCNP, 17°14'S to 21°11'S) and central (Dorob National Park, 21°11'S to 23°19'S) regions along the Namibian coast. Lower and upper 95% confidence intervals and p-values of the estimate are in parenthesis next to each parameter. The detailed model outputs for the historical (1994-1996) and contemporary (2018-2019) samples are in Appendix A7

Parameter	**Kirchner & Voges (1999)**	**Historical (1994-1996)**	**Contemporary (2018-2019)**
L_∞	112.0 (100-130)	138.04 (85.54–434.17, p = 0.03)	82.37 (60.19–151.37, p = 0.04)
K	0.094 (0.07-0.12)	0.058 (0.01–0.19, p = 0.26)	0.119 (0.04–0.45, p = 0.47)
t0	-2.29 (-3.03 – -1.70)	-4.22 (-9.15 – -0.696, p = 0.12)	-3.01 (-7.48–1.22, p = 0.53)
Age (years)	**Mean length-at-age (cm)**	**Mean length-at-age (cm)**	**Mean length-at-age (cm)**
0	21.69	30.16	24.94
1	29.79	36.28	31.42
2	37.17	42.05	37.17
3	43.88	47.50	42.28
4	49.99	52.64	46.80
5	55.56	57.49	50.82
6	60.62	62.06	54.38
7	65.23	66.37	57.54
8	69.43	70.44	60.35
9	73.25	74.27	62.83
10	76.72	77.89	65.04
11	79.89	81.30	67.00
12	82.77	84.52	68.73
13	85.39	87.56	70.27

* The expected length L_t (cm), at age group t, was calculated using the Von Bertalanffy growthfunction (VBGF): $L_t = L_\infty (1- e^{-K\ (t-t0)})$. For Kirchner & Voges (1999) the Von Bertalanffy parameters calculated for the northern region were used.

Table 4: Comparison of multiple Von Bertalanffy growth models of *Argyrosomus inodorus*, fitted to historical and contemporary age-length data. The column headings include the model type which refers to the model that was fitted, DF (degrees of freedom for fitted model and for the model comparison with full model in parentheses, -LL (negative Log-likelihood), χ^2 (the χ^2test statistic when comparing the specific fitted model with the full model) and Pr (> χ^2), the significance level of the comparison. *** denotes significant differences at the 0.001 % level.The fits of the different configuration of the multiple Von Bertalanffy growth models *Argyrosomus inodorus*, fitted to historical and contemporary age-length data are shown in Appendix A8

Model type	**DF**	**-LL**	χ^2	**Pr (>χ^2)**
Different L_∞, K, t_0 (full)	7	-773.07		
Common t_0	6 (-1)	-773.09	0.045	0.832
Common K	6 (-1)	-773.15	0.1745	0.6762
Common L_∞	6 (-1)	-773.23	0.335	0.5627
Common K and L_∞	5 (-2)	-774.80	3.4715	0.1763
Common K and t_0	5 (-2)	-773.48	0.8353	0.6586
Common L_∞ and t_0	5 (-2)	-773.78	1.4333	0.4884
Common All	4 (-3)	-789.75	33.36	<0.001 ***

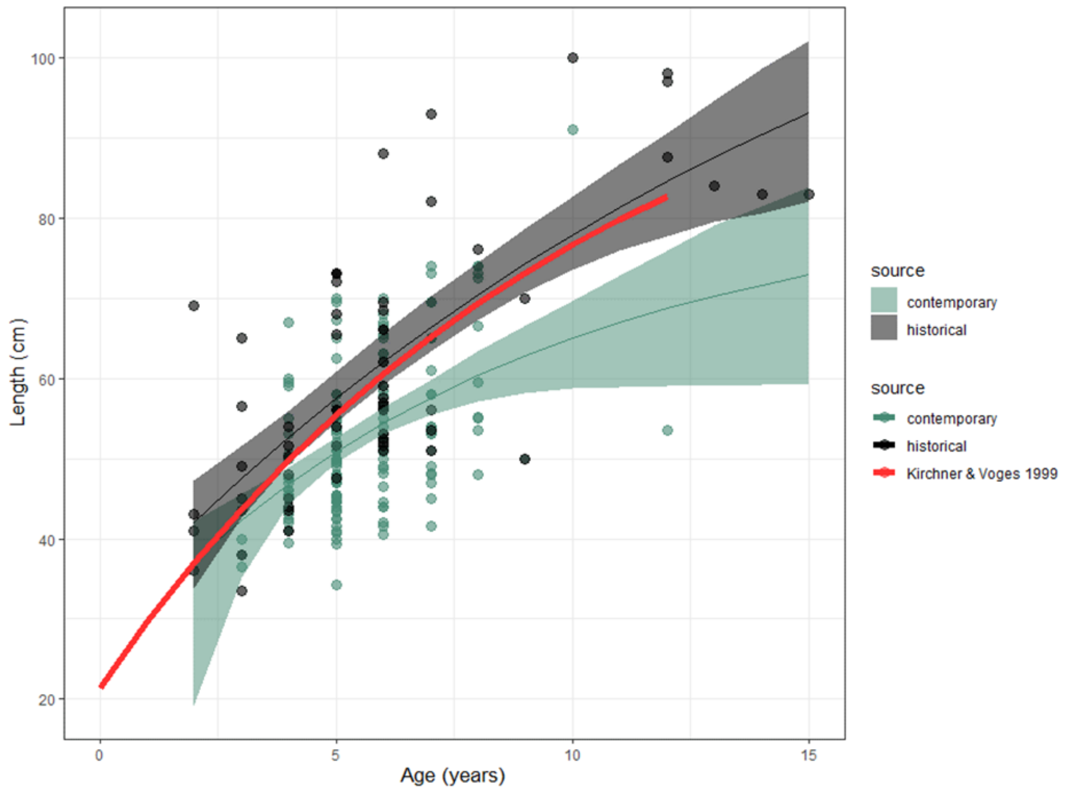

Figure 5: Plot of age-length data of *Argyrosomus inodorus* historical (black dots) and contemporary (green dots) with the fitted growth model for the contemporary and historical ageing data in lines of the same colours. The fitted growth model from Kirchner and Voges (1999) published data is shown in red. The 95% confidence interval from bootstrapping is shown in the shaded areas in grey (historical) and green (contemporary)

The mean length (± standard deviation) of *A. inodorus* at age 5 (n = 67) during the contemporary period was 52.3 ± 9.1. This was less than *A. coronus* (61 ± 14.1) and the hybrids (55.1 ± 4.4) at age 5 (n = 3 and n =2 respectively). However, the Kruskal-Wallis test results showed that there was no significant difference between their (*A. coronus*, *A. inodorus* and hybrids) mean lengths at age 5 (*H* (2) = 4.363, *P* = 0.113). Furthermore, there was a significant difference between the purebred species (*A. coronus* and *A. inodorus*) (Figure 6) at mean lengths at age 4 (*H* (1) = 8.264, *P* =

0.004), despite the higher median length of *A. coronus* (*Mdn* = 56 cm) when compared with *A. inodorus* (*Mdn* = 46 cm) (Appendix A9). A post-hoc Mann-Whitney test at mean lengths at age 4 for the two purebred species (*A. inodorus* and *A. coronus*) indicated that there was a significant difference between lengths of *A. coronus* and *A. inodorus* at age 4, *U* = 219, *z* = -2.875, *p* = 0.004) (Appendix A10). None of the other ages had significantly different lengths by species.

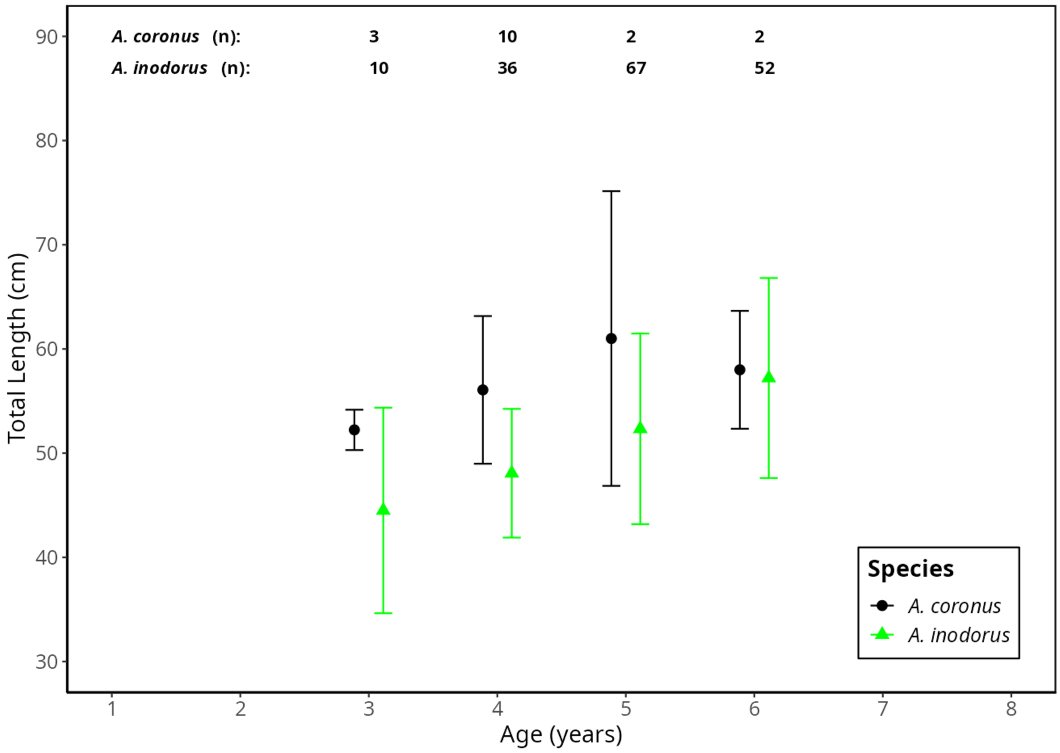

Figure 6: Mean lengths (± standard deviation) at ages 3 to 6 years of purebred *Argyrosomus coronus* (black) and *Argyrosomus inodorus* (green) sampled during the contemporary period (2018-2019). *Note that this is only where there was sample sizes *N* >1 for both species by agegroup

4.4 Otolith chronologies

A total of 1185 increments were measured on historical and contemporary *A. inodorus* otoliths. *A. inodorus* growth was highly synchronous across all individuals (Figure 7).

