ASSESSMENT OF CLIMATE CHANGE AND FISHERIES EFFECTS ON SARDINE (*SARDINOPS SAGAX*) AND CAPE HORSE MACKEREL (*TRACHURUS CAPENSIS*) OTOLITH GROWTH RATES IN THE BENGUELA

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GENERAL ABSTRACT

Assessing how fish populations reacted to previous environmental changes is valuable for predicting their future behaviours. However, this process is often constrained by the limited availability of long-term biological data. Two sardine (*Sardinops sagax*) stocks are found in Namibia (northern Benguela) and South Africa (southern Benguela). Sardine in the northern and southern Benguela has shown substantial changes in population size over the past 70 years. Heavy fishing pressure in the 1950s to early 1970s caused the collapse of South Africa's and Namibian sardine stocks. A fishery collapse happens due to significant alterations in the marine community, hindering the recovery of valuable commercial species and leading to cascading effects across multiple trophic levels in marine food webs. Despite a fishing moratorium since 2018 in Namibia, the population has shown no signs of recovery as of 2024. Cape horse mackerel (*Trachurus capensis*) is the most abundant commercial fish species in Namibia and has been heavily exploited since the early 1970s.

The overall objective of the study was to understand how growth rates of sardine (*Sardinops sagax*) and Cape horse mackerel (*Trachurus capensis*) are affected by environmental variability, long-term environmental changes and human exploitation within the Benguela region. Otolith increment widths, indicating alterations in fish growth, were analysed using linear mixed models to explore intrinsic (within individual) and extrinsic (fish biomass, sea surface temperature, upwelling, prey availability) factors contributing to variations in fish growth with the assumption that otolith increment growth is a proxy for somatic growth. In this study, three otolith biochronologies were developed using archived sardine otoliths: a 48-year biochronology (1974-2021) for sardine of northern Benguela, a 58-year sardine biochronology (1962-2019) for sardine of southern Benguela, and a 50-year Cape horse mackerel biochronology of northern Benguela. The predicted sardine biochronology in northern Benguela displayed short-term fluctuations but no significant change in patterns, due to the absence of otolith data from before the population collapse in the late 1960s. The predicted annual growth of sardine in the northern Benguela significantly correlated negatively with SST in spring, and positively correlated significantly with upwelling in summer.

Sequential t-test analysis of regime shifts (STARS) performed on the biochronology of sardine growth in the southern Benguela that indicated four regimes with three alteration points in 1986, 2006, and 2015 that correspond with periods of low, high, average and low biomass, respectively; i.e. high growth rates occurred during the high biomass period and vice versa. A series of mixed effects models was developed to determine increment width response to selected environmental, prey availability and sardine biomass factors with the assumption that otolith increment growth is a proxy for somatic growth. Predicted sardine growth positively correlated with sardine biomass, sea surface temperature and zooplankton abundance in the southern Benguela. This observation suggests that sardine population dynamics exhibit a depensation mechanism, potentially destabilizing populations after the fishery collapse in the southern Benguela. Depensatory population dynamics have caused sea surface temperature and zooplankton abundance primary factors influencing sardine growth in the southern Benguela.

The absence of otolith data from before the population collapse in the late 1960s meant that the analysis of predicted annual sardine otolith growth post-collapse showed short-term fluctuations but no significant long-term growth rate changes for sardine in the northern Benguela. Predicted annual sardine growth was significantly negatively linked with SST in Austral spring, and positively linked with upwelling in summer for the area 17-20 ºS (northern Namibia). The results suggest environmental conditions play a dominant role in driving sardine growth, exacerbated by the extremely low sardine biomass, which may be indicative of depensation in northern Benguela. Sequential t-test analysis of regime shifts (STARS) performed on the Cape horse mackerel biochronology of fish growth indicated three regimes with two alteration points in 1980 and 1990 for Cape horse mackerel. Otolith biochronologies revealed decadal variability that indicated rapid regime shifts in the southern and northern Benguela marine ecosystem. Therefore, integrating otolith chronologies provides a broader understanding of how fish respond to environmental changes. The utilization of preserved otoliths in this study enabled the analysis to identify prolonged shifts in sardine growth, which are influenced by a range of biological and physical factors.

Key words: Otolith biochronology, *Sardinops sagax*, *Trachurus capensis*, Benguela ecosystem, regime shift.

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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
DFFE	Department of Fisheries, Forestry, and Environment (South Africa)
EBUS	Eastern Boundary Upwelling Systems
ENSO	El Niño-Southern Oscillation
ICOADS	International Comprehensive Ocean–Atmosphere Dataset
IOW	Leibniz Institute for Baltic Sea Research Warnemünde
ITCZ	Intertropical Convergence Zone
MEIv2	Multivariate ENSO index MEI version 2
MFMR	Ministry of Fisheries and Marine Resources (Namibia)
nBUS	northern Benguela upwelling sub-system
NCEP	European Centre for Medium-Range Weather Forecasts ERA5
NOAA	National Centre for Environmental Prediction
SLP	Sea level pressure
SOI	Southern Oscillation Index
SST	Sea surface temperature
TRIATLAS	Tropical and South Atlantic Climate-Based Marine Ecosystem Prediction for Sustainable Management
VBGF	Von Bertalanffy growth function

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DEDICATION

This dissertation is devoted to my grandmothers, Nancy Brinkman and Elizabeth “Ellie” Brinkman, and to my beloved mother, Jackie Brinkman. Your unwavering love, wisdom, and support have been the foundation of my life, especially in my educational journey. I owe who I am to your influence. With deepest gratitude, I dedicate this work to honor all you have done for me. I am forever grateful to have had you as my grandmothers and to continue being blessed by your love, Mom.

"When he had finished speaking, he said to Simon, 'Put out into deep water, and let down the nets for a catch.' Simon answered, 'Master, we’ve worked hard all night and haven’t caught anything. But because you say so, I will let down the nets.' When they had done so, they caught such a large number of fish that their nets began to break… Then Jesus said to Simon, 'Don’t be afraid; from now on you will fish for people.'"

— Luke 5:4–10 (NIV)

DECLARATION

I, **Faye R.V Brinkman**, 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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Faye Rachel Volente Brinkman	Signature	Date

Research Ethics Statement

The present study utilised research data derived from archived otolith samples, as well as biological and commercial catch records pertaining to the Benguela region, encompassing Namibia and South Africa. This information was employed to generate primary data on Cape horse mackerel (*Trachurus capensis*) and sardine (*Sardinops sagax*). The otolith samples were obtained through annual scientific research surveys and from commercial fishing vessels, both of which operate under the legal frameworks established by the Marine Resources Act No. 27 of 2000 (Republic of Namibia) and the Marine Living Resources Act No. 18 of 1998 (Republic of South Africa). These legislative instruments govern the harvesting, movement, and transfer of marine species across territorial waters and jurisdictions. The research was conducted in collaboration with the University of Namibia, the Namibian government, and the South African government under the auspices of the Triatlas Project. Permission to access and utilize the archived otoliths was formally granted by the relevant governmental authorities in both Namibia and South Africa (see Appendix A). Ethical approval for the study was obtained from the University of Namibia's Decentralized Ethics Committee (DEC), under the clearance reference number SNC DEC 0001/03/2023 (Appendix A). Additionally, research authorization was provided by the University of Namibia's Centre for Research Studies (Appendix A).

CHAPTER ONE: INTRODUCTION

1.1 General Introduction

The Earth's climate has undergone unprecedented warming in recent history, and there is now undeniable evidence of human-induced contributions over the past 200 years (Intergovernmental Panel on Climate Change 2014). Global warming has led to numerous effects across all regions of the world, especially in eastern boundary upwelling system (EBUS) areas, which are regarded as some of the most susceptible to climate change. (Bakun et al. 2015; Sydeman et al. 2014; Wang et al. 2015). In the EBUS, upwelling events draw nutrient-rich cold water from the deep ocean to the surface, creating vital habitats that support marine biodiversity (Fréon et al. 2009). Therefore, although they represent only 2% of the global ocean surface, the EBUSs are among the most productive ocean ecosystems and have a strong economic impact through increased fish stocks (Fréon et al. 2009).

In addition to the impact of climate change, in the last decade, there has been growing interest in the possible evolutionary impacts of fishing on growth rates (Enberg et al. 2012). According to Enberg et al. (2012), fishing can selectively remove fast or slow growers from a population, but it also influences the growth of the remaining fish through modifications to density-dependent processes (Lorenzen and Enberg 2002), habitat (Rooper et al. 2011), or food webs (Audzijonyte et al. 2013). Several studies have made use of dendrochronological methods to demonstrate the diverse relationships between fish growth and external drivers and provide quantifiable reasons for year-to-year variability or long-term trends in growth, Bayesian techniques, and regime shifts (Ong et al. 2016; Helser et al. 2012; Smoliński and Mirny 2017). The study of fish growth is able to examine the impacts of fishing and environmental variability on population abundance because it is the phenotypic manifestation of the relationship between the individual (intrinsic) and the environmental or ecological (extrinsic) components that influences the acquisition and allocation of resources (Enberg et al. 2012)

1.2 Statement of the problem

Populations of small pelagic fish, such as sardine (*Sardinops sagax*) and Cape horse mackerel (*Trachurus capensis*), are highly sensitive to both anthropogenic pressures and environmental variability. The Benguela Current system, recognised as one of the world's most productive coastal upwelling regions, has experienced significant impacts on fish population dynamics due to historical fishing pressure, climate variability and climate change. Over the past 70 years, the sardine stocks in both Namibia and South Africa have experienced dramatic fluctuations in abundance, with stock collapses occurring in both countries between the 1950s and early 1970s due to excessive fishing pressure. These collapses triggered significant changes in marine community structure, impeding the recovery of sardine populations and altering trophic interactions across the ecosystem. Despite a fishing moratorium in Namibia since 2018, sardine populations have not shown signs of recovery as of 2024, indicating the potential influence of additional environmental or ecological constraints. Cape horse mackerel, currently the most abundant commercial species in Namibia, has also been heavily exploited since the early 1970s. However, the combined and potentially interacting effects of long-term fishing pressure and environmental change on the growth and productivity of these small pelagic species remain poorly understood. This knowledge gap is exacerbated by the limited availability of long-term biological datasets in the region (Morrongiello et al. 2012), and the scarcity of studies that integrate fishing and climate effects across different biological scales, particularly at the population, between-individual, and within-individual levels (Morrongiello et al. 2019).

Understanding how fish populations responded to historical environmental fluctuations is critical for predicting their future responses under on-going climate change. However, identifying causal relationships is difficult due to the complexity of fish responses across ecological levels (Parmesan et al. 2011) and the lack of detailed, long-term studies on key species in the Benguela ecosystem (Morrongiello and Thresher 2015).

Otolith-based biochronologies offer a powerful approach for overcoming these limitations. Otoliths provide continuous, individual-level records of somatic growth and can be used as proxies for environmental conditions and resource allocation over time (Morrongiello and Thresher 2015; Reynolds et al. 2017). These techniques have been successfully applied across multiple species and regions to reconstruct historical climate impacts (e.g., Black et al. 2005; Morrongiello et al. 2014; Izzo et al. 2016; Smoliński and Mirny 2017; Martino et al. 2019; Tanner et al. 2019; Vieira et al. 2020; Wilhelm et al. 2020) and to detect growth responses to rapid ecosystem changes (Smoliński and Mirny 2017) or forecast future growth under environmental scenarios (Rountrey et al. 2014). Despite the proven utility of otolith chronologies, no long-term growth studies have yet been conducted for sardine or Cape horse mackerel in the Benguela region. Furthermore, the role of environmental drivers and fishing pressure in shaping growth dynamics over time in these populations remains unexplored. This represents a critical gap in understanding the phenotypic responses and population-level consequences of environmental and anthropogenic change in one of the world’s most dynamic marine systems.

Therefore, the present study seeks to quantify long-term trends in the growth of sardine (*Sardinops sagax*) — in both northern and southern Benguela (Namibian and South African waters) — and Cape horse mackerel (*Trachurus capensis*) in the northern Benguela (Namibian waters), using otolith-based growth chronologies. By integrating long-term biological data with environmental and fisheries time series, this study aims to assess how growth variability reflects the interaction between intrinsic factors and extrinsic drivers, thereby providing insight into the population dynamics and resilience of small pelagic fishes under historical and future climate conditions (Enberg et al. 2012; Denechaud 2021).

1.3 Objectives

The overall objective of the study was to understand how growth rates of sardine (*Sardinops sagax*) and Cape horse mackerel (*Trachurus capensis*) are affected by environmental variability, long-term environmental changes and human exploitation within the Benguela region. More specifically the study objectives are discussed in the below paragraphs for each chapter.

(1) Long-term growth rates of sardine in the southern Benguela (South Africa) (Chapter 3)
   (a) To develop a multi-decadal biochronology of sardine during 1962 – 2019 to characterise long-term variability of the sardine population average growth in the southern Benguela (South Africa).
   (b) To determine if there has been any abrupt alteration in the annual otolith growth patterns that may be linked to the ecosystem regime shift.
   (c) To investigate the effects of sardine biomass on the sardine growth patterns during the study period.
   (d) To investigate the effects of environmental (SST and upwelling index) and biological (copepod abundance) variables on sardine growth patterns during the study period.

(2) Long-term growth rates of sardine in the northern Benguela (Namibia) (Chapter 4)

(a) To develop a sardine otolith biochronology for the northern Benguela (Namibia), to evaluate intrinsic (between-individual and within-individual) and extrinsic (environmental) factors that may influence the growth of sardine.

(b) To determine if there has been any abrupt alteration in the annual otolith growth patterns that may be linked to the ecosystem regime shift.

(c) To investigate the effects of sardine biomass on the sardine growth patterns during the study period.

(d) To investigate the effects of environmental (SST and upwelling index) and biological (copepod abundance) variables on sardine growth patterns during the study period.

(e) To perform a cross-wavelet coherence analysis to examine changes in sardine growth patterns and their relationships with environmental time series, exploring these dynamics across time, frequency, and spatial domains.

(3) Long-term growth rates of Cape horse mackerel in the northern Benguela (Namibia) (Chapter 5)

(a) To develop a Cape horse mackerel otolith biochronology for the northern Benguela (Namibia), to evaluate intrinsic (between-individual and within-individual) and extrinsic (environmental) factors that may influence the growth of sardine.

(b) To determine if there has been any abrupt alteration in the annual otolith growth patterns that may be linked to the ecosystem regime shift.

(c) To investigate the effects of Cape horse mackerel biomass (based on survey and stock assessment estimates) on the Cape horse mackerel growth patterns during the study period.

(d) To investigate the effects of environmental (SST and upwelling index) and biological (copepod abundance) variables on Cape horse mackerel growth patterns during the study period.

1.4 Hypotheses of the study

The hypotheses of the study based on the objectives for each chapter were the following:

(a) H_0: Annual otolith growth patterns of sardine and Cape horse mackerel in the Benguela remained constant each year without shifts in growth throughout the sardine and Cape horse mackerel otolith biochronology.

H_1: There was a significant variability by year or shift or change in annual otolith growth patterns over time of sardine and Cape horse mackerel biochronology in the Benguela.

(b) H_0: Population biomass does not significantly affect sardine or Cape horse mackerel annual growth patterns in the Benguela.

H_1: Population biomass significantly affects the annual growth patterns of sardine and Cape horse mackerel in the Benguela.

(c) H_0: Environmental variables (sea surface temperature and upwelling intensity) and biological variable (copepod abundance) do not significantly affect sardine or Cape horse mackerel annual growth patterns in the Benguela.

H_1: Environmental variables (sea surface temperature and upwelling intensity) and biological variable (copepod abundance) significantly affect sardine and Cape horse mackerel annual growth patterns in the Benguela.

1.5 Significance of the study

The study contributed towards improved knowledge of Cape horse mackerel and sardine growth responses to climate change and population size fluctuations with regard to environmental changes and fishing in the Benguela. Moreover, the study strengthened regional national and international institutional collaboration with the partners of TRIATLAS (South and Tropical Atlantic - climate-based marine ecosystem prediction for sustainable management), Ministry of Fisheries and Marine Resources (MFMR), University of Cape Town (UCT), South African Department of Forestry, Fisheries and Environment (DFFE), Polish Research Institute, and UNAM on mutual beneficial agreements towards improving an ecosystem approach to fisheries management in light of climate change. The utilisation of preserved otoliths in this study enabled the analysis to identify prolonged shifts in sardine and Cape horse mackerel growth, which are influenced by a range of biological and physical factors. Otolith biochronologies revealed decadal variability that indicated rapid regime shifts in the Benguela marine ecosystem. The integration of environmental factors driving interannual growth rate variability, which are frequently overlooked in stock assessment, could enhance the accuracy of predicting sardine stock dynamics (e.g. Denechaud et al. 2020; Smoliński 2019). For instance, the annual sardine and Cape horse mackerel growth anomalies can be used as a forcing function of sardine productivity in the Benguela Ecosystem (Ecosim) model or annual sardine and Cape horse mackerel growth variation could be incorporated into fisheries stock assessment models to improve estimation or management performance. This insight can be integrated into overarching management strategies to enhance their effectiveness, as highlighted by studies (Izzo et al. 2016; van der Sleen et al. 2018).

CHAPTER TWO: LITERATURE REVIEW

Globally, climate change is responsible for increased ocean temperature, increased or decreased wind stress, more extensive low-oxygen zones, increased stratification and changes in nutrient availability (e.g. Moloney et al. 2013; Poloczanska et al. 2016). These changes have been compounded by the intense fishing pressure in the Benguela region since the 1960s. (Jarre et al. 2015). Climate change is a major global force affecting marine ecosystems, and its influence on marine biodiversity (e.g., species abundance and distribution) is expected to intensify over time. However, the severity of these impacts, such as on the growth rates of individuals, will vary by location, depending on regional oceanic conditions and the vulnerability of species in specific areas (e.g. Roessig et al. 2004; Harley et al. 2006; Cheung et al. 2009; Lockerbie and Shannon 2019). However, the severity of these impacts will vary depending on the geographical location, influenced by oceanic conditions and the vulnerability of species in specific regions (Lockerbie and Shannon 2019). The Benguela Upwelling System, with its highly productive ecosystems, is characterised by the equatorward Benguela Current, vigorous shelf-edge jets and several distinct upwelling cells, which undergo large seasonal to decadal variability (e.g. Bordbar et al. 2021; Brandt et al. 2024).

The study aims to concentrate on the key commercial pelagic fish species in the Benguela region, specifically sardine in the northern and southern Benguela (Namibia and South Africa), and Cape horse mackerel in northern Benguela (Namibia). The South African and Namibian stocks of sardine as well as the Cape horse mackerel stock in Namibia experienced heavy fishing pressure, with the changes in the environment having an additional impact on their population somatic growth rates, productivity and population sizes (e.g. Boyer et al. 2001; Kirchner et al. 2010). The depletion of key resources in the Benguela ecosystem due to commercial fishing has amplified the effects on population dynamics, resulting in significant declines in the abundance and distribution of fish populations, a form of "top-down" regulation (Hampton 2012). Indirectly, this exploitation has disrupted the broader ecosystem by altering the structure and function of the food web (Hampton 2012; Heymans and Tomczak 2016). The collapse of sardine, an important forage species, has been linked to documented ecosystem impacts, including food shortages for dependent predators like seabirds and seals (Jarre et al. 2015). Cape horse mackerel plays a pivotal role in the marine food web especially after the decline in sardine populations in the northern Benguela compelled predators to search for other food sources (Mecenero et al. 2006, Mecenero et al. 2007; Mwaala et al. 2023). Shannon et al. (2010) emphasized, through the use of various ecosystem indicators across demersal and pelagic communities that despite the recognized impacts of fishing, changes in food webs within upwelling systems cannot be fully understood without thoroughly accounting for environmental drivers. Verheye (2000) found that decadal-scale (multi-decade) changes in the lower trophic levels in the southern Benguela were linked to a long-term increase in wind stress. This suggests that stronger winds, which enhance ocean upwelling and nutrient availability, likely drove these changes. Verheye (2000) also observed a long-term increase in zooplankton biomass after commercial fishing began in the early 1950s. These examples provide support for bottom-up control in small pelagic species, which influence their growth, reproduction, and survival.

2.2 The biophysical features of the BCLME and its decadal changes due to climate

The Benguela Current Large Marine Ecosystem (BCLME), characterized by coastal upwelling and belonging to the group of four extensive marine systems with eastern boundary currents, stands as a highly productive area (Figure 2.1). It supports crucial fisheries for the three coastal nations – Angola, Namibia, and South Africa (Jarre et al. 2015). One of the major forces driving dynamics in the BCLME is climate, rendering the system prone to alterations and heightened variability following shifts and increased fluctuations in the global climate (Hampton and Willemse 2012). The physical environment of the BCLME is influenced by extensive features at the basin scale during austral summer. These include the tropical waters from the South Atlantic and Indian Oceans (influenced by atmospheric teleconnections), the position of the intertropical convergence zone (ITCZ), the strength and location of the South Atlantic and South Indian Ocean High Pressure Systems, and fluctuations in the Agulhas Current. (Hutchings et al. 2009). Significant contributors to variability include the tropical Atlantic, the El Niño-Southern Oscillation (ENSO) signal, the Indian Ocean Dipole Zonal Mode (southern Benguela), and deviations in sea surface temperature (SST) within the Indian Ocean (southern Benguela) (Reason et al. 2006). These factors collectively influence both the intensity and positioning of frontal regions that demarcate subsystems within the Benguela. Additionally, they play a role in regulating the upwelling intensity, thereby affecting sea surface temperatures (SSTs) in the shelf zones of the three countries (Reason et al. 2006). During winter, the latitudinal fluctuations of the westerly wind belt to the south of the continent, along with interactions between the Intertropical Convergence Zone (ITCZ) and the Hadley Cells spanning the Tropics and Subtropics, impact the strength and location of the anticyclones. This, in turn, influences the variability of westerly winds in the southernmost region of the Benguela (Reason et al. 2006). Moreover, wind patterns at a regional scale are influenced by the pressure gradient between the high-pressure systems over the ocean and the low pressure over the continent. This modulation is further influenced by the eastward movement of cyclones within the westerly wind belt at 30–40°S, as highlighted by Nelson and Hutchings in 1983. These cyclones have the potential to impact patterns as far north as 25°S (Jarre et al. 2015).

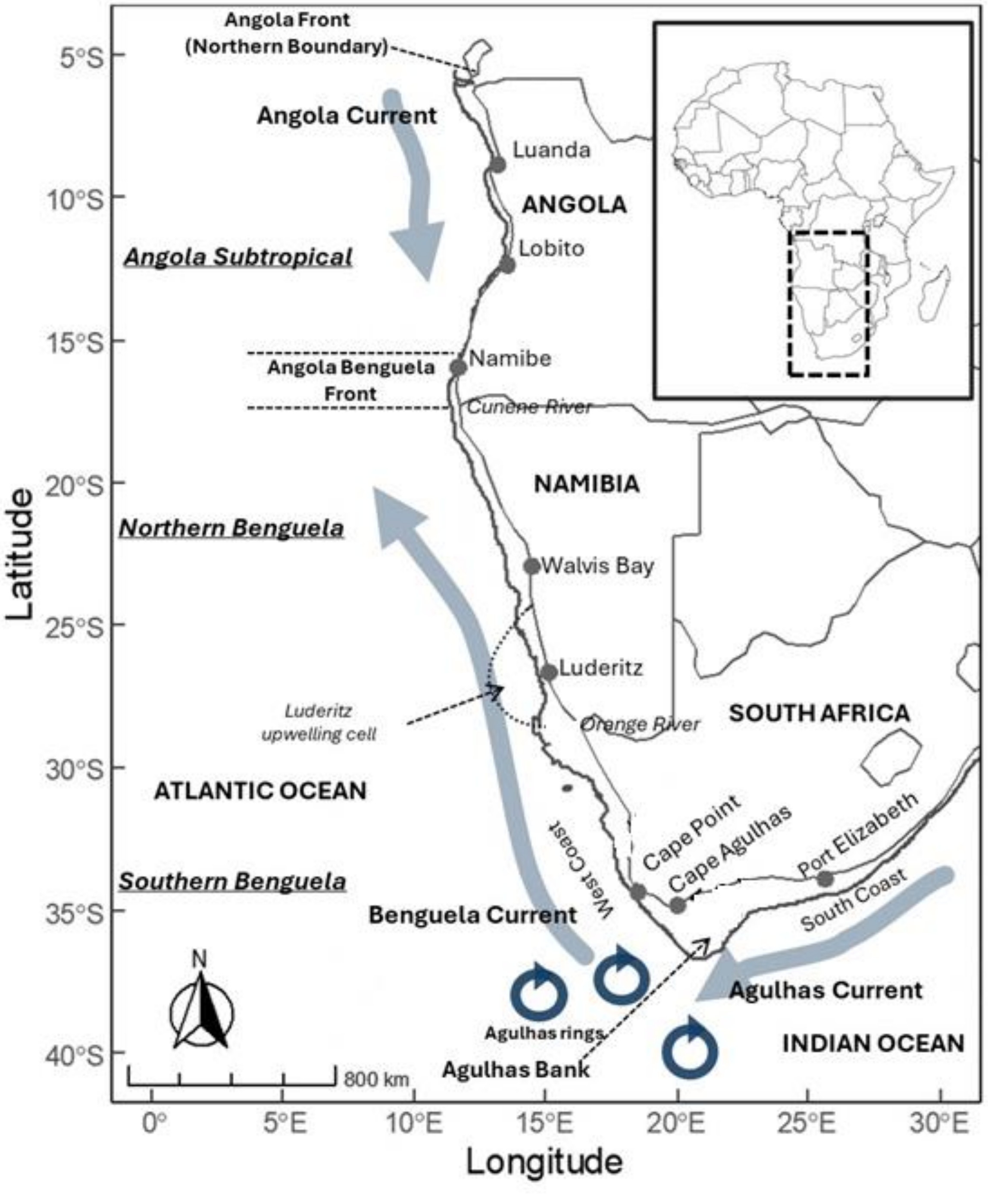


Figure 2.1 A map of Benguela Current Large Marine Ecosystem (BCLME) adapted from Jarre et al. (2015).