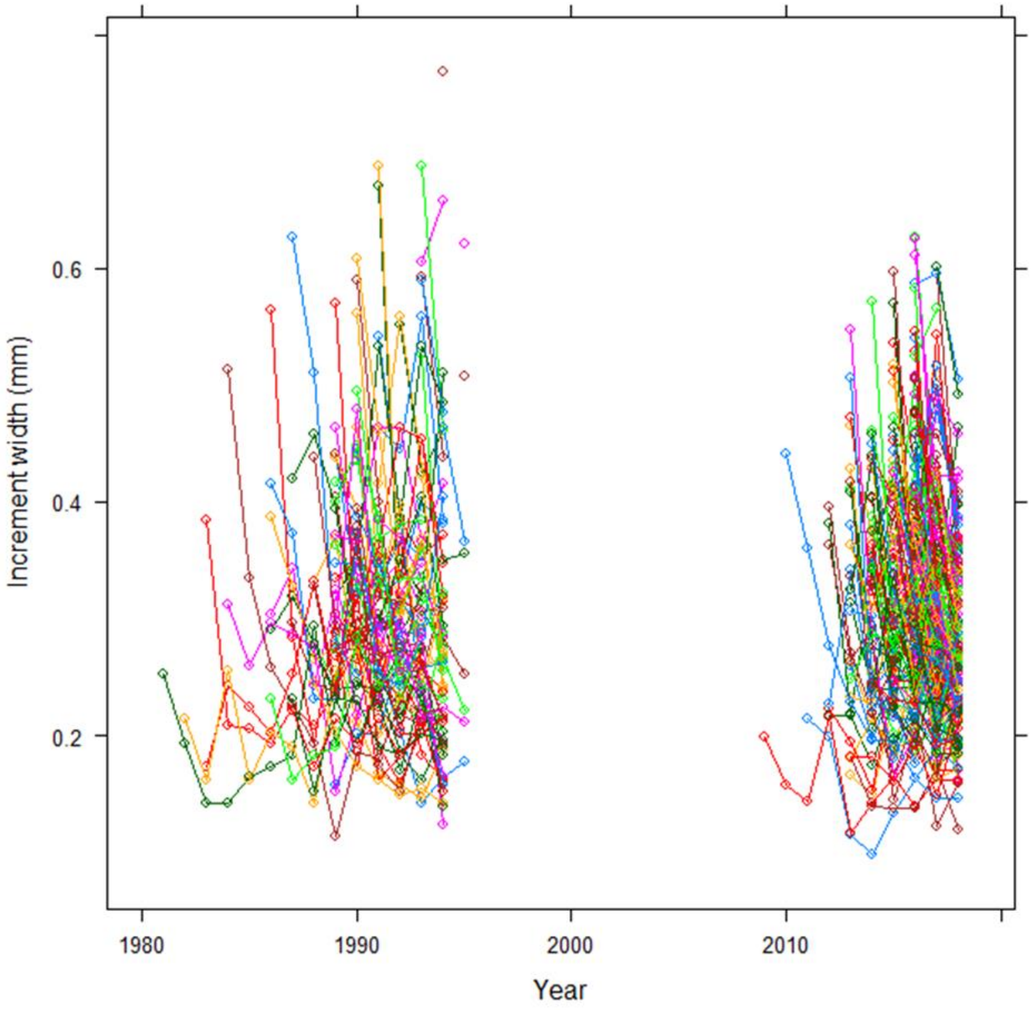

Figure 7: Absolute increment width (mm) against year of formation for all individual otoliths of *Argyrosomus inodorus* caught off Namibia from 1994-1996 and 2018-2019. The gap seen from the mid-1990s to the early 2000s is because no otoliths were collected during that time. Absolute increment width against age of formation for all otoliths of all individual otoliths of *A. inodorus* caught off Namibia from 1994-1996 and 2018-2019 are shown in Appendix A11

Based on a series of AICc comparisons (Table 5), the following most parsimonious mixed effects growth model was selected for *A. inodorus*:

Log (Inc) ~ log (age) + log (AAC) + log (age) |FishID + 1|Year 3,

where Inc = increment width measurement in mm, age = age at time of increment formation, AAC = age-at-capture, FishID = individual fish samples unique identification, Year = calendar year of increment formation, 1| denotes random effect intercept for Year and age| denotes slope and intercept for FishID. The best model was chosen as the most parsimonious (AICc = - 196.34, Conditional R^2 = 0.69, Table 5) as it differed from the model with the lowest AICc only by 0.06 with the fewest parameters and almost the same conditional R^2 as the model with the lowest AICc score. The best supported model of the growth increment data explained 69% of variation in the growth of *A. inodorus* (Table 5). Optimal model parameter estimates and test statistics describing fixed and random sources of growth variation in *A. inodorus* from 1994 to 2018 are shown in Table 6. Sex, cohort and area did not have a considerable influence on the variation in growth (otolith increment width). Age had the greatest influence on growth among the tested variables, with predicted increment widths strongly declining as fish grew older (Figure 8).

Table 5: Results of the intrinsic effects (mixed effects) model optimization based on the full dataset of 1981 to 2018 *Argyrosomus inodorus* otolith chronologies. The models were sorted by AICc, and the selected model is highlighted in bold. AAC = Age-at-capture; Random age slopes for FishID and Cohort denoted by “age|”; “1|” denotes only a random intercept was calculated*; K = degrees of freedom; AICc = Akaike’s information criterion, adjusted for small sample sizes; LL: Log-likelihood

Fixed effects	Random effects	K	AICc	Δ AICc	LL	Conditional R^2
log(age)) + log(AAC)	log(age)| Area + log(age)|FishID + 1|fYear	10	-196.40	0.00	108.2	0.70
log(age) + log(AAC)	**log(age)|FishID + 1|fYear**	**8**	**-196.34**	**0.06**	**106.2**	**0.69**
log(age) + log(AAC)	log(age)|FishID + 1|fYear + 1|Area	9	-194.62	1.78	106.3	0.69
log(age) + Sex + log(AAC)	log(age)|FishID + 1|fYear	12	-192.12	4.28	108.1	0.69
log(age) + age*Sex + log(AAC)	log(age)|FishID + 1|fYear	17	-191.89	4.51	112.9	0.68
log(age) + age*Sex + log(AAC)	log(age)|FishID + 1|fYear	17	-191.89	4.51	112.9	0.68
log(age) + log(AAC)	log(age)|FishID +1|fCohort	8	-191.72	4.68	103.9	0.69
log(age) + log(AAC)	log(age)|FishID	7	-191.51	4.89	102.8	0.69
log(age)) + log(AAC) + Area	log(age)|FishID	9	-189.63	6.77	103.8	0.69
log(age) + Sex + log(AAC)	log(age)|FishID	11	-187.70	8.7	104.9	0.69
log(age) + age*Sex + log(AAC)	1|FishID	14	-138.31	58.09	83.2	0.62
log(age)) + Area	log(age)|FishID	8	-137.29	59.11	76.7	0.64
log(age)	log(age)|FishID	6	-132.46	63.94	72.2	0.64
log(age) + log(AAC)	1|FishID	5	-131.87	64.53	70.9	0.62
log(age) + Sex	log(age)|FishID	10	-128.06	68.34	74.0	0.64
log(age)	1|FishID	4	-67.82	128.58	37.9	0.57

* Note that only intercept could be fitted for Year and Cohort because of the overall sample size.

Table 6: Optimal model parameter estimates and test statistics describing Fixed and Random sources of growth variation in *Argyrosomus inodorus* caught along the Namibian coast during the historical (1994-1996) and contemporary (2018-2019) period

Fixed effects

Covariate	**Estimate**	**SE**	**t-value**
Intercept	-1.26	0.014	-85.26
Age	-0.23	0.017	-13.29
AAC	-0.33	0.041	-7.86

Random effects

Covariate	**Variance component**	**SD**	**Correlation**
1|FishID	0.0223	0.1494	
Age|FishID	0.0172	0.1313	-0.07
1|Year	0.0009	0.0312	
Residual	0.0311	0.1764	

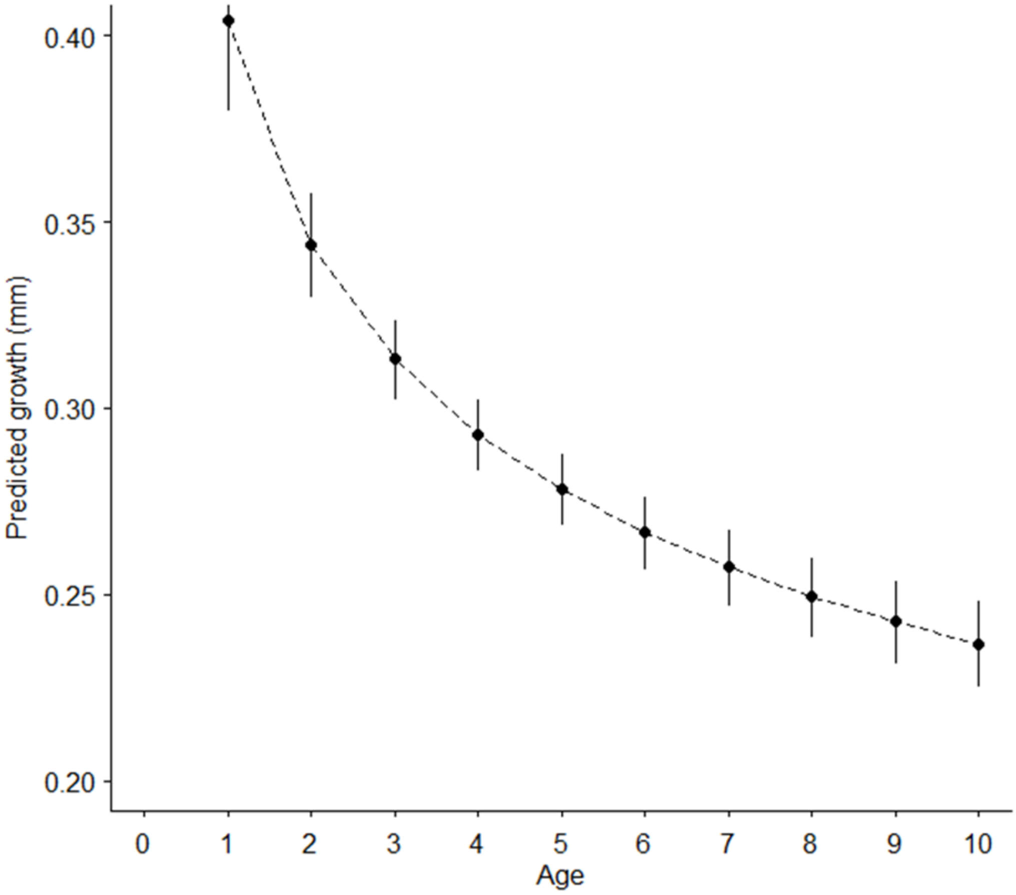

Figure 8: Predicted annual growth variation (mm) for *Argyrosomus inodorus* against age in years estimated in the full mixed effects model back transformed to the original scale

The *A. inodorus* growth time series that was extracted from the best linear unbiased predictor (BLUP) (from the random effects intercept of Year) of otolith growth showed relatively low inter-annual variations of growth over the period 1981-2018, but with exceptionally low growth in 1983, 1985, 2014 and 2015 and high growth in 1990 and 1993 (Figure 9).

Recent growth from the contemporary period appeared to be reduced, with annual growth largely below average from 2009 to 2018 (Figure 9).