What distinguishes the Benguela upwelling system globally is its positioning between warm water systems to both the north and south, specifically the equatorial eastern Atlantic in the north and the Agulhas Current of the Indian Ocean, along with its retroflection zone in the south (Figure 2.1; Shannon and O’Toole 2003). The primary upwelling centre located near Lüderitz in southern Namibia is the most intense within any upwelling system and acts as a natural internal boundary within the Benguela, resulting in distinct functional differences between the areas to its north and south (Shannon and O’Toole 2003). Warm surface waters primarily flow from the Indo-Pacific into the Atlantic Ocean as rings released from the retroflection of the Agulhas Current. The South Atlantic is unique in that it exhibits a net transport of heat toward the equator (Shannon and O’Toole 2003). As a result, the Benguela not only occupies a vital position within the global climate system but also faces significant vulnerability to climate changes or increased climate variability (Shannon and O’Toole 2003).

Hampton and Willemse (2012) provided a brief overview of the Benguela ecosystem’s primary characteristics, variations and decadal changes in the biophysical environment over the last 50 years. The key points to note are: 1) the system's inherent natural variability poses challenges in distinguishing long-term trends influenced by climate change, 2) a significant regime shift occurred in the northern Benguela mainly due to the substantial reduction in biomass due to fishing pressure on sardine and anchovy populations during the 1970s and 1980s, and 3) in recent decades, there has been a widespread warming of surface water at the northern and southern boundaries of the system. However, there is a general cooling trend closer to the shore along the west and south coasts of South Africa (e.g. Blamey et al. 2015; Hampton and Willemse 2012; van der Lingen et al. 2006c; Coetzee et al. 2008; Hutchings et al. 2009).

The Benguela ecosystem has undergone significant changes over the past six decades (Jarre et al. 2015; Hampton 2012; Hutchings et al. 2009) and the decadal changes are discussed in much detail in section 2.6.

The southern Benguela shelf experienced declines of chlorophyll *a* (Chl-*a*) and microphytoplankton across all seasons. In the southern Benguela open ocean, there were slight increases during the austral winter, followed by a decrease in spring. On the Agulhas Bank shelf, both Chl-*a* and microphytoplankton increased during the summer, but showed decreases in the other seasons. In contrast, the Agulhas Bank open ocean displayed a different pattern, with increases noted in winter and spring, and decreases in summer and autumn (Lamont et al. 2019). Fish catches have declined across the region, with small pelagic fish (sardine and anchovy) disappearing from the northern Benguela, and southern catches of small pelagic fishes have significantly decreased compared to the 1950s (Hampton 2012; van der Lingen et al. 2006a; Boyer et al. 2001). The distribution of sardine and anchovy biomass shifted eastward to the south coast of South Africa between 1985 and 2005 but has since reversed, likely due to environmental changes or fishing pressure (van der Lingen et al. 2006a; Coetzee et al. 2008). Top predator populations have also been affected. Cape fur seals have increased in the northern parts, though they experienced a sharp drop following low-oxygen events in the 1990s (MFMR 2021). Gannets have been in rapid decline, largely due to reductions in anchovy and sardine stocks, while penguin populations have also fallen, although they are currently stable (Green et al. 2015; Hampton 2012).

2.3 Sardine – stock identity, distribution, biology and fishing history

Sardine (*Sardinops sagax*) are a small pelagic fish inhabiting the upper layers (0 – 200m depth) of the ocean distributed globally (Figure 2.2). Sardines (*Sardinops sagax)* flourish in upwelling regions where increased nutrient levels support the growth of phytoplankton and zooplankton, serving as their main source of food. Sardines are characterised by a short lifespan 4–7 years. According to the "wasp-waist hypothesis," forage fish species like sardines play a key role in controlling the populations of both predators and prey within the ecosystem (Erasmus et al. 2021; Cury et al. 2000; Bakun 2006).

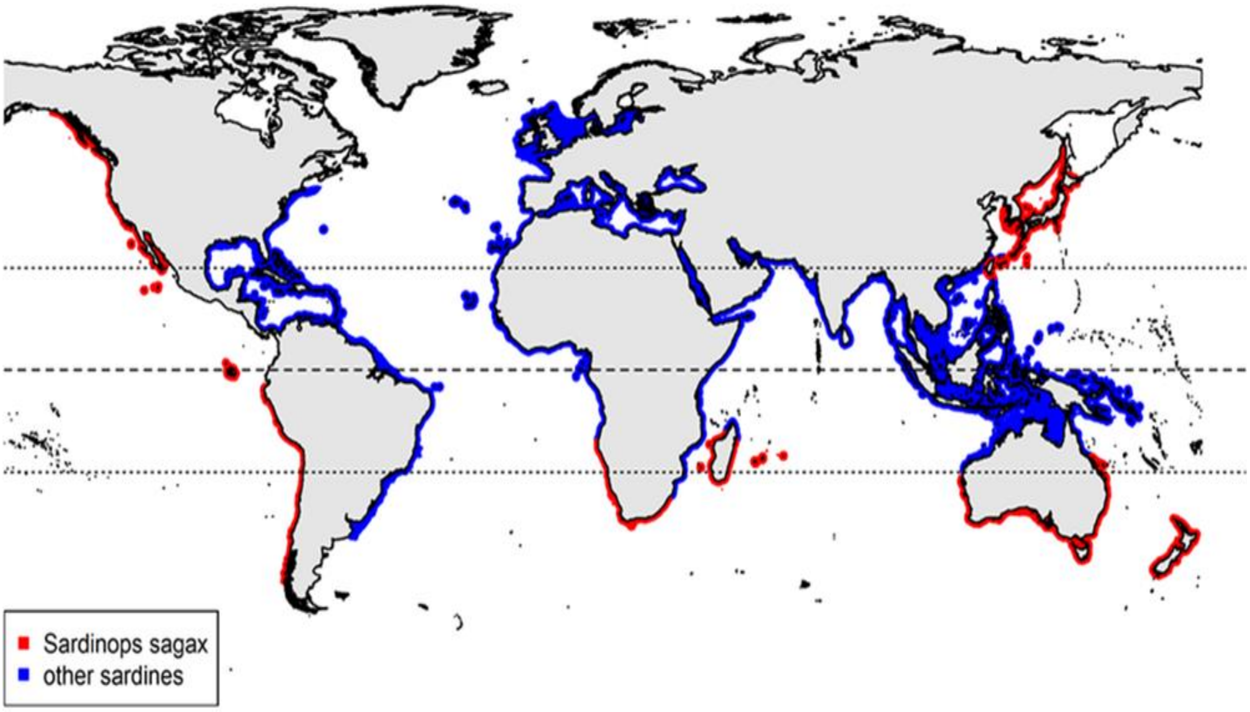


Figure 2.2. Global distribution of sardines, specifically showing the habitat range of *Sardinops sagax* - with the *Sardinops* genus indicated in red, and *Sardina* and *Sardinella* genus in blue. (Sourced from Crutchett et al. 2020).

Sardines in the Benguela region are found in temperate coastal and shelf waters stretching from southern Angola at Baia dos Tigres, (16°S) around the Cape of Good Hope (35°S) to KwaZulu-Natal at Durban (30°S) along the northeast coast of South Africa (Beckley and van der Lingen

1999). Notwithstanding extensive migratory patterns, it seems there are two distinct stocks namely: the southern stock inhabits the area southward from the Orange River around the Cape to KwaZulu-Natal and the northern stock inhabits the area from the Lüderitz upwelling cell (27°S) northward along the Namibian coast to the warm-water front of southern Angola (~15°S) (Parrish et al. 1989; Beckley and van der Lingen 1999). The presence of very cold upwelled water off Lüderitz throughout most of the year hinders the extensive mixing of the two sardine stocks (Beckley and van der Lingen 1999). Tagging research indicates that sardines do not migrate from the southern to the northern Benguela, and there is minimal movement in the opposite direction (Newman 1970). Sardines from the two subsystems are treated as distinct stocks with minimal interaction, and they are managed separately by Namibia and South Africa (Boyer and Hampton 2001). In areas north of the Angolan front and in KwaZulu-Natal, the marine ecosystem displays a tropical composition, shaped by the warmth and southward flow of the Angolan and Agulhas currents (Beckley and van der Lingen 1999).

2.3.1 Sardine – stock identity, distribution and biology in the northern Benguela (Namibia)

Sardines in the northern Benguela (Namibia) reproduce to the north of the prominent Lüderitz upwelling centre (27°S) and extend their spawning activity up to the Angola–Benguela Front (16–19°S) (Hutchings et al. 2002). The spawning grounds are situated in the region between Cape Frio (19°S) to Walvis Bay (24°S) (Parrish et al. 1989). In the northern region of these two areas, the peak of spawning, primarily by young adults, occur near the 200-meter isobaths during late summer and autumn, with water temperatures ranging between 19 and 21°C (Boyer and Hampton 2001). On the other hand, in the southern of the two areas, spawning, mainly by older fish, occurs in summer within cooler waters near upwelling zones (Boyer and Hampton 2001). The peak of sardine spawning takes place 30–80 km offshore in September–October off the central Namibian shelf (Hutchings et al. 2002). Adult fish seem to migrate northward towards

Angola before eventually returning south (Armstrong and Thomas 1989). The distribution patterns are connected to the age of the fish, and, similar to the situation in South Africa, there is a variation in size composition of the stock along latitudinal lines (Armstrong and Thomas 1989).

The larvae of the sardine stock in the northern Benguela (Namibia) are found slightly farther offshore, while recruits appear in close proximity to the shore. Thus, there seems to be a straightforward movement from inshore to offshore across the expansive Namibian shelf (Hutchings et al. 2006). The sardine larvae are carried southward along the coast, becoming part of the fishery as 0-group fish (pre-recruits) and inhabiting the nursery ground within the cold upwelling regions near Walvis Bay (Beckley and van der Lingen 1999; Boyer and Hampton 2001). Subsequently, there are a migration northward of juveniles and young adults to the initial spawning grounds in the northern mixing area. Older fish then made a return journey south to spawn near Walvis Bay, while younger fish stayed in the northern region (Boyer and Hampton 2001).

Reproduction also takes place during mid-summer in the area around the Angola–Benguela Front (Crawford 1987). In the late summer months (December–March), the southward movement of warm water from the Angolan Current reaches central Namibian waters, facilitating the transport of pelagic spawning products into the nursery grounds off the central Namibian coast (Hutchings et al. 2002). Additionally, there is a strong probability of significant offshore movement linked to this converging frontal area (Hutchings et al. 2002).

The collapse of sardine in northern Benguela (Namibia) has been linked to documented ecosystem impacts, including food shortages for dependent predators like seabirds and seals

(Jarre et al. 2015). Sardines feed by filter-feeding and particulate feeding (van der Lingen et al. 2006a). They are generalist planktivores and can consume a variety of prey sizes, including phytoplankton (van der Lingen et al. 2006b). However, their feeding strategy seems to have adapted specifically to target smaller zooplankton, such as cyclopoid and small calanoid copepods (van der Lingen et al. 2006b). Sardines are a high-energy prey species (Roux et al. 2013; Hutchings et al. 2009) and serve as a fundamental food source for numerous predators, including seabirds (Matthews and Berruti 1983), demersal fish (Pillar and Barange 1998), pelagic fish (Crawford 1987), marine mammals (Marçalo et al. 2015), and sharks (Cliff and Dudley 1992). Sardines play a crucial role as a key trophic link connecting lower and upper levels of the food web in upwelling ecosystems (Erasmus et al. 2021; Cury et al. 2000).

2.3.2 Sardine – stock identity, distribution and biology in the southern Benguela

The sardine population in the southern Benguela upwelling ecosystem (South Africa) has shown significant changes in biomass over the last 5 decades (van der Lingen et al. 2006). A large population that initially supported high catches collapsed in the early 1960s, recovered in the 1990s, increased again at a maximum in the early-2000s before declining rapidly once again thereafter in the mid-2000s such that the sardine population has remained low and depleted (Beckley and van der Lingen 1999; van der Lingen 2021). The significant decrease in sardine biomass, in both the western and eastern segments of the population since 2004–2005 has been attributed to an extended period of low recruitment and a sudden rise in adult mortality, which cannot be explained by fishing activities (Coetzee et al. 2008). Moreover, changes to sardine life history parameters: length at 50% sexual maturity (L50), condition factor (CF), and standardized gonad mass (SGM) have occurred since the 1950s (Beckley and van der Lingen 1999).

Historically, in South Africa, the majority of the adult sardine biomass has been limited to the southern west coast and Agulhas Bank, extending as far east as Port Alfred, throughout a significant portion of the period covered by hydro-acoustic survey data (Coetzee et al. 2008). However, alterations in the distribution patterns of the southern Benguela sardine along the west and south coasts, varying at different abundance levels, have been noted over the last three decades (Coetzee et al. 2008). The species occupies two clearly defined areas, consistently separated by the region between Cape Agulhas (recognised as the boundary between the west and south coasts) and Mossel Bay at low and moderate biomass levels (Idris et al. 2016). Sardines participating in the annual 'sardine run' off the east coast of South Africa during the austral winter may constitute a third stock, as consistent spawning has been observed in that region during winter and spring (Connell 2010). While earlier publications suggested that the sardine run resulted from the eastward extension of suitable habitat in winter, a recent and comprehensive analysis has dismissed that hypothesis. Instead, it proposes that the sardine run is a 'reproductive migration of a genetically distinct subpopulation. (Fréon et al. 2010).

In South Africa, the sardine spawning season is prolonged, happening throughout the year, but predominantly from August to late March. Within the primary spawning season, there are two notable peaks, one in September to October and another in February to March (van der Lingen and Huggett 2003). Sardine spawning seemed to occur during the spring and summer seasons, primarily taking place on the Agulhas Bank between Cape Point and St. Sebastian Bay. However, there were instances of spawning recorded off St. Helena Bay (Beckley and van der Lingen 1999). The addition of 0-year-old fish to the population took place across the entire west coast starting in May, with the highest numbers observed in September. One-year-old fish also concentrate in the west coast regions (Beckley and van der Lingen 1999). However, 4-year-old fish occurred in the southern spawning region during spring and summer and, with the advent of autumn, they appeared to migrate east past Cape Agulhas (Beckley and van der Lingen 1999).

There have been observed shifts in some biological elements of the southern Benguela, specifically in the distributions and primary spawning habitats of sardine, throughout the past few decades (Mhlongo et al. 2015). Sardines have demonstrated a sudden change in their spawning behaviour between 2000 and 2001, transitioning from the western Agulhas Bank to the south coast. Since 2001, the majority of spawning has occurred on the south coast with some spawning observed on the west coast during the years 2007–2009 (Mhlongo et al. 2015). The patterns observed in the distribution of sardine eggs, revealed two clearly defined spawning grounds, and indicative of the potential presence of at least two distinct groups of adults involved in spawning (van der Lingen and Huggett 2003; van der Lingen et al. 2015). Eggs spawned in the two distinct regions have divergent outcomes such that those spawned to the west of Cape Agulhas (WAB) are transported to a nursery area on the west coast, while those spawned to the south coast are primarily retained in a nursery area on the south coast Agulhas Bank (Miller et al. 2006; van der Lingen and Huggett 2003). The reduction in sardine spawning intensity in the WAB during summer, when the levels of chlorophyll *a* are low, along with the second spawning peak in late summer (February) that aligns with peak upwelling and heightened primary production, supports this hypothesis (Fowler 1998). Therefore, the timing of sardine spawning behaviour may be linked to the food availability for spawners, specifically in relation to phytoplankton rather than zooplankton (Fowler 1998).

2.3.3 Sardine – fishing history and assessment in the Benguela

In Namibia, the sardine stock level was approximated to be several million tonnes in the late 1950s and 1960s (Thomas 1985; le Clus 1988). Heavy fishing pressure in the 1950s and 1960s off Namibia led to the collapse of sardine stocks in the early 1970s (Jarre et al. 2015; Roux and Shannon 2004). The sardine catches experienced a significant decline, dropping to approximately 50,000 tons from the late 1970s to the late 1980s. Although there was a slight recovery in the early 1990s, with catches reaching around 100,000 tons, the overall trend continued to decrease. Subsequently, catches have remained under 30,000 tons with no indications of improvement (De Oliveira et al. 2007).

Despite minimal fishing pressure on the sardine stock in Namibia over the past twenty years, and a recent moratorium on fishing since 2018, there is no sign of recovery. Despite scientists advocating for a sardine fishing moratorium since 1995, only a one-year moratorium was implemented in 2002, which did not succeed in recovery of the sardine population. A three-year moratorium was announced in 2018, which is still in place due the continued low levels of sardine biomass. The sardine biomass in Namibia, as determined by stock assessment models, indicated a notable increase in the mid-1960s followed by a substantial decrease in the late 1960s, and subsequent years have not demonstrated any significant signs of recovery (Kirchner et al. 2009; van der Lingen et al. 2006). Although there were signs of a partial recovery of the sardine biomass in the early 1990s, the biomass declined once more following occurrences of low-oxygen and warm-water events in 1994 and 1995 (Boyer and Hampton 2001). Along with the reduction in biomass, there have been significant alterations in the stock structure of sardines (Kreiner et al. 2011). The average total length of sardines has decreased by over 4 cm from the 1950s to the 2000s, and the length at which 50% of sardines reach maturity has dropped by more than 3 cm from the 1980s to the 2000s (Jarre et al. 2015; Kreiner et al. 2011). The near-complete removal of sardine from the northern BCLME in the 1970s and 1980s due to overfishing has led to a shift toward a less efficient and less environmentally stable regime (Hampton and Willemse 2012).

Namibia received a significantly diminished sardine stock upon gaining independence in 1990 (Boyer et al. 2001). Prior to independence in 1990 the sardine fishery was managed and overexploited by the International Commission for the South-East Atlantic Fisheries (ICSEAF), an organization that involved the participation of a total of 17 nations from around the globe such that the sardine stock fell to only 2 per cent of its previous level between 1976 and 1986.

In South Africa, historically, sardine constituted the majority of catches in this small pelagic fishery. However, due to overfishing in the early 1960s, sardine stocks collapsed, prompting a shift in fishing gear to smaller-meshed nets in 1964, targeting the smaller anchovy instead (van der Lingen and Huggett 2003). Sardine catches remained low for thirty years, but the fishery started targeting this species along the south coast in the 1990s, leading to an increase that reached a second peak in the mid-2000s before dropping again to very low levels in recent years (van der Lingen 2021). The sardine fishery operates off the west and southwest coasts, while sardine are caught farther offshore and over a broader geographical range compared to anchovy (van der Lingen and Huggett 2003). Juvenile sardines that gather in groups with anchovies are incidentally captured as bycatch in the anchovy fishery (van der Lingen and Huggett 2003).

The decrease in the sardine population and its current depleted condition has resulted in significant consequences for the small pelagic fishery, posing a crucial and urgent issue. To address this change and anticipate future developments, the fishery must adjust by optimizing the use of existing and new resources, particularly in the short term (van der Lingen 2021). Implemented strategies for adaptation include the importation of frozen sardines to maintain operational factories and fulfil local demand. Additionally, an experimental fishery for the mesopelagic lanternfish *(Lampanyctodes hectoris*) has been established in South Africa (van der Lingen 2021).

Other possible adaptation strategies involve restoring the sardine population, creating consumer products from anchovies (such as fillets and dried products) and exploring market opportunities, examining the utilization of larger vessels with diverse fishing gear (such as pelagic and midwater trawls instead of purse-seiners) for harvesting anchovies and round herring, exploring anchovy fishing off the South Coast and establishing processing infrastructure, increasing the current minimal exploitation rates on round herring and creating canned products for human consumption, and formulating an integrated research plan to enhance predictions of potential climate change impacts on these species and the associated fisheries (van der Lingen 2021).

2.4 Cape horse mackerel – stock identity, distribution, biology and fishing history

2.4.1 Cape horse mackerel – stock identity and distribution in the Benguela

The Cape horse mackerel (*Trachurus capensis*) plays a significant role in the Benguela ecosystem (Crawford 1987). Genetic studies on *T. capensis* populations of the Benguela (Namibia and South Africa) have found no evidence of distinct population structure (Karaiskou et al. 2004; Naish 1990). Despite this, the species is currently managed as two arbitrarily defined stocks, one in the northern and the other in the southern Benguela Upwelling System (Hecht 1990; Naish et al. 1991; Healy et al. 2020).

The Cape horse mackerel resides in the cool Benguela Current region, ranging from south of the Lüderitz upwelling cell to the Angola-Benguela Front, with most of its abundance between 25°00'S (slightly north of the Lüderitz upwelling cell) and 17°15'S (Axelsen et al. 2004; Krakstad and Kanandjembo 2001; Ndjaula et al. 2013). The adult population forms large shoals with varying densities, showing a general trend of increasing abundance from the southern regions to the north. Axelsen et al. (2004) indicated that the most substantial concentrations of horse mackerel are located in the region between 17° S to 20° S, which lies in the northern Namibian of the continental shelf making it the species' primary distribution area in Namibia. However, lesser and more dispersed groupings have been discovered to the south, spanning between 19° S and 23° S, with limited amounts of mature fish located in deep waters south of 23° S (Axelsen et al. 2004; Krakstad and Kanandjembo 2001; Ndjaula et al. 2013). This overall distribution pattern undergoes seasonal variations, exhibiting more sporadic and concentrated groupings during the summer months (December–February) compared to the winter months (June–August) (Ndjaula et al. 2013).

The distribution of fish size corresponds to both latitude and isobaths: smaller fish are more prevalent in the northern area, around the Kunene River, particularly at depths shallower than 200 meters (Bauleth-D’Almeida et al. 2001). As juveniles, the species is epipelagic, but as they age, they become mesopelagic, spending much of their pre-adult and adult life at greater depths (Axelsen et al. 2004). Juvenile Cape horse mackerel typically inhabit areas closer to the shore than the 100-meter isobath, with the smallest individuals being located furthest to the north (Crawford 1987). Mature Cape horse mackerel are located at greater distances from the shore, specifically over the isobaths ranging from 200 meters to 500 meters (Bauleth-D’Almeida et al. 2001; Kanandjembo et al. 2004; Krakstad et al. 2002). Larger fish seem to undertake a southward migration, particularly toward Walvis Bay, especially during austral winter (Boyer and Hampton 2001). As fish mature, they shift offshore and move northward for spawning, with adults typically found north of 21°S (Boyer and Hampton 2001). At the end of their lifespan the older adult fish adopt a semi to exclusively demersal lifestyle and they tend to migrate southward and disperse in waters south of 25°S where they are mainly detected in demersal trawls (Axelsen et al. 2004).

The biomass of Cape horse mackerel fluctuates between 500 thousand to 1.8 million tonnes during 1990-2021 with the lowest estimates of approximately 0.5 million tonnes in 2006 and 2007. This increase in Cape horse mackerel biomass occurred after a previous decline from about 3 million tonnes in the early 1960s (Kirchner 2012). The significant variability in biomass estimates is due to the species' tendency to aggregate, particularly during warmer periods when thermal fronts form and concentrate nutrients along these temperature gradients (Kanghono 2022). Shifts in the stock structure of the horse mackerel population in the northern Benguela have been noted. Kirchner (2012) reported that the length at 50% maturity dropped from 25.9 cm total length (TL) to 18.9 cm TL during the 2000s. Moreover, the modal TL of commercial catches shifted from about 29 cm in the 1980s to an average of approximately 23 cm over the period from 2003 to 2012.

Cape horse mackerel typically engage in feeding activities during daylight hours, with peak activity occurring in the late afternoon in proximity to the seabed (Pillar and Barange 1998). In this location, they can capitalize on the near-bottom daytime concentrations of copepods and euphausiids, which are their primary prey off the Namibian and South African coast (Andronov 1983; Hecht 1990; Pillar and Barange 1998). Approximately 95% of the adult horse mackerel's diet comprises euphausiids and fish, although a diverse array of invertebrate prey is typically observed. The extent of predation on fish was negligible (Barange et al. 2005). In contrast, juvenile horse mackerel predominantly consume copepods belonging to the genus Calanus (Barange et al. 2005). Cape horse mackerel larvae were identified as highly effective and voracious feeders, exhibiting a strong feeding success (Geist et al. 2015). Cape horse mackerel larvae displayed the high daily biomass growth rates and maintained good nutritional condition (Geist et al. 2015). They preyed on various copepod taxonomic groups, including small *Oithona* sp. and *Oncaea* sp.