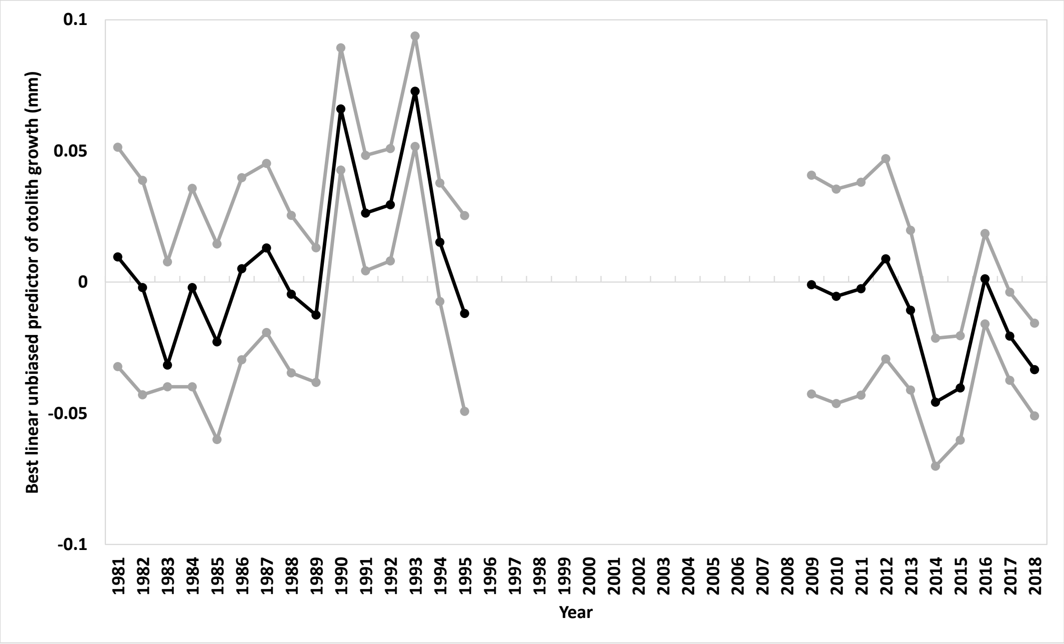

Figure 9: Best linear unbiased predictor (BLUP) of growth (black solid line) against year of *Argyrosomus inodorus* caught off Namibia estimated from the most parsimonious mixed effects model on otolith increments. The 95% confidence limits are indicated by the grey solid lines and the mean growth is indicated by the dashed grey line

4.5 <u>The effects of sea surface temperature on *A. inodorus* growth</u>

Argyrosomus inodorus BLUP of annual growth from otolith increments was significantly positively correlated (Pearson's correlation coefficient) to spring SSTs (October y-1) in the area 17-20˚S, 10-12˚E (r = 0.476, n = 25, *p* < 0.01). For the area 20-24˚S, 12-14˚E, *A. inodorus* BLUP of annual growth from otolith increments was significantly positively correlated (Pearson's correlation coefficient) with winter (July of the year of formation) mean SST (r =0.541, n = 25, *p* < 0.05, Figure 10) and was significantly negatively correlated (Pearson's correlation coefficient) with mean spring-summer SSTs (October to December of year-1) (r = -0.512, n = 25, *p* < 0.05) (Figure 10). Figure 10 also shows that in recent years the summer temperatures have warmed,with the warmest summers matching the reduced growth in 2014 and 2015 and the warmest winters in the 1990s matching the increased growth in 1991 and 1993. Figure 11 shows that fast annual growth was associated with warmer water temperatures in winter (above 15℃) with a decrease in annual growth noted during summer when temperatures were below 17℃, suggesting that the optimal temperature for growth is somewhere between 15℃ and 17℃.

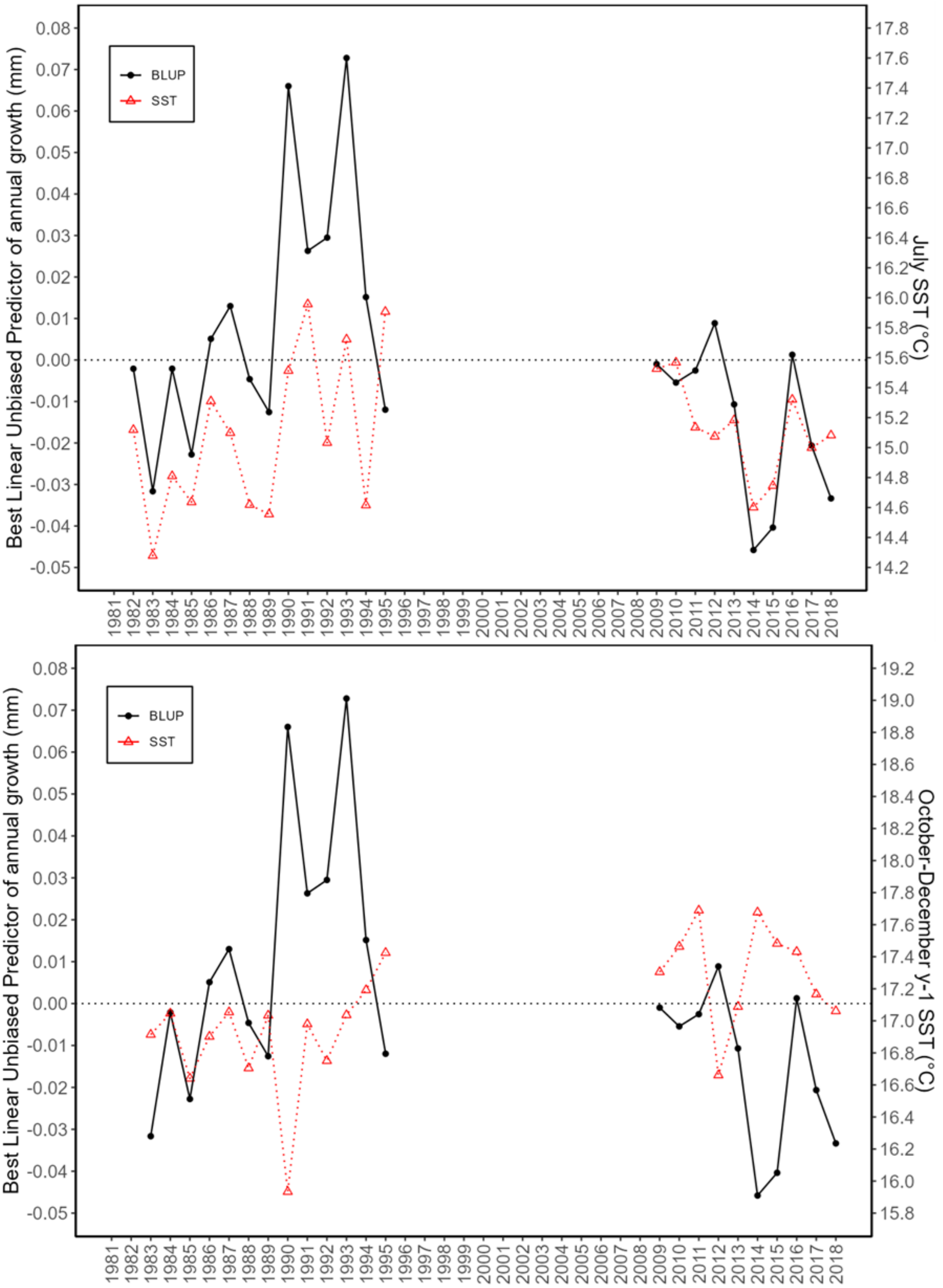

Figure 10: Best linear unbiased predictor (BLUP) of annual growth increments against growth year for *Argyrosomus inodorus*, from Namibia, superimposed with July (of year of formation) SST (top) and spring-summer SST (October - December y-1) (bottom) in the area 20-24◦S, 12- 14◦E against year

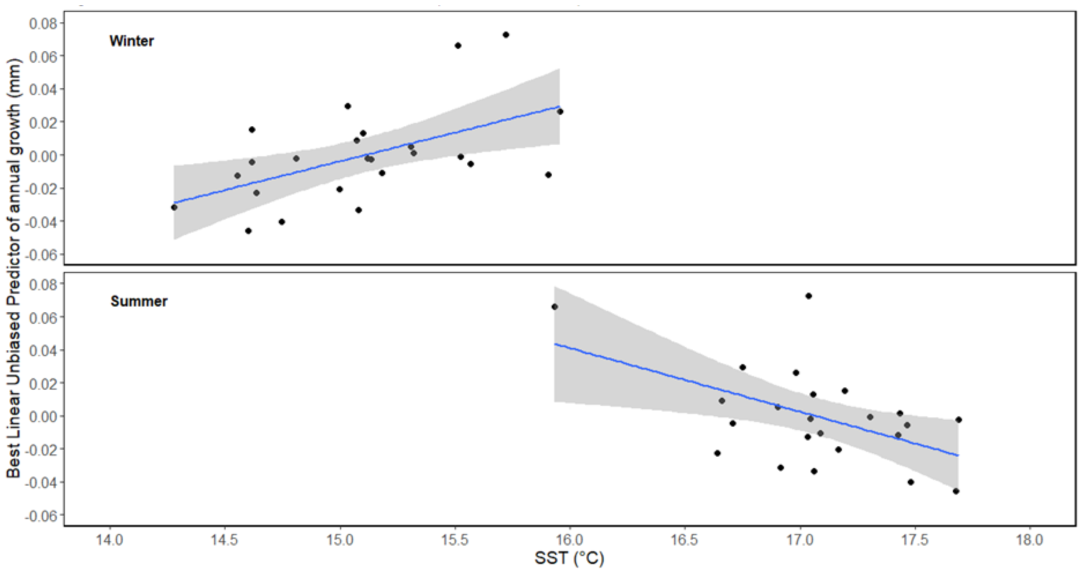

Figure 11: Relationship between the best linear unbiased predictor of annual growth (BLUP) mm and winter (July) (top) and summer (October-December y-1) (bottom) sea surface temperatures (SST) and of *Argyrosomus inodorus* in the area 20-24◦S, 12-14◦E. Linear regression of BLUP against SST is shown by the blue line with the grey shaded envelopes around the regression being 95% confidence interval

Chapter 5: Discussion

The findings of this study show that there has been a significant decline in the growth of *A. inodorus* between the 1990s and 2010s. During this time, the otolith biochronology information (predicted growth) for *A. inodorus* was significantly correlated with SST. Annual growth appeared to be positively correlated with SST in July (austral winter) and negatively correlated with the spring and summer (October to December) SST. Based on these findings, it appears that the warmer summer temperatures in recent times may have negatively influenced the growth of the species. The comparisons of the growth rate of *A. inodorus* and *A. coronus*, although preliminary, suggested that *A. coronus* and hybrids may grow faster than *A. inodorus* in contemporary conditions. This comparative growth information and the identification of the drivers of *A. inodorus* growth have improved our understanding of the status of the fishery and the likely changes that may be seen for the future of the *Argyrosomus* fisheries in this ocean warming hotspot.

The significant difference in the growth rate observed between historical and contemporary populations of *A. inodorus* is a concern from a fisheries perspective. This may suggest that the productivity of the stock is declining. While it is possible that there may have been methodological problems and the estimates were biased, the similarity between the historical growth curve and the one estimated by Kirchner and Voges (1999) (Figure 5), suggests that the growth curve estimates in this study were valid and indicate that growth of this species has changed significantly over the last 20 - 30 years. This is a major concern to the sustainability of the *A. inodorus* fishery, and it is recommended that stock assessments incorporate the contemporary growth curve to avoid (further) overexploitation.

Understanding how the growth rate has changed is important for predicting its consequences and understanding the mechanisms driving the change. The results of the Likelihood-ratio chi-square tests suggested that the Brody coefficient (*K*) for both historical and contemporary periods were similar, while L_∞ differed significantly; with the historical population having a much higher length-at-age compared to the contemporary *A. inodorus* (Table 3, Figure 5). In addition, the confidence intervals overlapped at 2-3 years, suggesting that the early growth rates during the historical and contemporary period were similar. Differences in the growth of fish in the older age classes may suggest that exploitation is impacting the cumulative growth of the fish after maturity, and/or that environmental drivers may be having a disproportionate impact on the larger *A. inodorus*.

Marginal increment analysis for both purebred *Argyrosomus* species showed that growth increments were formed annually in austral spring. The growth increments consisted of one opaque and one translucent zone which was observed for both *A. inodorus* and *A. coronus* and it also highlighted the annual periodicity of zone formation. The formation of a single opaque and translucent zone agrees with the findings from other *Argyrosomus* spp. growth studies in the Benguela, for example *A. japonicus* (Griffiths 1996a); *A. inodorus* (Griffiths 1996b); *A. inodorus* (Kirchner and Voges 1999) and *A. coronus* (Potts et al., 2010).

The opaque zones for contemporary *A. inodorus* appeared to start forming during the austral winter (June) (lowest mean marginal increment) and appeared to complete by October (highest mean marginal increment) when the translucent zone would have formed. This indicated that the growth period for this present study which was measured from the end of the translucent zone to end of the next translucent zone was measured from October (previous year) to September (present year). The *A. coronus* marginal increment seemed to start forming in winter (July) (lowest mean marginal increment) and appeared to complete by autumn (April) (highest mean marginal increment) when the translucent zone would have formed. More sample size in the missing months is however needed to confirm the exact formation of translucent and opaque zones for the *A. coronus*.

The forming of the translucent zone appeared to be around October for *A. inodorus* which coincides with the onset of the 6 months protracted spawning season (October-March) for Namibia’s *A. inodorus* (Kirchner & Holtzhausen 2001b). Similar to this present study, Griffiths (1996b) also observed large standard deviations of mean marginal increments for *A. inodorus* whereby the mean marginal increment was highest during February and March which are also known as the peak of the South African *A. inodorus* spawning season (Griffiths 1996b). This suggests that both the Namibian *A. inodorus* and that of South Africa have translucent zones forming during their spawning seasons. There is a general understanding that otolith pattern formation may be related to metabolic processes, i.e. metabolic processes change during spawning periods as well, which may be directly related to the fish physiology or indirectly to the underlying environmental changes that coincide with spawning periods (e.g. Wilhelm et al., 2018). Nonetheless, the results from this present study add to what many studies already demonstrated; that zone formation (or the presence) coincides with spawning periods (e.g. Brouwer & Griffiths, 2004). Although there have not been any reports of spawning occurrence for *A. coronus* in Namibian waters, a spawning migration that is concurrent with the movement of the ABFZ (moving north in early winter and south in spring) is believed to take place (Potts et al., 2010), which could also be concurrent with zone formation of *A. coronus*.

While this study attempted to obtain a comprehensive and representative sample of the

Argyrosomus species in Namibia, it is likely that larger-sized and older-aged individuals were underrepresented. This is also reflected by the significant inclusion of the AAC parameter in the mixed effects model (Table 6). The maximum age reported for Namibia's *A. inodorus* to date is 28 years at a total length of 102.3 cm TL (Kirchner & Voges, 1999) while the oldest fish caught in this present study was 12 years old (contemporary *A. inodorus*) at a total length of 53.5 cm. Ideally, for a better comparison of the Von Bertalanffy growth curves, more representative sampling has to be done (by area and size class). The growth rates found in this study for *A. inodorus* (historical) were nonetheless in agreement with other studies (e.g., Kirchner & Voges, 1999; Kirchner & Holtzhausen, 2001a; Potts et al., 2010).

A significant difference in the total lengths at age 4 was observed between *A. inodorus* and *A. coronus* found along the Namibian coast. These findings agree with Griffiths and Heemstra (1995), who stated that the *A. inodorus* and *A. coronus* have two contrasting life histories and also with Potts et al. (2010), who showed that L_{50} for *A. inodorus* (350-360 mm TL) and *A. coronus* (870 mm TL) differ significantly. The present study's results also showed that there was considerable variability in the size-at-age for both purebred *Argyrosomus* species. For instance, the total lengths in this present study at age 4 for contemporary (2018-2019) *A. inodorus* and *A. coronus* ranged between 39.5 cm to 71.7 cm TL and 46 cm to 71.7 cm TL, respectively. This was also reflected in the between-individual growth rate variation shown by the mixed effects model for *A. inodorus*.

The significant difference in the growth curves of *A. inodorus* during the historical (1994-1996) and contemporary (2018-2019) periods was supported by the otolith chronologies, which showed that the *A. inodorus* mean annual growth rates from 1981-2018 changed from above and average growth in the 1980s to mostly below average growth from 2009 onwards, which was positively related to warm winters and negatively related to warm spring-summer sea surface temperatures.

The Age-at-capture (AAC) was described by Morrongiello and Thresher (2015) as a “Measure of potential selectivity on growth” (p. 98). The individual growth rates from this present study for *A. inodorus* were negatively related to AAC (Table 6), suggesting growth-based selectivity occurrence, which means that individual fish who grow faster do not commonly reach the same age as those individual fish who grow slower (Morrongiello & Thresher, 2015), because individual fish who are fast-growing are usually susceptible to being caught at younger ages when compared to those who grow slower (Smoliński & Mirny, 2017). This suggests fisheries selectivity influencing growth rates is occurring in *A. inodorus*.

Mirimin et al. (2016) stated that fishing-induced evolutionary changes in the growth of heavily fished species such as *A. inodorus* (who have been exploited since the 1960s) are likely to be taking place already. Exploitation may be a primary mechanism driving the observed changes in the growth of fish, through altering a population’s resilience to environmental change when the older age classes are removed through fishing, which ultimately leads to age-class truncation (Stewart, 2011). Age-class truncation often indicates changes in intrinsic population growth rates due to an instability in population dynamics as the young, small in size, and more quickly maturing individuals seem to be the main target, thus exerting pressure on fish populations (Anderson et al., 2008; Kuparinen et al., 2016). For example, Swain et al. (2007) showed evidence of a decline in growth rates of cod (*Gadus morhua*) in eastern Canada and suggested that selective fishing had influenced this decrease. However, this was disputed by Hilborn and Minte-Vera (2008) who used a meta-analysis of 73 commercially fish stocks and showed that there was no relationship between fishing intensity and the change in growth rate (Hilborn & Minte-Vera, 2008). All things considered, conclusions around fisheries-induced changes cannot be made from this present study as it was not the focus, however there is a great possibility that it is already occurring for fish populations such as *Argyrosomus* spp. that have been exploited for decades.

While exploitation may be a mechanism driving the observed changes in the growth of *A. inodorus*, it also may have other impacts. For example, Stewart (2011) suggested that a population's resilience to environmental change is reduced when the older age classes are removed through fishing. The otolith chronology component of this study identified a significant correlation between SST and growth (Figure 10), with growth positively correlated to the SST in July and negatively correlated with the SST in October-December y-1. When considered together, it appears that the overall optimal growth temperatures for Namibian *A. inodorus* are narrow and likely range from 15 – 16 °C, during both warm winters and cold summers (Figure 11).

Based on this narrow thermal range for optimal growth, it is likely that the slower growth seen in the recent years (contemporary period) may be attributed to rapid climate change observed in the northern part of the northern Benguela region. The negative correlation between the spring-summer SSTs and the growth of *A. inodorus* observed in this study suggests that the growth of the species is related to the timing and movement of the Angola-Benguela frontal zone (ABFZ) in the region. Warming in central and northern Namibia in spring-summer are generally determined by the extent of the southward intrusion of warm and saline waters from the ABFZ (Lass et al., 2000; Lass & Mohrholz, 2005; Potts et al., 2014a; Koseki & Goubanova,2019). The southward intrusion of warm and saline waters from the ABFZ into central Namibia usually strengthens during austral spring/summer (around September- October) (Lass et al., 2000; Lass & Mohrholz, 2005; Potts et al., 2014a; Koseki & Goubanova, 2019). Therefore, the below average growth that is observed for *A. inodorus* in warm austral spring-summers from this present study could be linked to the southward intrusion of warm and saline waters from the ABFZ into central Namibia during this period or also be linked to the weakening trade winds in the western equatorial Atlantic, which may also seem to be the start of Benguela Niño's in austral fall (Lübbecke et al., 2010). So, it appears that the contemporary trends of theABFZ, which included comparatively cold winter and warm spring and summer SSTs may have negatively influenced the growth of this heavily exploited population.

The findings in this study are not unique to the region. For example, a chronology study on *M.paradoxus* found off the Namibian coast (Wilhelm et al., 2020) showed that the annual growth rates for this species for the years 1982–2013 were significantly negatively correlated with October (austral spring) sea surface temperatures in the area 24–28°S. However, different to the present study, the sea surface temperature reflected indirect relationships shown by their positive correlation for *M. paradoxus* annual growth rates with the July–September upwelling index and a positive correlation with the August mean chlorophyll-*a* concentrations for the years. Their study further noted that the growth sensitivity of *M. paradoxus* towards the variability of the Benguela upwelling may have changed over time, indicating a stronger correlation with upwelling indices in the present than the past (Wilhelm et al., 2020).

In addition to directly affecting fish growth through higher energy conversion, Ottersen et al. (2004) states that environment temperature also has an indirect effect on fish growth through aspects such as 1) influencing ecosystem productivity; 2) altering the distribution of many fish by influencing them to move towards areas where the temperature is optimal and food availability is abundant; and 3) affecting the spawning and feeding seasons. The concept of temperature-dependent growth in marine fish is therefore indisputable and well-established (Pörtner et al., 2001; Matta et al., 2010), because it is not unfamiliar for fish species to show a significant relationship between their environmental temperature and growth rate during a certain period of the year as shown in other studies (e.g. Smoliński & Mirny, 2017; Duncan, 2018; Wilhelm et al., 2020) though usually the growth rate was only affected by temperature in one direction (positive or negative effect by indirectly being linked to upwelling).

The rapid oceanographic changes predicted for the Namibian coast will have implications for the *Argyrosomus* spp. and their fisheries. While the biochronology results suggest that growth of *A. inodorus* may continue to decline with increased warming, a mechanistic understanding of this is necessary to understand when temperatures will no longer be suitable for the growth and survival of the species. Pringle (2020) recently compared the thermal physiology of *Argyrosomus* spp. caught along the Namibian coast. He showed that the aerobic scope (the temperature where most energy is available for activity) of *A. inodorus* was highest at temperatures between 12°C and 16°C (Pringle, 2020). He also suggested that the aerobic scope of the species would decline rapidly above 24°C. These findings explain the pattern seen in the present study, i.e., *A. inodorus* grew faster in warmer winters (<17°C) but slower in warmer summers (>17°C).

The northern Benguela's Angola-Benguela Front - with its current rapid increase in SSTs are further likely to exert more negative effects on *A. inodorus* growth as it gets warmer. As a global warming hotspot, the northern region of the northern Benguela serves as an important early indicator to what is likely to be expected with regard to global climate change (Hobday & Pecl, 2014; Potts et al., 2014a). Extreme cold and warm SST events (Benguela Niña and Benguela Niño, respectively) are common in the Benguela region and when occurring, these events are known to have drastic effects on fish populations through affecting their biological productivity and climate change in the region (Florenchie et al., 2004). This not only means that *A. inodorus* is likely to shift distributional range, but it also means that there is a possibility that its migratory patterns would likely be affected due to this restriction in its distribution. The adult and juvenile feeding grounds (central and northern Namibia) might be warmer than average if this predicted rise in SSTs continues and this could alter their feeding behavior during certain warmer than usual periods which might in return lead to lower growth rates. Additionally, an increase in competition for prey may also lead to reduced growth rates. An example of this is the interspecific competition which was observed among the sunfish (*Lepomis* spp.) and the yellow perch (*Perca flavescens*) which led to negatively influencing the yellow perch through reducing their growth when an abundance in sunfish was seen (Schoenbeck & Brown, 2010). Overall, it is likely that the suitability of the Namibian coastal environment is declining rapidly for *A. inodorus*.