Cape horse mackerel plays a pivotal role in the marine food web. The decline in sardine populations in the northern Benguela compelled predators to search for other food sources. Cape fur seals in the northern Benguela thus increased their diet of pelagic gobies (*Sufflogobius bibartus*), Cape horse mackerel and mesopelagic fish (mainly *Lampanyctodes hectori*) and have ended up at a lower trophic level post-exploitation (Mecenero et al. 2006; Mecenero et al. 2007; Mwaala et al. 2023). Seals play a crucial role as significant predators of horse mackerel, particularly targeting juvenile fish (Mecenero et al. 2007; Mwaala et al. 2023). Additionally, hakes, considered the most valuable fishery stocks in Namibia, along with certain sharks and rays, are among the other predators preying on Cape horse mackerel (Bauleth-D'Almeida et al. 2001; Wilhelm et al. 2015). Pelagic gobies, along with mesopelagic fish, are less nutritious but capable of living in oxygen minimum zones (Roux et al. 2013). Cape horse mackerel, on the other hand, is a larger and more mobile prey, making it harder to capture. As a result, alternative prey species are either of lower nutritional value or demand more effort to catch and consume, both of which contribute to reduced trophic efficiency.

Cape horse mackerel in the northern Benguela (Namibia) spawn consistently throughout the year, with a concentrated spawning period occurring predominantly from December to March (Wysokiński 1985). However, Ndjaula et al. (2013) described the spawning period spanning from December to July. The highest Gonadosomatic Index (GSI) peak was recorded in February, with the peak in actual spawning observed between late March and early April. Moreover, the frequency of spawning remained elevated until May (Ndjaula et al. 2013). The spawning of Cape horse mackerel typically occurs in the area between Cape Frio (18° S) and Cape Cross (22°S) (Ndjaula et al. 2013; O'Toole 1977). Examinations of eggs and larvae off the coast of Namibia in the 1970s indicated that the most intensive spawning activity occurs in the northern region between October and March (O'Toole 1977). This coincides with the mixing zone of warm oceanic water and cool coastal water, with the timing of spawning closely tied to the duration and intensity of this mixing. Cape horse mackerel species are described as indeterminate, exhibiting the characteristic of being multiple batch spawners (Ndjaula et al. 2009). Hence, females undergo spawning on multiple occasions within a single spawning season (Ndjaula et al. 2013). The ovaries carry numerous asynchronous oocytes, particularly when their maturity is well progressed leading up to the commencement of spawning and the continuous size frequency distribution of oocytes persists until a distinct batch of hydrated oocytes was formed separately, signalling a pattern consistent with serial spawning (Ndjaula et al. 2013).

Nursery habitats are present in both the southern and northern regions of the Benguela ecosystem, located near the spawning grounds but closer to the shore (Boyer and Hampton 2001). Additionally, significant movements occur along the shoreline and across the shelf for both juvenile and adult individuals (Boyer and Hampton 2001).

2.4.2 Cape horse mackerel in Namibia – fishing history and assessment

The Cape horse mackerel stock in Namibia is harvested through two primary fisheries, namely pelagic purse-seine and midwater trawl. The purse seine industry ceased operations in 2014, and currently only adult fish are being harvested for whole round production by the midwater fishery. Research has shown that allocating resources for juveniles is not sustainable, as it results in decreased overall stock levels, reduced recruitment, and lower profitability for the adult Cape horse mackerel fishery (Mukumangeni and Viium, 2006). The fishery boasts the largest stock volume and catch among all fish species in the region (Kirchner et al. 2010). Between the early 1970s and the late 80s, calculations of Cape horse mackerel stock size relied on stock assessment models utilising catch data from commercial vessels that primarily focused on horse mackerel (Kirchner et al. 2010). Between 1980 and 1989, the International Commission for South East Atlantic Fisheries (ICSEAF) initiated the regulation of horse mackerel exploitation by implementing catch limits, referred to as Total Allowable Catches (TAC) (Boyer and Hampton 2001). During that period, annual catches reached their peak, surpassing 600,000 tons.

Following Namibia's independence in 1990, stock monitoring has been carried out by integrating catch statistics from commercial vessels (the fishery-dependent information) and acoustic surveys from survey vessels (the fishery-independent data) (Boyer and Hampton 2001). Hydro-acoustic surveys take place annually in February and March. Stock assessment involves the application of two methods: the VPA, an age-based approach, and acoustic biomass assessment (Krakstad and Kanandjembo 2001). Due to the absence of precise information regarding the age and growth of horse mackerel, the outcomes derived from the majority of stock assessment models are viewed as unreliable. Advice on the Total Allowable Catch (TAC) was originally based on harvesting around 26% of the estimated survey biomass, aiming for a fishing mortality rate (F) of 0.3 (Bauleth-D’Almeida et al. 2001). However, since 2002, survey estimates (from 1999–2010, excluding 2008) have not been treated as absolute measures of abundance. Instead, TAC recommendations are now derived from stock assessment models. Acoustic survey estimates are still used as relative indicators and are incorporated into an age-structured production model to assess the stock's condition (Kirchner et al. 2010).

The species exhibited a consistently high abundance over the years, characterized by significant year-to-year fluctuations, as indicated by abundance survey estimates (Uanivi 2018).

Commercial catch data shows that the average lengths of commercial catches and the size at maturity derived from survey trawls have been declining over time (MFMR unpublished data). Nevertheless, the commercial catch per unit effort (CPUE) in the midwater fishery has nearly tripled in recent years and has remained exceptionally high (Uanivi 2018). Starting in 1990, the catch size rose significantly until 1994, followed by fluctuations in subsequent years due to variations in fishing conditions and reductions in the total allowable catch (TAC). Catch levels below the TAC might indicate potential recovery and rebuilding of fish stocks over time. In general, midwater trawl catches have remained below the Total Allowable Catch (TAC), except for 1994, 2002, 2003 and 2013 when catches exceeded the TAC (Kanghono 2022). The fishing industry has expressed concerns about low catch volumes and the small size of fish density (Mundjulu 2009). The decrease observed in recent years (since 2019) is attributed to inadequate allocation responses (Mundjulu 2009).

2.5 Decadal Changes in the Benguela ecosystem

Ecosystem alterations in the Benguela encompass both biological and oceanographic components (Howard et al. 2007; Blamey et al. 2012). These ecosystem alterations, also known as regime shifts, refer to a sudden transition from one stable ecosystem state to another, impacting multiple trophic levels within a relatively short period compared to contrasting regimes (Blamey et al. 2012). Regime shifts are defined as infrequent and abrupt alterations in the whole ecosystem structure and function, occurring at multiple trophic levels and over large geographic scales. They are able to cause losses of ecological and economic resources with significant management consequences (Möllmann et al. 2009). While changes in ocean and atmospheric climate are the main drivers of regime shifts (Polovina 2005), biotic factors, alterations in habitat structure, and fishing also contribute significantly (Scheffer and Carpenter 2003; Daskalov et al. 2007)

Regime shifts may be triggered by environmental changes that influence the food web either through bottom-up processes involving phytoplankton or zooplankton, or through wasp-waist dynamics that directly affect the recruitment of pelagic fish (Cury and Shannon 2004). Bottom-up control, a typical form of trophic flow regulation, appears to impact most ecosystems (Cury et al. 2003). A climatic regime shift, often described in literature as a warm or cold phase, can set off a cascade of linked physical and biological processes that initiate and sustain a regime shift (e.g. Lluch-Belda et al. 1991; Schwartzlose et al. 1999; Cury and Shannon 2004). Predation can be as influential as resource availability in shaping ecosystem dynamics. Since most fish species are linked through predator-prey relationships, top-down control—where one or more higher-level predators regulate populations of lower food-web organisms—is likely essential for the health and stability of marine ecosystems (Cury and Shannon 2004). Fishers, acting as top predators, have consistently targeted larger fish species. This focus has led to a global reduction in the average trophic level of catches, a trend referred to as 'fishing down marine food webs' (Pauly et al. 2000).

In ecosystems regulated by predation, this process typically drives a shift from ecosystems dominated by large predatory fish to those dominated by smaller, pelagic fish species (Cury and Shannon 2004). When large predatory fish are removed from ecosystems, pelagic fish species (which are particularly responsive to environmental changes) tend to increase in abundance (Cury and Shannon 2004). In upwelling systems, fish biomass is often primarily composed of one sardine (or sardinella) species and one anchovy species, with only one of these typically being dominant at any given time. Dominant pelagic fish species, especially in upwelling regions, can significantly shape ecosystem dynamics, impacting other pelagic species along with organisms at both higher and lower trophic levels (Cury et al. 2000, 2003). In such an instance, the subordinate fish species might be compelled to form schools with the dominant species, sacrificing foraging benefits in exchange for the protection provided by larger schools, creating what is referred to as a "school trap" (Bakun and Cury 1999). This phenomenon can effectively entrench a specific regime (Cury and Shannon 2004).

Over the past 50 years, the northern Benguela system has undergone substantial reorganisation, likely driven by a combination of overfishing and environmental influences like the Benguela Niño events. This period saw a significant regime shift occurred in the northern Benguela mainly due to the substantial reduction in biomass due to fishing pressure on sardine and anchovy populations during the 1970s and 1980s (Roux and Shannon 2004; Watermeyer et al. 2008; Hampton and Willemse 2012; Jarre et al. 2015). Key environmental features influencing the northern Benguela consist of the Angola Current, the Angola-Benguela front (ABF), low-oxygen water (LOW), and the upwelling cells located at Cape Frio and Lüderitz (Hutchings et al. 2009). The South Atlantic high-pressure system and its seasonal movement promote the wind patterns favourable for upwelling, which prevail year-round in the northern Benguela (Hutching et al. 2009; Hampton and Willemse 2012). There has been a southward shift and strengthening of the ABF since 1980, linked to the southward movement of the South Atlantic subtropical anticyclone and may be connected to, but are not always synchronised with El Niño Southern Oscillation (ENSO) (Hampton and Willemse 2012). This has led to periodic southward incursions of warm, saline, nutrient-poor, and low-oxygen water onto the Namibian shelf, associated with significant southward displacement of the ABF, a phenomenon known as Benguela Niños (Rouault et al. 2007) and their cold equivalents, the Benguela Niñas (Koungue et al. 2021). The northern Benguela has experienced a steady rise in sea surface temperature (SST), with the highest recorded temperatures occurring during the 1980s, while the late 1960s and 1970s saw a significant drop in SST (Shannon et al. 1992; Hardman-Mountford et al. 2003; Cury and Shannon

2004). Heymans and Tomczak (2016) demonstrated that SST, which is the primary environmental factor, was not a significant driver in the ecosystem changes and did not affect the overall structure. However, the substantial fluctuations in primary production linked to major Benguela Niño events in 1972 and 1984 were associated with alterations in the system's emergent properties (Heymans and Tomczak 2016). Winds at Lüderitz exhibit significant decadal variability with southerly winds reaching their highest levels during 1970–1973, 1976–1989, and 1997/1998. Conversely, lower wind levels were recorded from 1961 to 1969 and again from 1990 to 2006. These patterns align with sea surface temperature anomalies in the northern Benguela region, which also display distinct decadal cycles (Hutchings et al. 2009). Low-oxygen water (LOW) on the northern Namibia shelf arises from a complex interaction of various processes, including (i) the southward movement of oxygen-poor water from the Angola dome area; (ii) the upward flow of water onto the shelf at Cape Frio; (iii) localized decay processes occurring on the shelf; (iv) the arrival of relatively oxygenated central water from the Cape Basin due to upwelling at Lüderitz; and (v) the stratification of the shelf waters (Hutchings et al. 2009). Dissolved oxygen levels off the coast of Namibia exhibit significant seasonal and inter-annual variability without a clear trend (Bartholomae and van der Plas 2007; Hutchings et al. 2009). Trends of increasing chlorophyll *a* (Chl-a) and microphytoplankton were observed in the northern Benguela shelf and open ocean from 1997 to 2017, along with an upward trend in upwelling intensity during both summer and winter seasons. (Bartholomae and van der Plas 2007; Reason and Rouault 2006; Lamont et al. 2019).