While the consequences of warming have been shown to put forth negative effects for *A. inodorus,* a number of studies have shown that a slight increase in SSTs are favorable for the growth of some marine species while other studies indicated the opposite. For example, Morgan et al. (2001) showed that the rainbow trout (*Oncorhyncus mykiss*) showed an increase in their appetite, growth, and other aspects when the temperature was 2℃ higher during winter, while showing the opposite (negative effects) in summer with the same increase (2℃) (Brander, 2007). Ottersen et al. (2004) on the other hand showed how a decline in SSTs caused approximately 50% of an observed decrease in size-at-age in the mid-1980s till mid-1990s for the

Atlantic cod on the northeastern Scotian Shelf (Campana et al., 1995) and off Newfoundland (de Cárdenas, 1996; Shelton et al., 1996). Another study recently done by Nicolle et al. (2022) for the mulloway *Argyrosomus japonicus*, showed a positive growth response to an increase in temperature with a mean annual growth rate for this species predicted to increase by 8.9% by the year 2099 in south-eastern Australia. This study area (south eastern Australia) by Nicole et al. (2022) is also classified as a global hotspot similar to the northern region of the northern Benguela (Hobday & Pecl, 2014).

Though the rapidly changing ocean temperature in Namibia may have negative consequences for the growth of species such as *A. inodorus*, it is possible that future conditions may favour other species. The core distribution of *A. coronus* is in the warmer waters of southern Angola and it is possible that the contemporary and future conditions in Namibia will be increasingly suitable for this species. Although the sample sizes were low, it appeared that the growth of *A. coronus* was not significantly different to *A. inodorus* in Namibia during the contemporary period. However, when there was a larger sample size, it appeared that the mean length of *A. coronus* at age 4 was significantly larger than that of *A. inodorus* at the same age. This may suggest that the growth rate of *A. coronus* is faster at least up to age 4.There was insufficient data to develop a biochronology for *A. coronus* in Namibia. However, the study by Pringle (2020), found that the aerobic scope for *A. coronus*, unlike *A. inodorus*, increased from 18℃ to 24℃, suggesting that the conditions for growth for the species may be improving in Namibia. Presently, it appears that the growth of *A. coronus* in Namibia is slow. *A. coronus* is believed to have similar life history traits such as a larger maximum size, a faster growth rate, and a similar size-at-maturity and age-at-maturity when compared to *A. regius*, *Totoaba macdonaldi* and the *A. japonicus* (South Africa) (Potts et al., 2010). The oldest species in this study was 9 years and had a total length of 46.5 cm. A study by Potts et al. (2010) in southern Angola showed that the mean length of *A. coronus* at 9 years of age was over 120 cm TL. This suggests that while the thermal regime is not suited for optimal growth, there is enormous potential for an increase in the growth rate of *A. coronus* in Namibia.

The hybridization between *A. inodorus* and *A. coronus* in the northern region of the northern Benguela seems to be in favour of the Namibian *Argyrosomus* spp. fishery because the genetics show that there is a possibility that the hybrids might have genetic material from both species that may result in the optimization of growth in the short-term. Potts et al. (2014a) described a positive aspect of the hybridization event by stating that rapid adaptation could potentially be promoted through the mixtures of genotypes that arise from hybridization after secondary contact between related species which are likely to enable evolution in response to the pressures from new environments (Stemshorn et al., 2011) and from climate change (Hoffmann & Sgro, 2011). Another positive aspect was made known by Pringle (2020), who showed that the physiological performance of the hybrids was high at the warmer (18-24℃) temperatures. In the present study, the hybrids tended to grow faster than *A. inodorus* during contemporary times and more similar to the historical period. Pringle et al. (2023) found that the physiological performance of the hybrids of *A. inodorus* and *A. coronus* were above average and concluded that hybridization may provide both species with additional genetic material for adaptation to the rapidly warming Namibian coastal environment. This may suggest that future studies that monitor the growth rate of the hybrids will be necessary to better assess their fitness and in so may be a mechanism to facilitate adaptation to the rapidly changing climate. It is important that researchers and managers understand the mean annual growth rate of hybrids in order to better assess their fitness and in so ensure that their adaptation to the rapidly changing SSTs are appropriately monitored.

Many studies have shown how climate change is expected to affect the distribution of marine species globally (e.g. Potts et al., 2014a, b; Assan et al., 2020). On the other hand, Roessig et al. (2004) stated that changing distribution of marine and estuarine fish stocks are also likely to affect harvesters who rely on them. This suggests that harvesters in Namibia from the recreational and commercial line-fishery, are likely to be negatively affected since this fishery relies on the currently already over-exploited *A. inodorus* stock as one of the major targeted linefish species (Kirchner, 1998), who are expected to do worse in warmer temperatures according to the present study. On the other hand, harvesters could also potentially benefit from a lucrative *A. coronus* fishery ("bigger in size kob") as future warming of SSTs could potentially allow for this species becoming more dominant (and abundant) along the rocky shores of Namibia (Potts et al., 2014a).

Izzo et al. (2016) highlighted that some species may pose environmental sensitivity with climate change and classified them into "sensitive" and "insensitive" species. The "sensitive" species are believed to be those who are likely to have a drastic change in their biological processes (e.g., growth) and their distributional range, while the "insensitive" species were described to be those who are likely to have a minor change in their biological processes by means of a slight shift in distribution when exposed to change in their environment (Izzo et al., 2016). It is therefore important that one understands climate-induced temperature effects on growth performance (Pörtner et al., 2001). For instance, Roessig et al. (2004) highlighted the importance of understanding the physiological responses of marine and estuarine fisheries under the current changing climate conditions, by way of contributing towards understanding the uncertainties related to the impacts that climate change will have on these species.

From the results of this present study and of Pringle (2020), *A. inodorus* growth seems to be directly temperature-driven. It is therefore evident that *A. inodorus* is a "sensitive" species, likely to experience a vulnerability to climate-induced environmental change or warming, which can alter their biological adaptations, and their distributional range (Huang et al., 2021). Results from Pringle (2020) indicate a likelihood that *A. coronus* could fall within the classification of an "insensitive" species as they fall within the descriptions given by Izzo et al. (2016).

The Benguela Niña and Benguela Niño usually occur along the Angola-Benguela area (southern Angola and northern Namibia) (Florenchie et al., 2004). The Benguela Niño according to Shannon et al. (1986), dates as far back as 1934 (Florenchie et al., 2004). During the early 1980s and 1990s as well as during the late 1990s these extremely cold and warm SST events were experienced along the Benguela region (Florenchie et al., 2004). Boyer and Hampton (2001) showed how the Benguela marine ecosystem was affected due to a southward shift of the sardine population after the extreme warm event of the 1995 Benguela Niño. In 2011 another Benguela Niño occurred which was caused by a reduction of the trade winds in the western equatorial Atlantic. This 2011 Benguela Niño had an interannual seasonal monthly SST anomaly which was 4°C larger than the previous major warm event in 1995, thus making the 2011 warm event (Benguela Niño) much warmer than the 1995 Benguela Niño (Rouault et al., 2018), and in so the warmest Benguela Niño for the purpose of this present study. These extreme coastal events (Benguela Niña and Benguela Niño) can last from a few months to half a year or more (Rouault, 2012; Koungue, 2018). Therefore, one can postulate that the below average growth of *A. inodorus* seen in the year 2014 and 2015 from this present study could be linked to the "after-effects" of the 2011 Benguela Niño as well as a "pre-effects" of the warm event that occurred in January and February of 2016, whereby sea surface temperature anomalies reached 3°C (Lübbecke et al., 2019). One should however also investigate other environmental parameters such as oxygen, wind, upwelling, chlorophyll a, etc. to try and understand what caused the below average mean annual growth in the above-mentioned years for *A. inodorus*. It is reported that SSTs can be 3°C higher (Benguela Niño) or lower (Benguela Niña) than the normal climate in the Angola-Benguela area during these extreme weather events (Koungue et al., 2021). With an increase in greenhouse gases in the atmosphere, it is expected that climate will continue warming in the 21st century (IPCC, 2014) which may cause impacts on fisheries, marine ecosystems (Koungue et al., 2021).

As one of the main targeted linefish species off the Namibian coast (Kirchner, 1998), the high fishing intensity exerted on the *A. inodorus* could bring dire consequences to the stock. For example, the fishing pressure on *A. coronus* in Namibia (which are believed to be mostly juveniles) could have a negative effect on the Angolan population (Potts et al. (2014a) since it is fished in Namibian waters under management regulations that are based on *A. inodorus* life history traits. Namibian regulations allow for recreational anglers to retain a daily bag limit of 10 fish per angler of which *Argyrosomus* spp. should be 40 cm TL and over. The regulations further limits anglers to obtain not more than 2 *Argyrosomus* spp. over the size of 70 cm TL in order to protect spawning stock (Kirchner & Beyer, 1999). These regulations might have seemed sensible for *A. inodorus* when they were introduced, however for *A. coronus* in Namibia it seems to be another case as it means they (*A. coronus*) are and have since the introduction of these regulations been fished before they reach maturity of which their size- and age-at-maturity is 87 cm TL at ages 4–5 years, respectively. This present study is therefore in agreement with other studies (i.e., Potts et al., 2014a; Pringle, 2020, etc.) that there is a need to revise the Namibian regulations specifically for *Argyrosomus* spp. to avoid the overfishing of *A. coronus* population in Namibian waters.

Faster growing fish tend to be more vulnerable to size- selective fishing because a fishery usually tends to select and remove larger fish from a population because of the many regulations placed on minimum size selection for harvesting in order to protect the juvenile resources (Biro & Post, 2008). In the long-run, if continually exploited, this could affect the genetic diversity of fish populations by reducing their resilience when confronted with climate change and variability (Biro & Post, 2008; Mudjirahayu et al., 2017). Results from the present study and that of Pringle (2020) could serve as an early indicator to show that *A. inodorus* resilience to high summer SSTs in the northern region of the northern Benguela might have changed given that the SSTs have considerably been increasing during the recent years. In short, this means that the capacity to withstand the rapid warming of this region could be decreasing for *A. inodorus* in the region; making them more vulnerable to exploitation due to the decrease in their resilience to the warm SSTs over time. It is therefore critical that there is a continuous monitoring of the growth and composition of *Argyrosomus* spp. found off Namibia, in order to manage the fishery as well as to understand the consequences of rapid ocean warming on coastal fish and fisheries.

The Namibian MFMR currently has a moratorium in place since 2008 on retaining *Argyrosomus* spp., *Lithognathus aureti* and *Dichistius capensis* for the linefish boats and commercial skiboats who usually caught large spawning fish in high quantities. Despite these measures in place, *Argyrosomus* spp. are still fished under recreational permits by recreational skiboats and anglers. The present study partly agrees with Pringle (2020)'s recommendation on the current regulations to remain as is (retain fish between 40-70 cm TL), provided that they are amended: The present study recommends that all fish above 70 cm TL be released, thus implementing a slot limit between 40 and 70 cm total length, to protect the maturing large adults from both *A. inodorus* and *A. coronus* populations. General catch-and-release guidelines would have to be followed in order to improve catch- and-release techniques in order to minimize the mortality of the fish post release. In this way the effort on the temperature "sensitive" *Argyrosomus* spp. fishery is controlled and large spawning fish for both are protected.

5.1 Conclusions and recommendations

In conclusion, this study was able to use genetic analysis to determine whether there was a hybrid of the two purebred species *Argyrosomus inodorus, A. coronus* in the sample for age determination and comparison. The study also validated the periodicity of translucent zone formation on the otoliths of *A. inodorous* using marginal increment analysis, even though the sample size was small for *A. coronus*.

As a first of its kind for one of Namibia's main coastal fish species, the study was able to correlate the mean annual growth rates of *A. inodorus* with sea surface temperature (SST) using Pearson correlation coefficient. The impact of thermal variability on *A. inodorus* growth was assessed and results demonstrated the significant role SSTs play on driving annual growth. Through examining their long-term (1990s to 2019) trends, the otolith biochronology showed how *A. inodorus* mean annual growth is negatively affected by both cold (<16°C) and warm (>17°C) temperatures. The results further give us an indication that there is a likelihood that *A. inodorus* growth rates will at one stage continue decreasing if temperatures continue warming in the northern region of the northern Benguela, which will in the end, lead to high mortality rates when exposed to increasing temperatures. It was also clear that *A. coronus* and *A. inodorus* are found concomitantly along the Namibian coast thus implying that both resources are important to sustain the Namibian line-fishery. Therefore, given that these two purebred *Argyrosomus* spp. exhibit different biological characteristics, it is important and recommended that their fisheries are managed separately.

It is further recommended that future otolith chronology studies for *A. inodorus* include the use of other environment parameters to see what effects they are likely to have on their mean annual growth rate. With a long-time series (±30 years) of environment data (oxygen index, upwelling index, ENSO index, chlorophyll-a, etc.) collected by the Namibian MFMR, this information can be easily incorporated into future otolith chronology studies which will in return be helpful towards fisheries scientists and managers in the region to further better understand how this species and similar species are likely to react to environmental shifts over time in response to ocean warming and exploitation.

The contemporary growth rates of *A. coronus, A. inodorus* and their hybrids (F1 and backcrosses) were compared using Likelihood-ratio chi-square tests. The results showed that there was a significant difference for the historical (1994-1996) and contemporary (2018-2019) period, thus indicating that *A. inodorus* stock used to grow older and faster in the historical period when compared to the contemporary.

Since there was not an adequate sample size for *A. coronus* from this present study, it is recommended that a proper growth study be done for *A. coronus* with a larger sample size as well as an otolith shape analysis method to distinguish between stocks. The sample size should be increased through collecting *A. coronus* samples throughout its entire distribution range during all seasons and over more than one calendar year as well as across its entire distribution range, including Angola for which permits were not available for the present study. An adequate sample size would help in understanding how *A. coronus* growth rate changes are affected by the current rapid increase in temperature and fishing or both in the northern Benguela. The findings of such a study would then contribute towards planning for a coherent exploitation of *A. coronus* and through doing so also effectively manage these species in the BCLME.

Despite the shortcomings of this study, which mainly included a small sample size for *A. coronus* and the hybrids of *A. inodorus* and *A. coronus*, there were key life-history information for Namibia's *Argyrosomus* spp. discovered. For instance, the marginal increment results showed that *A. inodorus* marginal increment forms in October which coincides with the onset of the Namibian *A. inodorus* spawning season. The results for *A. coronus* showed that the marginal increment forms in April, however another age and growth study using marginal increment analysis is recommended to confirm this with an increased sample size.

An otolith shape analysis study for *Argyrosomus* spp. based on the genetic results of the present study is also recommended as otolith shape analysis has proven to be a useful indicator of stock identity in fish as reported by Griffiths (1996b) and can thus assist with the first ever biological description of the hybrids. Ferguson et al. (2011) used two methods to investigate the stock structure of *A. japonicus* (Australia) and this can therefore serve as a guideline for a similar study to see how the hybrids differ from the purebred *Argyrosomus* spp.

All in all, this present study has filled gaps in knowledge on the biology and ecology of *Argyrosomus* spp. which now include the hybrids in order to contribute towards effective conservation and sustainable harvesting management for these species and similar species in the northern Benguela.

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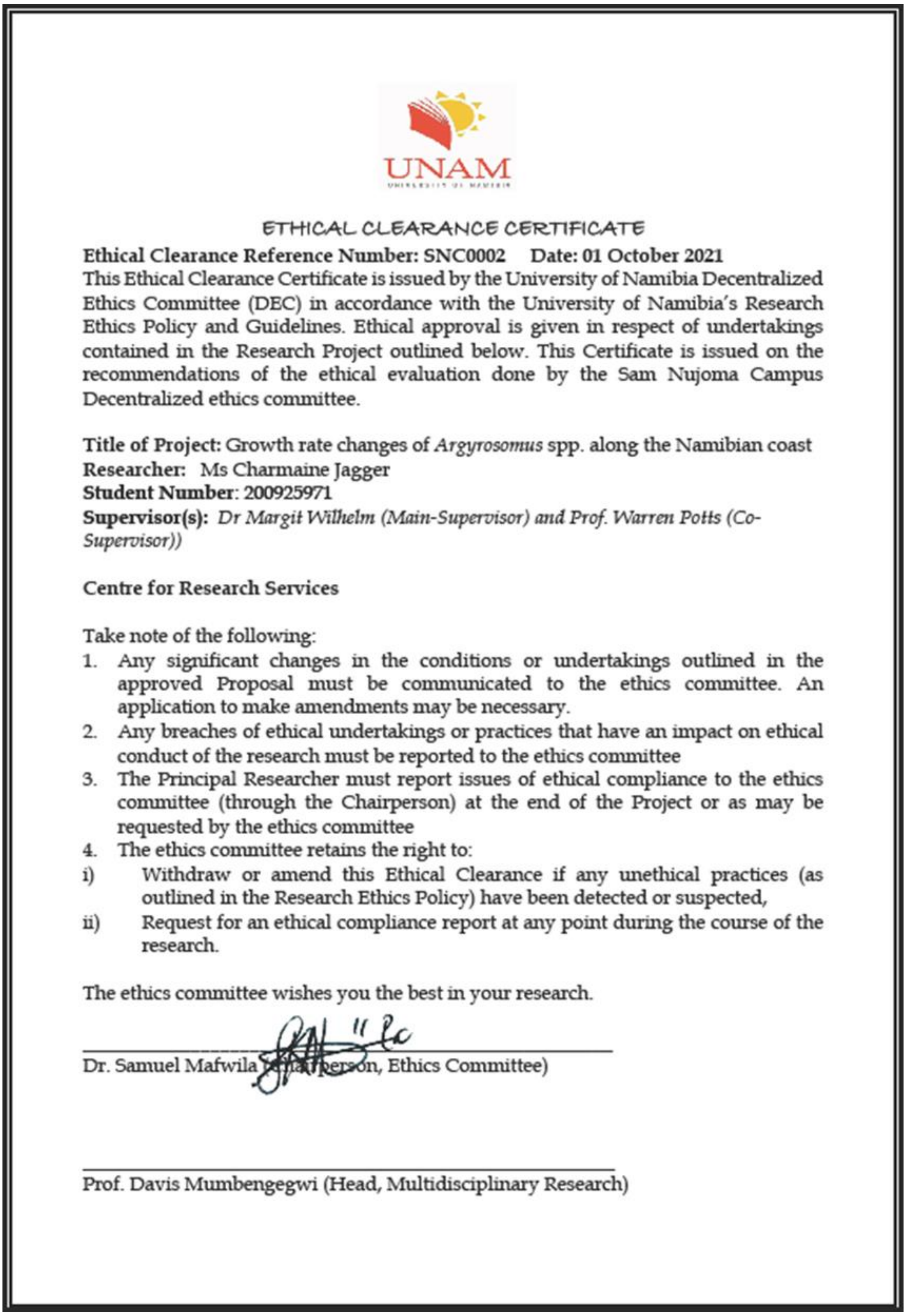
Appendices

Appendix A1: Ethical clearance certificate



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ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SNC0002 Date: 01 October 2021

This Ethical Clearance Certificate is issued by the University of Namibia Decentralized Ethics Committee (DEC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the Sam Nujoma Campus Decentralized ethics committee.

Title of Project: Growth rate changes of *Argyrosomus* spp. along the Namibian coast
Researcher: Ms Charmaine Jagger
Student Number: 200925971
Supervisor(s): *Dr Margit Wilhelm (Main-Supervisor) and Prof. Warren Potts (Co-Supervisor))*

Centre for Research Services

Take note of the following:

1. Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the ethics committee. An application to make amendments may be necessary.
2. Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the ethics committee
3. The Principal Researcher must report issues of ethical compliance to the ethics committee (through the Chairperson) at the end of the Project or as may be requested by the ethics committee
4. The ethics committee retains the right to:

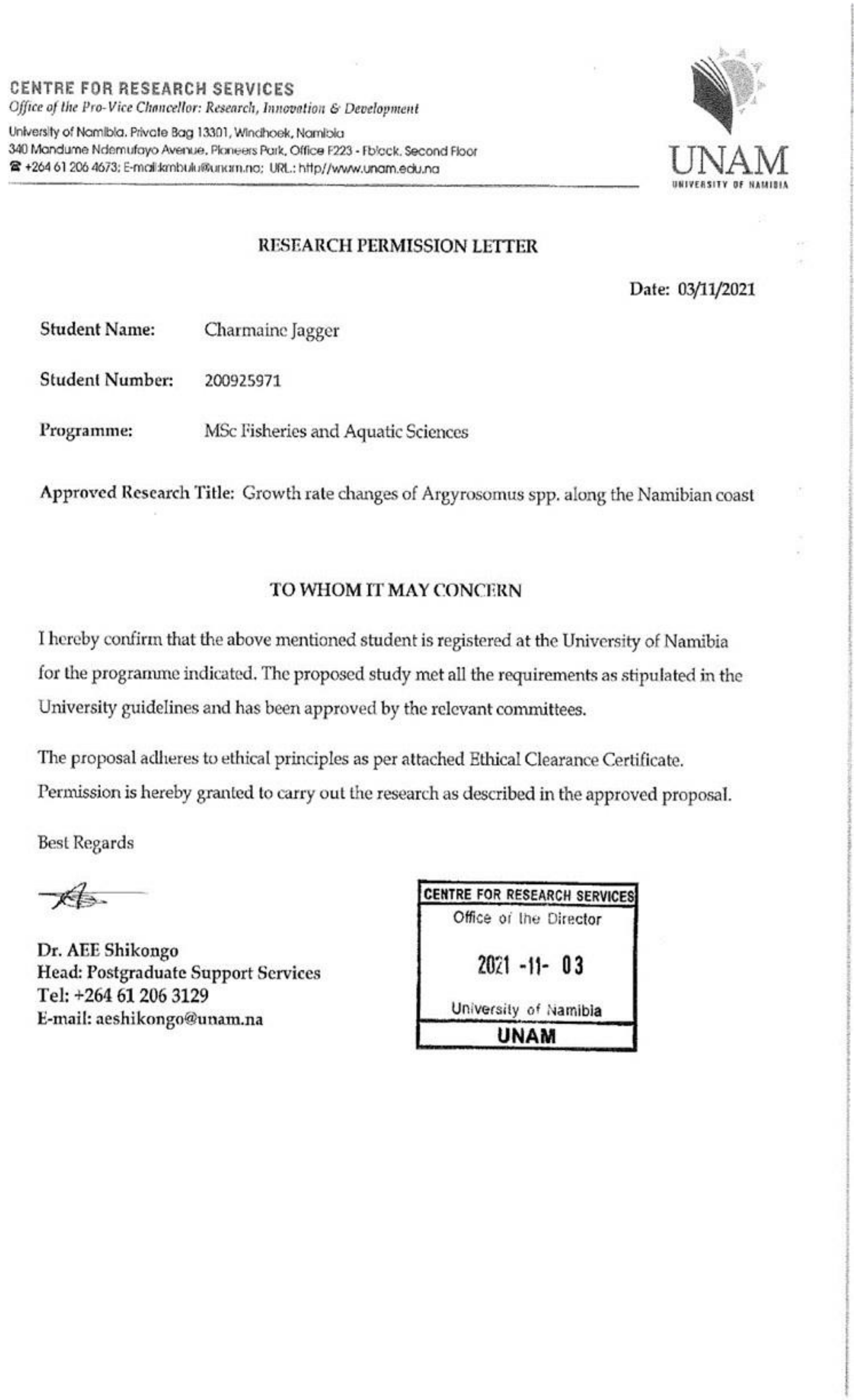
i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,
ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

____
Dr. Samuel Mafwila (Chairperson, Ethics Committee)

____
Prof. Davis Mumbengegwi (Head, Multidisciplinary Research)

Appendix A2: Research Permission letter



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RESEARCH PERMISSION LETTER

Date: 03/11/2021

Student Name: Charmaine Jagger

Student Number: 200925971

Programme: MSc Fisheries and Aquatic Sciences

Approved Research Title: Growth rate changes of Argyrosomus spp. along the Namibian coast

TO WHOM IT MAY CONCERN

I hereby confirm that the above mentioned student is registered at the University of Namibia for the programme indicated. The proposed study met all the requirements as stipulated in the University guidelines and has been approved by the relevant committees.