Alterations in sardine abundance may have contributed to regime shifts in the northern Benguela Upwelling System (nBUS), a phenomenon that has been well documented by various studies (Boyer et al. 2001; Heymans and Tomczak 2016). The northern Benguela ecosystem was significantly restructured by intensive fisheries targeting small pelagic and demersal fish. The biomass of most exploited groups, particularly sardines and hake, has significantly decreased over time. The small pelagic fish that typically dominate upwelling systems have been supplanted by a broader variety of species, while the biomass of gelatinous zooplankton seems to have surged dramatically in recent decades (Boyer and Hampton 2001; Watermeyer et al. 2008). The dominant planktivorous fish in the northern Benguela ecosystem shifted from sardines to horse mackerel, bearded gobies, and jellyfish (Cury and Shannon 2004; Utne-Palm et al. 2010; Kirkman et al. 2015). As a result, much of the pelagic energy flow shifted towards jellyfish and gobies, which were less important as prey for top predators compared to sardines and anchovies before the mid-1970s (Heymans and Tomczak 2016). However, due to limitations related to diet or habitat, these new species do not effectively transfer this production to their predators (Shannon et al. 2008). Between 1967 and 1990, fish catches declined alongside the biomass of target species, despite the trophic level (TL) of the catch during these periods. The ecosystem was so altered that sea surface temperature (SST) anomalies became a dominant force driving change (Watermeyer et al. 2008; Heymans and Tomczak 2016).

In the southern Benguela, wind patterns have intensified especially during the summer, driving stronger offshore winds (Shannon et al. 1992; Hardman-Mountford et al. 2003; Veitch 2007; Hutchings et al. 2009; Rouault et al. 2010; Hampton 2012). SSTs in the inshore waters along South Africa's west and southern coasts have cooled, while SSTs in offshore waters have risen, leading to heightened temperature gradients (Taunton-Clark and Shannon 1988; Shannon et al. 1992; Bartholomae and van der Plas 2007; Jarre et al. 2015; Hampton 2012). Chlorophyll-a and microphytoplankton levels showed a decline across all seasons on the southern Benguela shelf (Lamont et al. 2019). In the open ocean of the southern Benguela, slight increases were noted during the austral winter, followed by a decline in spring. Conversely, the Agulhas Bank shelf experienced rises in chlorophyll-a and microphytoplankton during the summer, while declines were observed in the other seasons (Lamont et al. 2019). The Agulhas Bank open ocean displayed a different trend, with increases in winter and spring, but decreases in summer and autumn (Lamont et al. 2019). Copepod abundance in the southern Benguela experienced a 100-fold surge from 1950 to 1995, followed by a tenfold reduction in 1996 on the west coast, coinciding with a significant ecological regime shift from larger to smaller copepod species dominance in 1995 (Verheye et al. 2016). Larger copepods, such as *Centropages brachiatus*, *Calanoides natalensis* (previously *C. carinatus*), and *Rhincalanus nasutus*, which are the preferred prey of anchovy (James 1987), were prevalent in the 1950s–1960s and in recent years (from late 2000s), while smaller copepods, such as *Oithona* spp., *Metridia lucens* and small calanoid species, the preferred prey for sardine van der Lingen (2021) increased from the late 1980s and declined in recent years (from late 2000s) (Verheye et al. 2016). This shift was likely triggered by environmental changes, such as ocean warming, and intensified by a change in predation pressure based on prey size by pelagic fish stocks along the west coast (Verheye et al. 2016).

Currently, two major regime shifts have been documented in the southern Benguela – the first regime shift took place in the aftermath of the sardine collapse during the early-mid 1960s and was fishing-induced (Jarre et al. 2015). The second regime shift, known as the eastward shift of sardines in South Africa, occurred during the mid-1990s to early 2000s, triggered by environmental changes and aggravated by fishing pressure (Blamey et al. 2012; van der Lingen 2021). The prominent transformation in the southern Benguela during the last two decades has been the relocation of sardine from the west coast subsystem to the south subsystem (Agulhas Bank) in the late 1990s/early 2000s (Coetzee et al. 2008). The relocation observed, involving the movement of sardine from the West Coast subsystem to the south subsystem in the late 1990s/early 2000s, is thought to be less extensive and less likely to be irreversible compared to the shift seen in the northern Benguela, which involved the decline of sardine (Cury and Shannon 2004). From 1985 to 1998, more than half of the sardine biomass was situated west of Cape Agulhas. However, this pattern shifted between 1999 and 2007, with over 50% of the biomass now located to the east of Cape Agulhas (Coetzee et al. 2008).

Managing marine ecosystems is challenging due to a lack of comprehensive information, difficulties in sampling across all trophic levels, and limited understanding of ecosystem structure (Travis et al. 2014) and how it responds to external pressures. As a result, it is hard to identify "tipping points" that signal an approaching regime shift and to manage ecosystems that have transitioned into a new regime. These regime shifts cause significant disruptions to ecosystem structure and alter the potential fish stock harvest, with human activities being a major driving force (Folke et al. 2004). Managing ecosystems that have shifted into new regimes, often referred to as novel ecosystems (Hobbs et al. 2009), is particularly challenging. Decisions on how much effort and resources to allocate towards restoration depend on factors such as local species diversity, livelihood priorities, sustainability goals, and attachment to past ecosystems. In systems with incomplete information, making these decisions becomes even more difficult (Hobbs et al. 2009). This study aims to investigate whether there have been any abrupt changes in the annual otolith growth patterns of sardine and Cape horse mackerel, potentially associated with previously identified ecosystem regime shifts in the Benguela, as documented in the literature.

2.6 Environmental and fishing-induced drivers of changes in fish growth

Body growth and size are interconnected, meaning selection on one can indirectly affect the other, and both may be linked to other traits under selection (Enberg et al. 2012). Measuring growth directly involves tracking size changes over time, with growth rate defined as size increase per unit of time. Common measures of growth rate in fish include increases in length or body mass over time (Enberg et al. 2012). A key distinction between these measures is that length growth is typically irreversible (usually no skeletal shrinkage), while weight can fluctuate (i.e. also shrink) as energy reserves are stored or used, or as gonad mass is developed and spawned (Enberg et al. 2012). While growth is often observed as the rate of size change, it actually involves two main processes: resource acquisition and their allocation to various functions (Enberg et al. 2012). Body growth is highly influenced by environmental factors, and any phenotypic effect must account for both genetic factors and phenotypic plasticity (Enberg et al. 2012).

The study of fish growth is able to examine the impacts of fishing and environmental variability on population abundance because it is the phenotypic manifestation of the relationship between the individual (intrinsic) and the environmental or ecological (extrinsic) components that influences the acquisition and allocation of resources (Enberg et al. 2012). In fact, growth influences not only individual fitness as it relates to body size, behaviour, reproductive output and mortality rates but it contributes to the population parameters such as recruitment success, generation time and stock biomass (Enberg et al. 2012). The life-history theory predicts that increased mortality selects for “faster” life histories that are categorised by rapid juvenile growth, early maturation, smaller body size and reduced life span. Fishing can selectively remove fast or slow growers from a population but it also influences the growth of the remaining fish through modifications to density-dependent processes (Lorenzen and Enberg 2002; Enberg et al. 2012), habitat (Rooper et al. 2011), or food webs (Audzijonyte et al. 2013).

The environmental factors that shape body growth rate include water temperature and the availability of food. Food availability can be impacted by density dependence. For instance, a large population may deplete its food sources, limiting body growth. Social dynamics can also play a role body growth rate where a reduction in older, larger individuals may remove a constraint on the maturation of smaller, younger fish (Kolluru and Reznick 1996). Fishing influences many of these interactions by directly reducing fish numbers, potentially increasing prey availability and, in turn, boosting resource access. Additionally, phenotypic traits can be shaped by environmental factors through mechanisms like developmental pathways or phenotypic plasticity (Enberg et al. 2012). As a result, it can be challenging to determine whether observed changes in size-at-age during fishing periods are due to evolutionary pressures from fishing or indirect environmental changes caused by fishing (Enberg et al. 2012).

Water temperature significantly impacts the biology, and life history of fish and other aquatic organisms influencing fish body growth by affecting their metabolic rates, reproductive cycles, food availability, and overall physiology. (e.g., Magnuson et al. 1997; Casselman et al. 2002). Jagger (2024) and Jagger et al. (2025) determined a positive link between the mean annual growth rates of *Argyrosomus inodorus* and SST. Jagger et al. (2025) found an optimal thermal window that revealed that both cooler (<16°C) and warmer (>17°C) SSTs negatively impacted *A. inodorus* growth, as shown through otolith biochronology. The findings suggest that continued warming in the northern Benguela region could lead to further declines in growth rates for *A. inodorus,* potentially resulting in higher mortality under prolonged exposure to elevated temperatures (Jagger et al. 2025). Furthermore, in the northern part of the northern Benguela (Angola-Benguela Front), a temperate marine environment, rising inshore temperatures in a warming ocean hotspot have led to species mixing and even hybridization between two Sciaenid species of *Argyrosomus* (Potts et al. 2014; Wilhelm et al. 2020; Jagger et al. 2025). Vieira et al. (2020) identified a correlation between predicted otolith growth of European hake (*Merluccius merluccius*) and winter sea surface temperatures (SSTs) as well as spring bottom temperatures.

Vieira et al. (2020) demonstrated that these temperature variables influenced growth in distinct ways across various age groups. Thus, changing water temperatures affect various processes, including body growth rates, the timing of seasonal events (phenology), species distributions, species interactions, and overall productivity levels (e.g., Carey and Zimmerman 2014; Morrongiello et al. 2014; Tanner et al. 2019; Jagger 2024; Jagger et al. 2025; Wilhelm et al. 2020).

Climate change is anticipated to harm many freshwater ecosystems due to lower stream-flow and rising temperatures, conditions already present in areas undergoing severe drought. Morrongiello et al. (2011) linked year-to-year growth variations to large-scale changes in temperature and water regimes, finding that golden perch (*Macquaria ambigua*) growth decreased as lake water levels fell during drought periods, though warmer years helped to counterbalance this effect by boosting growth. Morrongiello et al. (2011) proposed that golden perch respond to shifts in food availability and competition within the species due to water level changes, while also benefiting from extended growing seasons that optimize physiological growth. Morrongiello et al. (2011) found that although climate models forecast considerable reductions in future water availability, fish growth could potentially rise due to a substantial extension of the growing season.

In addition to climate-driven changes in fish populations' life history strategies and productivity, selective fishing can also alter these strategies. For instance, Morrongiello et al. (2019) used a biochronology approach to examine a newly exploited temperate reef fish in Tasmania, finding that fishing pressure not only accelerated adult growth rates but also increased the fish's sensitivity to temperature over a short period of ten years. Fisheries-induced alterations in growth rates have been attributed to density-dependent processes or selection favouring early growth and reproduction, as discussed by Lorenzen and Enberg (2002) and Enberg et al. (2012).

Density-dependent growth regulation is a crucial mechanism in numerous marine fish species, frequently linked to competition for food (Trenkel et al. 2014). Vieira et al. (2020) demonstrated that the predicted otolith growth of European hake was associated with recruitment, attributing this relationship to density dependence. Duncan (2019) revealed that younger fish (under 12 years old) exhibited higher growth rates in the exploited population compared to those in the protected population in a marine protection area.

Currently, there are no studies done on the long-term growth rate changes of small pelagic fish species in the Benguela, and how these are influenced by different drivers, environmental, or biomass and how they relate to regime shifts. The present study aimed to address this gap in knowledge.

2.7 The application of otolith biochronologies fish population dynamics and environmental change studies

Age information forms the basis and is the most influential of biological parameters for calculations of growth rate, mortality rate and productivity (Campana 2001). Fish have indeterminate growth patterns, meaning they continue to grow throughout their lives, although growth rates typically slow with age, and these patterns are severely impacted by environmental conditions (Campana and Thorrold 2001). Therefore, fisheries science requires regular age determination if population dynamics in response to environmental adaptation are to be better understood (Campana and Thorrold 2001). Campana and Thorrold (2001) postulated that for a conjectured fish population, climate change could bring about increased growth rate, reduced longevity, reduced age of sexual maturity, and increased rate of natural mortality. Age data are valuable for constructing population models, conducting stock assessments, and facilitating the effective management of harvested species (Campana 2001). The most common way to obtain age estimates and growth parameters for fish is by counting growth rings in calcified tissues such as otoliths or scales (Campana and Therrold 2001).

A key property of otoliths is that they grow continuously throughout the life of an individual even when somatic growth slows (Casselman 1987). This distinctive feature enables otoliths to document entire individual growth histories and provide precise age information for the majority of studied species. In contrast to other structures like scales, where errors and discrepancies in aging are more common, especially as fish grow older (Beamish and McFarlane 1995). Each otolith has the potential to yield three comprehensive and complementary long-term biological data sets. These include: (1) life-history and demographic information extracted from structural features like growth-increment counts and widths; (2) environmental and physiological records obtained from structural features, as well as isotopic and elemental proxies present in the composition of otoliths; and (3) genetic data sourced from the organic fraction of otoliths or attached tissue (Morrongiello et al. 2012).

Traditionally, the examination of fish growth based on otolith data has depended on two approaches. Initially, calculations of the maximum size and growth rates of fish at the population level can be determined using specific equations like the von Bertalanffy growth curve (von Bertalanffy 1938), utilising data on fish size and age-at-capture (Baudron et al. 2014). The second method involves utilising otolith increment widths and size-at-capture to back-calculate an individual's length at the time of each increment's formation (Li et al. 2008). In employing this method, it is essential to assume a proportional correlation between fish somatic length and otolith length. The width of each yearly increment on a fish otolith can be measured to estimate the individual's annual growth throughout its life. Typically, each increment consists of a pair of zones: one translucent and one opaque. The translucent zone is believed to form during periods of slow growth, while the opaque zone forms during faster growth, usually aligning with more productive times. As a result, the width of the annual increment generally represents the fish's period of rapid growth each year. Back-calculation of otolith growth can serve as a valuable method for analysing individual fish growth, frequently applied in ecological studies (Tonkin et al. 2011). However, it is prone to notable biases when the connection between somatic and otolith growth becomes disrupted or is inaccurately estimated or when the fish experiences growth-selective survival (Campana 1990; Hare and Cowen 1995).

Traditional methods have a limitation in that growth is a multifaceted biological response influenced by numerous processes. Approaches that exclusively rely on population-level data, such as size-at-capture, might not adequately capture the ongoing processes that trigger individual responses (Enberg et al. 2012; Morrongiello and Thresher 2015). This is because these processes are influenced by both intrinsic factors (ontogenetic or individual-specific) and extrinsic factors (environmental or population-specific) that impact the availability and distribution of essential resources (Enberg et al. 2012). Otolith biochronologies provide valuable insights into fish growth patterns, age structure, and the influences of environmental conditions on fish populations, thereby aiding in effective fisheries management and conservation efforts (Morrongiello and Thresher 2015; Smoliński et al. 2017). It is essential to dissect the sources of growth variation to account for ecological and environmental impacts (Morrongiello and Thresher 2015). Connecting diverse individual growth histories across various cohorts (year-classes) can enhance comprehension of distinct growth variations and assist in interpreting historical growth patterns. This, in turn, can be applied to address population-level inquiries (Morrongiello and Thresher 2015).

The utilisation of mixed-effects modelling has proven effective in examining the chronology of otolith growth across various species and environments. Mixed-effect models prove highly beneficial, as the incorporation of random effect structures in otolith growth can more precisely capture the hierarchical nature of the ecological and biological data (Morrongiello et al. 2014). These models are adequately adaptable, enabling the examination of distinctions in phenotypic expression both intrinsic and extrinsic effects including age, environmental conditions, and population density (Morrongiello and Thresher 2015). This approach has been successfully applied over time scales spanning from a decade to nearly a century (e.g. Doubleday et al. 2015; Matta et al. 2018; Smoliński 2019). As a result, otolith chronologies have been utilised to examine fluctuations in annual fish growth rates and investigate the environmental factors influencing them.

Examples of otolith biochronologies in the northern Benguela demonstrated a significant negative correlation between sea surface temperature (SST) and the growth of *Merluccius paradoxus* (Wilhelm et al. 2020) and *Argyrosomus inodorus* (Jagger 2024; Jagger et al. 2025). In the southern Benguela, Brinkman et al. (2025a) identified four sardine growth regimes with shifts in 1986, 2006, and 2015, showing positive correlations between sardine growth, biomass, sea surface temperature, and copepod abundance. This suggests depensatory dynamics may destabilise sardine populations post-fishery collapse, with temperature and copepods as key growth factors. Thus, otolith biochronologies are ideal for analysing growth trends in sardine and Cape horse mackerel, providing insights into how environmental variability, climate shifts, and fishing affect growth rates in the Benguela region over time. This approach allows reconstruction of individual growth histories and correlation with environmental changes across long periods. Alternative options, like tagging, stock modeling, or genetic studies, would not yield the historical growth data needed for such an extensive time series or may be less precise for historical growth data. Thus, otolith biochronologies capture high-resolution, long-term data essential for understanding species responses to changing ecosystems and informing sustainable management. Otolith biochronologies aid in understanding species responses to changing ecosystems, and informing management strategies for these commercially important fish.

CHAPTER THREE: UNVEILING ECOSYSTEM SHIFTS IN THE SOUTHERN BENGUELA THROUGH OTOLITH BIOCHRONOLOGIES OF SARDINE (*SARDINOPS SAGAX*)

Abstract

Sardine (*Sardinops sagax)* in the southern Benguela has shown substantial changes in population size over the past 70 years. Heavy fishing pressure in the 1950s to early 1970s caused the collapse of sardine stocks in South Africa. A fishery collapse happens due to significant alterations in the marine community, hindering the recovery of valuable commercial species and leading to cascading effects across multiple trophic levels in marine food webs. In this study, a robust 58-year biochronology (1962-2019) was developed using archived sardine otoliths from the West of Cape Agulhas in South Africa. Sequential t-test analysis of regime shifts (STARS) performed on the biochronology of fish growth indicated four regimes with three alteration points in 1986, 2006, and 2015 that correspond with periods of low, high, average and low biomass, respectively; i.e. high growth rates occurred during the high biomass period and vice versa. A series of mixed effects models was developed to determine increment width response to selected environmental, prey availability and sardine biomass factors based on the assumption that otolith increment growth is a proxy for somatic growth. Predicted sardine growth positively correlated with sardine biomass, sea surface temperature and copepod abundance estimates. This observation suggests that sardine population dynamics exhibit a depensation mechanism, potentially destabilizing populations after the fishery collapse. Sea surface temperature and copepod abundance have been primary factors influencing sardine growth, partly due to depensatory population dynamics. Furthermore, the study improves understanding of how different factors have affected sardine growth following the collapse of the sardine fishery.

3.1 Introduction

Climate change is recognised worldwide as a major factor impacting marine biodiversity, with its effects expected to increase in the coming years (e.g. Lockerbie and Shannon 2019). However, the severity of these impacts will vary depending on the geographical location, influenced by oceanic conditions and the vulnerability of species in specific regions (Lockerbie and Shannon 2019). The Benguela Upwelling System, with highly productive ecosystems, is characterised by the equatorward Benguela Current, vigorous shelf-edge jets and several distinct upwelling cells, which undergo large seasonal to decadal variability (e.g. Shannon 1985; Bordbar et al. 2021; Brandt et al. 2024). The southern Benguela, in South Africa is primarily affected by alongshore winds, exhibiting seasonal variations and occasional overflow of warm events from the Agulhas Current (Jarre et al. 2015).

Observations along the west coast of South Africa suggest notable environmental shifts likely attributable to climate change. Coastal temperatures on the west coast have decreased by roughly 0.5°C per decade over the last forty years, potentially influenced by stronger, unusual upwelling-promoting winds and a northward extension of the South Atlantic Subtropical Anticyclone (Blamey et al. 2015). There has been a slight upward trend in upwelling since 1979-2014 on the west coast, the south coast has experienced a significant increase in upwelling intensity over the past 35 years, leading to more pronounced local upwelling events (Lamont et al. 2018). Coastal temperatures on the south coast have also declined by approximately 0.4°C per decade (Blamey et al. 2015). In contrast, the Agulhas Current, pivotal for regional oceanic dynamics (Augustyn et al. 2018), has warmed by up to 0.6°C per decade, causing heightened thermal gradients across the south coast shelf (Rouault et al. 2010; Blamey et al. 2015). This region is identified as one of the 23 global marine hotspots experiencing rapid ocean warming (Hobday and Pecl 2014).

Ecosystem alterations in the southern Benguela, influenced by sea surface temperature, wind and upwelling patterns, encompass both biological and oceanographic components (Howard et al. 2007; Blamey et al. 2012). These ecosystem alterations, also known as regime shifts refer to a sudden transition from one stable ecosystem state to another, impacting multiple trophic levels within a relatively short period compared to contrasting regimes (Blamey et al. 2012). While changes in ocean and atmospheric climates are the main drivers (Polovina 2005), biotic factors, alterations in habitat structure, and fishing also contribute significantly (Scheffer and Carpenter 2003; Daskalov et al. 2007). Copepods, as the primary constituents of the zooplankton community and essential food for numerous organisms such as sardines, demonstrate remarkable sensitivity to environmental shifts due to their short life spans, rendering them valuable indicators of changes in marine ecosystems (Verheye et al. 1998; Verheye 2000; Hutchings et al. 2006). Drivers of ecosystem alterations can arise from natural, human-induced, or combined influences (de Young et al. 2012). Currently, two major regime shifts have been documented in the southern Benguela – the first regime shift took place in the aftermath of the sardine collapse during the early-mid 1960s and was fishing-induced (Jarre et al. 2015). The second, known as the eastward shift of sardines in South Africa, occurred during the mid-1990s to early 2000s, triggered by environmental changes and aggravated by fishing pressure (Blamey et al. 2012; van der Lingen 2021).

Sardine (*Sardinops sagax*) in South Africa fishery covers a vast area, extending from the west coast, including the western Agulhas Bank up to Cape Agulhas (20ºE), to the south coast, ranging from Cape Agulhas to approximately East London, which includes the south and east Agulhas Bank. Additionally, it encompasses the east coast of South Africa, covering the coasts of Eastern Cape and KwaZulu- Natal (van der Lingen and Hampton 2019). Historically the sardine fishery was considered targeting one population however recently it has been postulated that subpopulations (west and east of Cape Agulhas) exist (Beckley and van der Lingen 1999; de Moor and Butterworth 2015).

The sardine population in the southern Benguela upwelling ecosystem has shown significant changes in biomass over the last 50 years (van der Lingen et al. 2006). A large population that initially supported high catches collapsed in the early 1960s, recovered in the 1990s, increased again at a maximum in the early-2000s before declining rapidly once again thereafter in the mid-2000s such that the sardine population has remained low and depleted (Beckley and van der Lingen 1999; van der Lingen 2021). The significant decrease in sardine biomass in both the western and eastern segments of the population since 2004-2005, has been caused by an extended period of low recruitment and a sudden rise in adult mortality that cannot be attributed to fishing activities (Coetzee et al. 2008). Moreover, changes to sardine life history parameters: length at 50% sexual maturity (L50), condition factor (CF), and standardized gonad mass (SGM) have occurred since the 1950s (Beckley and van der Lingen 1999). Indeed, growth plays a crucial role not just in individual fitness concerning factors like body size, behaviour, reproduction, and mortality rates, but it also significantly contributes to population-level parameters such as recruitment success, generation time, and the overall biomass of the stock (Enberg et al. 2012). The "Rosa Lee phenomenon" (Lee 1912) arises from the natural variation in individual growth rates within fish populations, coupled with the preferential removal of faster-growing individuals through selective mortality mechanisms such as fishing (Kraak et al. 2019). Additionally, it exerts an influence on the growth of the remaining fish by introducing changes to density-dependent processes (Lorenzen and Enberg 2002), habitat (Rooper et al. 2011), or food webs (Audzijonyte et al. 2013).

The study of long-term changes in fish growth can provide important insights into the impacts of fishing and environmental variability. Growth is the phenotypic manifestation of the relationship between the individual (intrinsic) and the environmental or ecological (extrinsic) components that influences the energy budgeting within an individual (Enberg et al. 2012). Several studies have made use of dendrochronological methods to demonstrate the diverse relationships between fish growth and external drivers and provide quantifiable reasons for year-to-year variability or long-term trends (Ong et al. 2016), Bayesian techniques (Helser et al. 2012) and regime shifts (Smoliński and Mirny 2017).

The overall objective of this study was to understand how the growth rate of sardine is affected by its population size (in terms of biomass), variability in environmental conditions, and long-term environmental changes, and population size within the southern Benguela off South Africa. More specifically the objectives were:

(1) To develop a multi-decadal biochronology of sardine during 1962 – 2019 to characterise long-term variability of the sardine population average growth.

(2) To determine if there has been any abrupt alteration in the annual otolith growth patterns that may be linked to the ecosystem regime shift.

(3) To investigate the effects of sardine biomass on the sardine growth patterns during the study period.

(4) To investigate the effects of environmental (SST and upwelling index) and biological (copepod abundance) variables on sardine growth patterns during the study period.

Moreover, this chapter addresses the following hypotheses:

a) H_0: Annual otolith growth patterns of sardine in southern Benguela remained stable over time, with no abrupt shifts in the biochronology.

H_1: There are significant temporal changes in the annual otolith growth patterns of sardine biochronology in southern Benguela.

b) H_0: Population biomass does not significantly affect the annual growth patterns of sardine in southern Benguela.