The proposal adheres to ethical principles as per attached Ethical Clearance Certificate. Permission is hereby granted to carry out the research as described in the approved proposal.

Best Regards

Dr. AEE Shikongo
Head: Postgraduate Support Services
Tel: +264 61 206 3129
E-mail: aeshikongo@unam.na

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2021 -11- 03
University of Namibia
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Appendix A3: Results of Likelihood-ratio chi-square test, χ^2 comparison between the contemporary Northern and Central Regions. Residual sum of square values were calculated by fitting the von Bertalanffy growth model to fish total length against age data of either the reduced (three parameters) or full model (6 parameters).

Comparison between North and Central regions *A.inodorus*			
	Residual sum of squares		
Northern area alone	6761.55	L1 (full model)	1018.12
Central area alone	3419.57		
North and Central area combined (reduced model)	10809.64 = Lo		
		χ^2	0.12
		$p>0.05$	

Lo = Likelihood (Residual sum of squares) of reduced model (Parameters = 3)

L1 = Likelihood (Residual sum of squares) of full model (Parameters = 6)

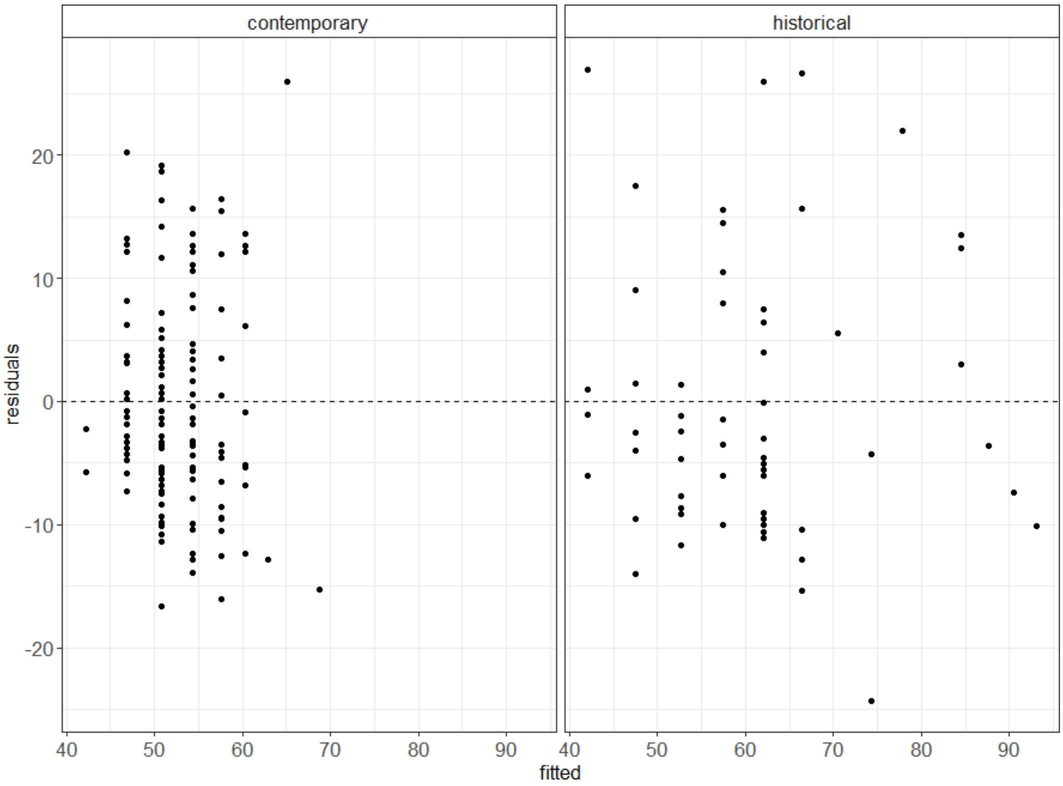
K (DF) = 3

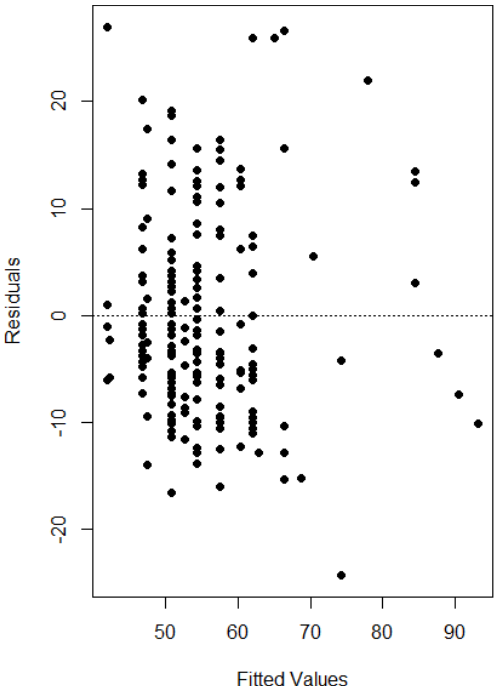
Critical χ^2, 0.05, 3 DF = 7.82

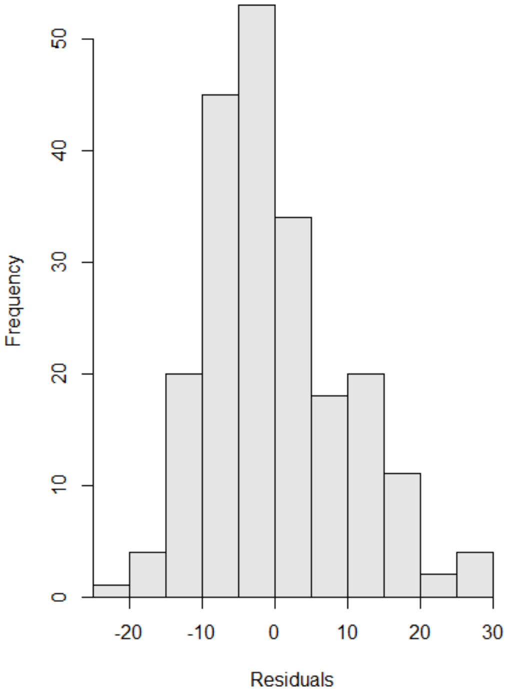
Ho: Full = Reduced

Accept H_0

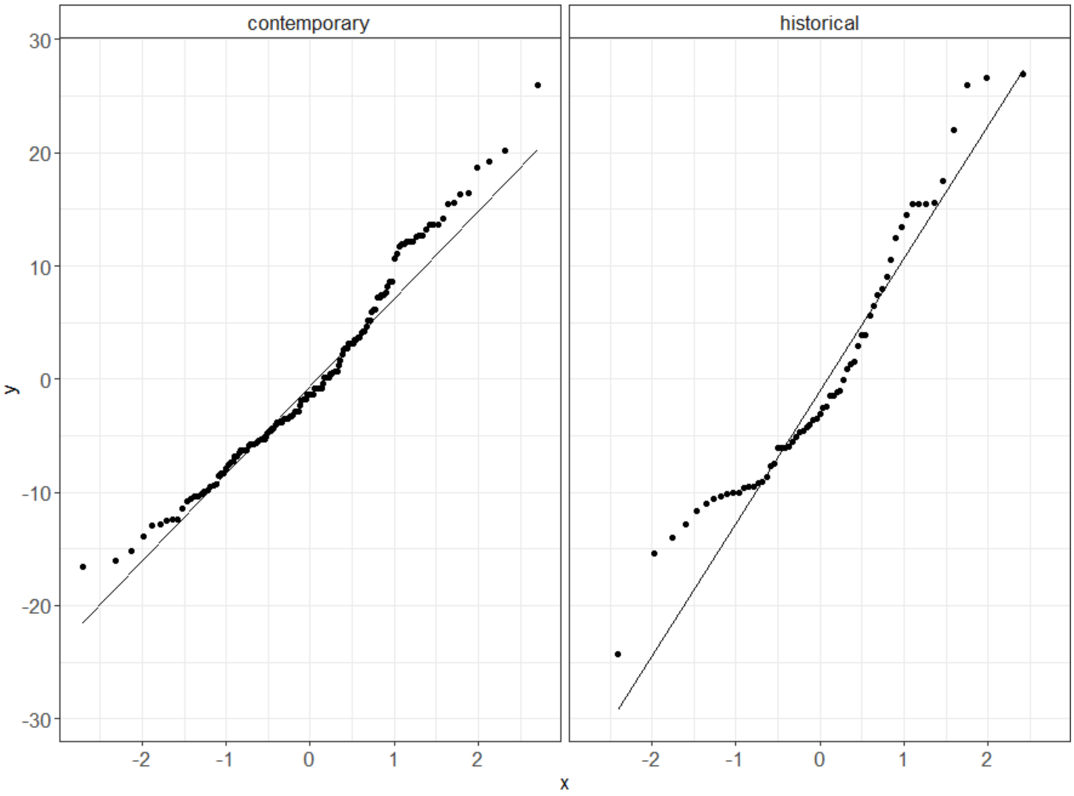
Appendix A4: Model diagnostics, fitted values vs. residuals, for the growth model fitted to the historical and contemporary ageing data for *A. inodorus*



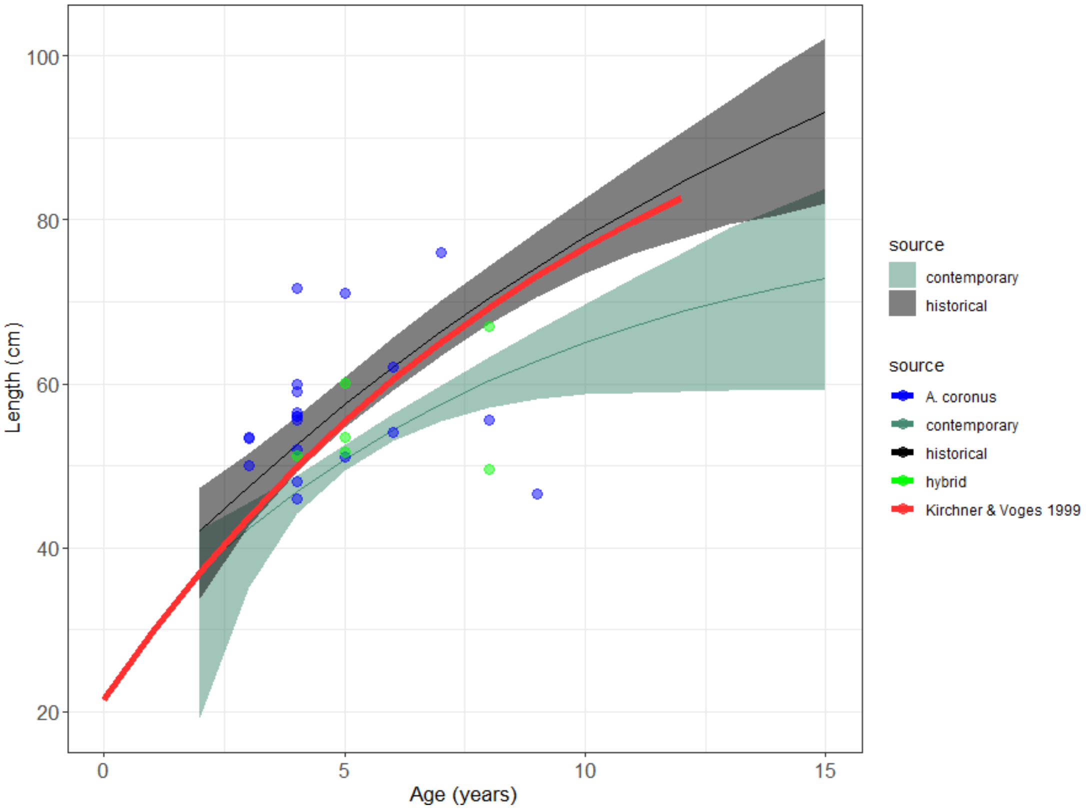




Appendix A5: Model diagnostics, quantile-quantile plots of residuals, for the growth model fitted to the historical and contemporary ageing data for *A. inodorus*



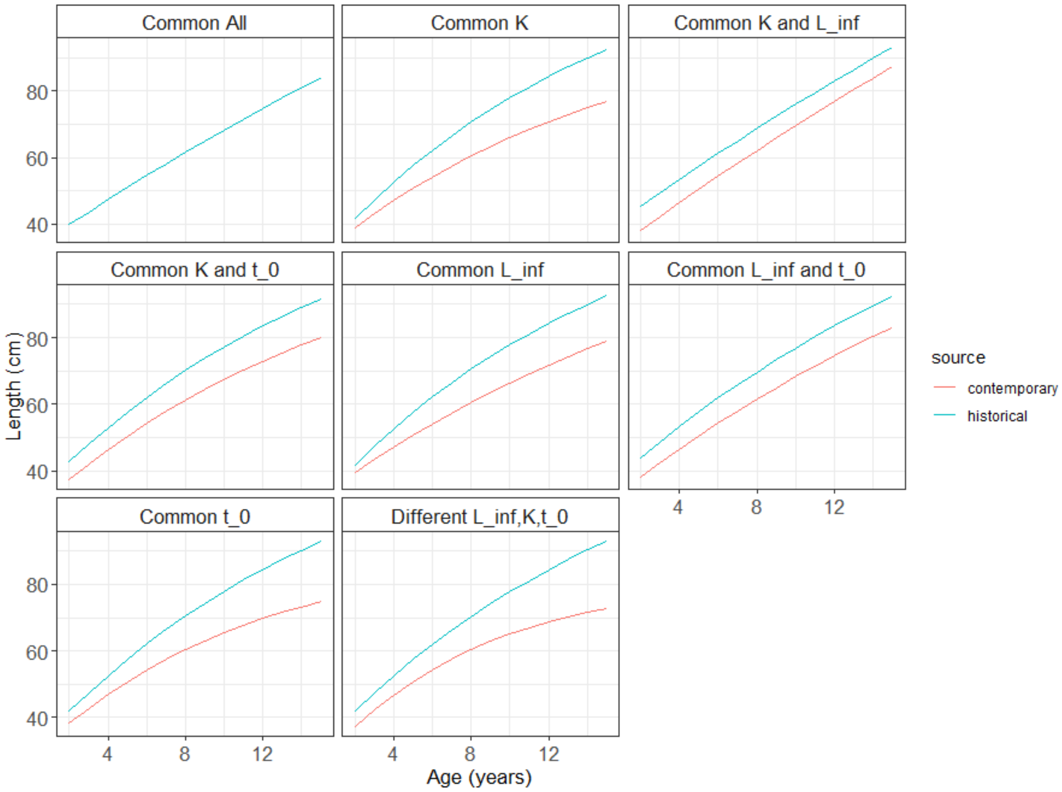
Appendix A6: Visual comparison of length against age data from *A. coronus* and the hybrid population to the fits of the growth model for *A. inodorus* from the historical and contemporary ageing data



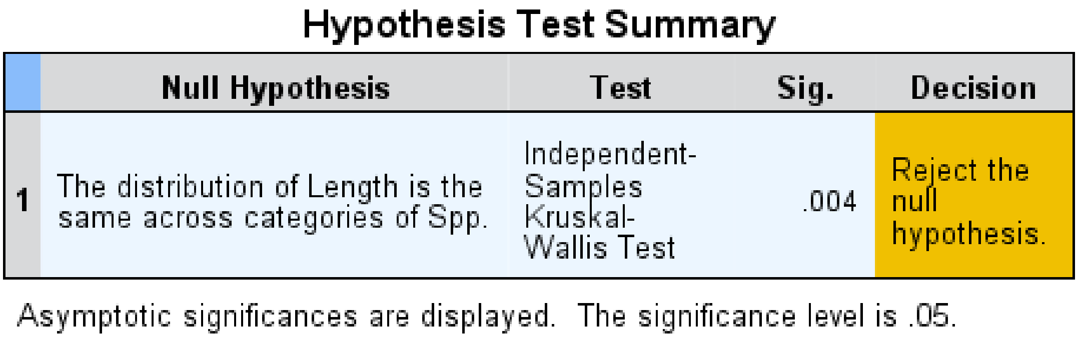
Appendix A7: Growth parameter estimates for historical (1994-1996) and contemporary (2018-2019) samples of *Argyrosomus inodorus* captured along the northern (SCNP, 17°14’S to 21°11’S) and central (Dorob National Park, 21°11’S to 23°19’S) regions along the Namibian coast. The column headings descriptions are as follows: source (refers to the period either contemporary or historical); term (the Von Bertalanffy parameters); estimate (the estimate values of the Von Bertalanffy parameters from the model); std.error (is the standard error which is a measure of the statistical accuracy of an estimate); statistic (t. value); p.value (number, calculated from a statistical test, that describes how likely you are to have found a particular set of observations if the null hypothesis were true); low_CI (lower confidence interval) and up_CI (upper confidence interval).

Source	**Term**	**Estimate**	**std.error**	**statistic**	**p.value**	**low_CI**	**up_CI**
Contemporary	L_∞	82.37	39.115	2.106	0.0364	60.199	151.371
	K	0.12	0.167	0.718	0.4733	0.037	0.495
	t_0	-3.01	4.831	-0.623	0.534	-7.479	1.224
Historical	L_∞	138.04	63.022	2.19	0.0296	85.541	434.175
	K	0.05842	0.052	1.23	0.2626	0.011	0.19
	t_0	-4.22	2.667	-1.582	0.1151	-9.152	-0.696

<u>Appendix A8:</u> The fits of the different configuration of the multiple Von Bertalanffy growth models *Argyrosomus inodorus*, fitted to historical and contemporary age-length data



Appendix A9: Kruskal-Wallis test results (Age 4)



Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Length is the same across categories of Spp.	Independent-Samples Kruskal-Wallis Test	.004	Reject the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

Test Statistics[a,b]

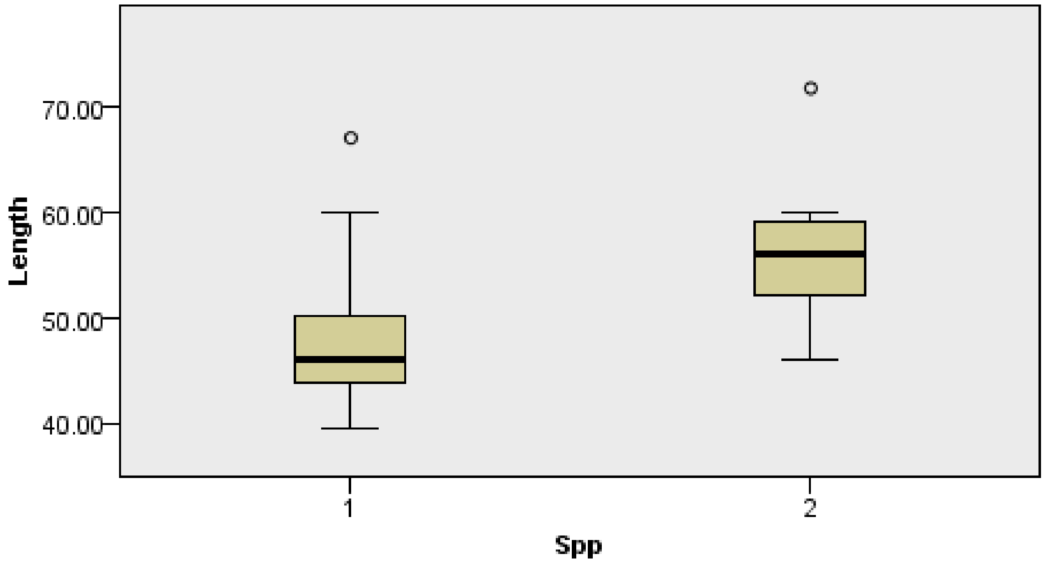
Length

Kruskal-Wallis H	8.264
df	1
Asymp. Sig.	.004

a. Kruskal Wallis Test

b. Grouping Variable: S

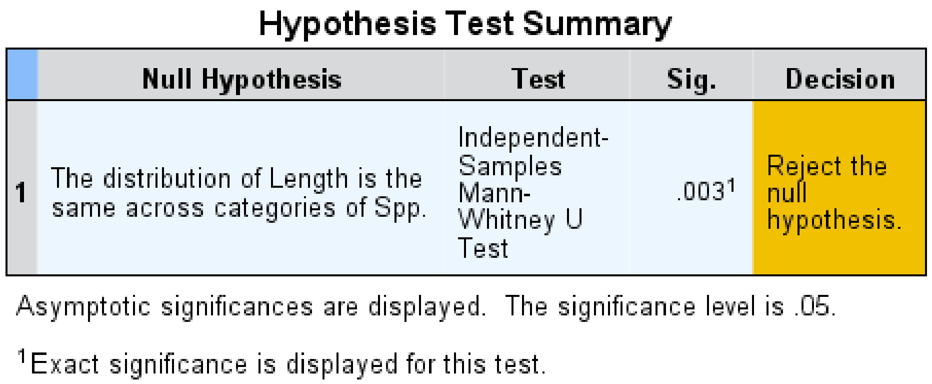
Independent-Samples Kruskal-Wallis Test



Total N	37
Test Statistic	8.264
Degrees of Freedom	1
Asymptotic Sig. (2-sided test)	.004

1. The test statistic is adjusted for ties.
2. Multiple comparisons are not performed because there are less than three test fields.

Appendix A10: Mann- Whitney U test results (Age 4)



Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Length is the same across categories of Spp.	Independent-Samples Mann-Whitney U Test	.003[1]	Reject the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

[1] Exact significance is displayed for this test.

Appendix A11: Absolute increment width against age of formation for all otoliths of all individual otoliths of *A. inodorus* caught off Namibia from 1994-1996 and 2018-2019