H_1: Population biomass significantly influences the annual growth patterns of sardine in southern Benguela.

c) H_0: Environmental factors (sea surface temperature, upwelling intensity) and copepod abundance do not significantly affect the annual growth patterns of sardine in southern Benguela.

H_1: These environmental and biological variables have a significant effect on growth patterns of sardine in southern Benguela.

3.2 Materials and Methods

3.2.1 Study Area

The study area (Figure 3.1) was located within the southern Benguela and extends southwards from Orange River mouth on the west coast to the Agulhas Bank off the south-west coast of South Africa. The Cape Agulhas (20°E) (Figure 3.1) is considered the boundary between the two stocks and movement of sardine of all ages are assumed to be exclusively from west to south coast (Coetzee et al. 2008). However, some eggs spawned on the south coast may be transported to the west coast nursery area and thus contribute to recruitment to the west coast (Coetzee et al. 2008).

3.2.2 Otolith Sampling and Measurements

A comprehensive analysis was conducted using 808 archived sardine otoliths sourced from the Department of Forestry, Fisheries, and the Environment (DFFE) in South Africa, spanning the years 1962 to 2019 (Figure B1). Only archived otoliths originating from sardines caught west of Cape Agulhas were used for analysis (Figure 3.1). Otoliths were collected from fish caught during DFFE annual surveys in November as well as from commercial port samples sampled west of Cape Agulhas off commercial purse-seine vessels.

The otoliths were cleaned with distilled water and mounted whole in black Perspex plate moulds and embedded in epoxy resin, following the FAO protocol approved in Kaliningrad in 2001 (Tandstad and Caramelo 2002), which is the standard method used in the Mediterranean and northwest African regions (Soares et al. 2005). Calibrated images of the sardine otoliths were taken using Zeiss Stemi 508 stereo microscope that is fitted with a Carl Zeiss Axiocam 208 colour camera. The assumption that otolith growth is proportional to somatic growth was tested by correlating fish length with otolith radius showing a significant relationship between fish length and otolith radius ($r=0.704$, $p<0.05$, Figure B2).

The otolith images were analysed using the ObjectJ macros, an ImageJ plugin (Schneider et al. 2012). For each otolith, the length of each annual increment was measured along the posterior region from the nucleus to edge (Figure 3.2). The otolith increment widths were recorded together with the year when the increment was formed, and age at the time of increment formation (Age) for each fish. The cohort was assigned as the year of birth for each fish. The age-at-capture (AAC), defined as the final age at time of capture, was assigned for each fish. The analysis incorporated measurements from a total of 2,352 increments spanning ages 2 to 7 years, with a mean age of 4 years, over a time period from 1962 to 2019. Thus, fish with ages less than 2 were not included in the sample. However, the first increment was measured for all fish older than 2 years. Sardines were assumed to spawn in austral spring to summer (September to March) (van der Lingen and Huggett 2003). Thus, the translucent zones were assumed to start forming mainly in spring (September-October), while most of the fish were caught in November. The sardines date of birth was set as 1 January (FAO 2002). One increment consisted of the relatively broad opaque zone and the relatively narrow translucent zone.

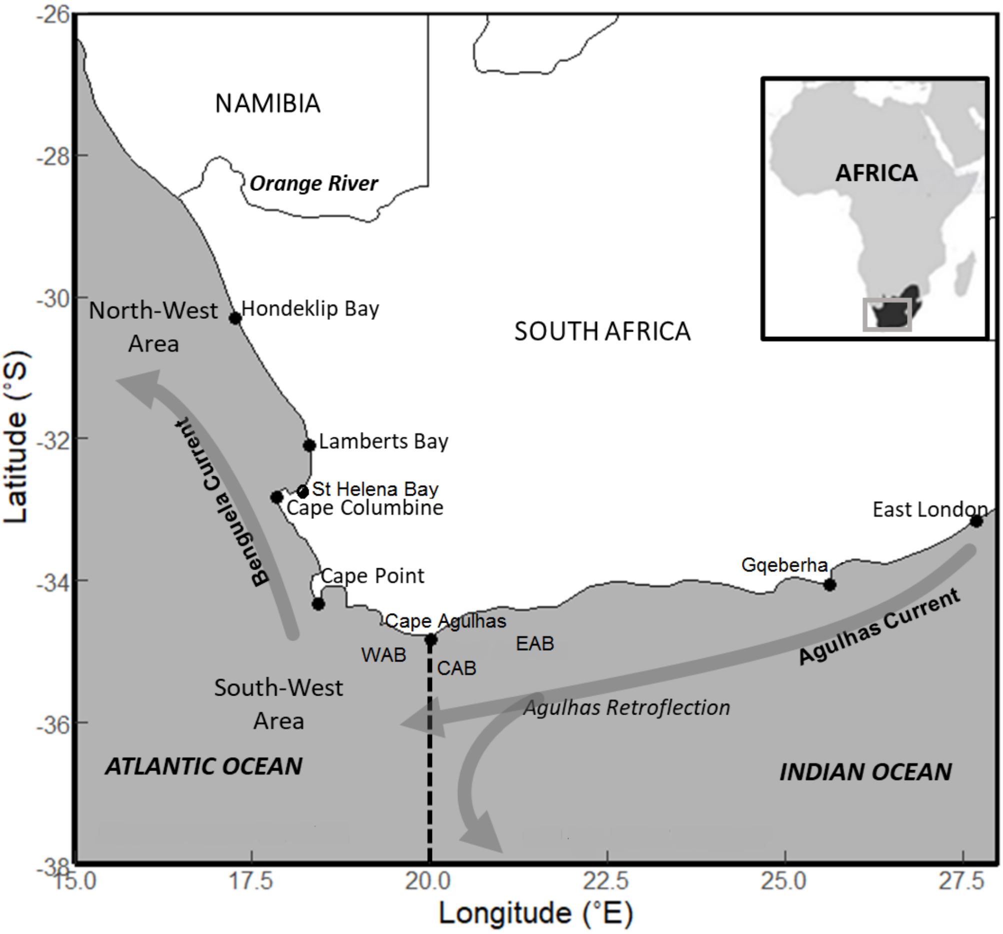


Figure 3.1. Geographical map of the southern Benguela off South Africa. In this study, the west coast is defined as the area West of Cape Agulhas from Cape Point northwards to the Orange River mouth and includes the western Agulhas Bank (WAB), the south coast is the area East of Cape Agulhas to Gqeberha (previously Port Elizabeth) and includes the central Agulhas Bank (CAB) and eastern Agulhas Bank (EAB), and the East coast from Gqeberha to KwaZulu-Natal.

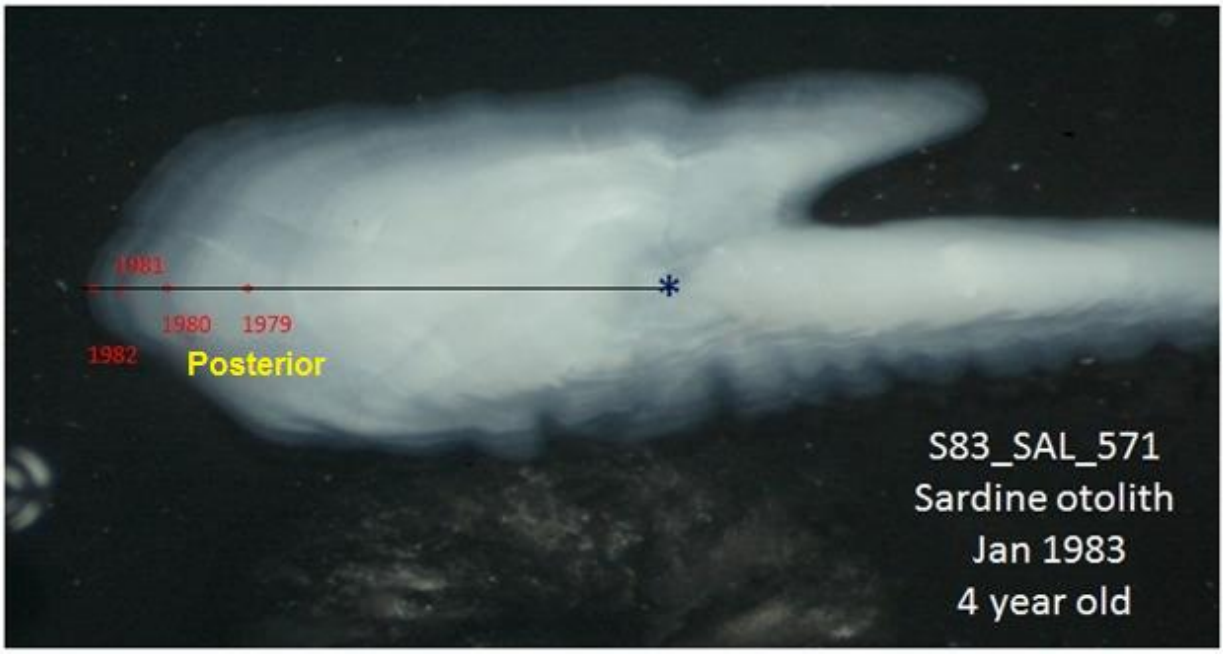


Figure 3.2. Posterior view of an otolith from a 4-year old sardine (Sardinops sagax) caught in January 1983 in South Africa. Increment measurements were taken from the nucleus (blue asterisk) to the edge of the otolith on the posterior region (black line) of the annual rings (red asterisks). All otolith samples were viewed under reflected light at 32x magnification.

3.2.3 Environmental, Sardine Biomass and Zooplankton Data

All environmental (SST and upwelling), sardine biomass and copepod abundance variables used in the growth model are listed in Table 3.1. Two sea surface temperature (SST) datasets were utilised in the growth models during two periods namely: Hadley SST dataset (during 1962-2019) and the SST dataset described by Reynolds et al. (2002) during 1984-2019. The Hadley SST dataset was available for the entire sardine growth time series (1962-2019), while the Reynolds et al. (2002) SST data was available from 1981 to 2019. The Hadley SST dataset offers lower spatial resolution (e.g., 5° x 5° grid) and mainly depends on in-situ measurements, which can result in data gaps or reduced accuracy. This dataset was chosen for analysing the entire sardine growth time series because it is well-suited for studying long-term climate trends, emphasizing long-term averages and larger spatial scales. However, the Reynolds et al. (2002) SST dataset includes finer spatial and temporal resolution, integrates satellite data and offers a more detailed and accurate representation of SST in the southern Benguela. This dataset was selected to analyse the shorter sardine growth time series (1984-2019) due to its ability to capture short-term variability. The Hadley SST dataset and the Reynolds et al. (2002) SST dataset were independently evaluated against the entire and short sardine growth time series, respectively, ensuring that overlapping time periods were excluded from each separate assessment. Furthermore, the Hadley SST dataset describes the entire area west of Cape Agulhas while the SST described by Reynolds et al. (2002) was divided into two major areas to describe the area west of Cape Agulhas. Firstly, average monthly SSTs for the entire area west of Cape Agulhas (30–36°S and 17–22°E) were extracted from the Met Office Hadley Centre's, HADSST.3.1.1.0 dataset (HADSST), a monthly global field of SST, for January 1962 to December 2019. HADSST data were taken from ICOADS and were produced by taking in situ measurements of SST from ships and buoys (Kennedy et al. 2011). Secondly, average monthly SST values were extracted from the National Oceanic and Atmospheric Administration (NOAA) National Centre for Environmental Prediction (NCEP) database described by Reynolds et al. (2002) for two major areas west of Cape Agulhas. The mean monthly SST values were extracted for two major areas (corresponding to areas identified by van der Lingen et al. 2006a) namely: northwest (30°S - 33°S) representing the area between the Orange River and Cape Columbine (NW), southwest (34°S - 36°S, 18°E - 20°E) representing the area between Cape Columbine and Cape Agulhas (SW) in (Figure 3.1). The Hadley SST dataset is represented by 'HADSST' and the Reynolds et al. (2002) SST dataset is represented by 'SWSST' and 'NWSST' in Table 3.1.

The monthly Southern Oscillation Index (SOI), which is a normalized index derived from the observed sea level pressure (SLP) variations between Tahiti and Darwin (Australia), was extracted for the area between 32-34°S and 16-18°E for January 1962 to December 2019. The Southern Oscillation and El Niño datasets are known as El Niño/Southern Oscillation (ENSO), a periodic fluctuation (i.e., every 2–7 years) in sea surface temperature (El Niño) and the air pressure of the overlying atmosphere (Southern Oscillation) across the equatorial Pacific Ocean (Wang et al. 2017). It serves as an indicator of the extensive changes in air pressure between the western and eastern tropical Pacific, characterizing the state of the Southern Oscillation during El Niño and La Niña events (Ropelewski and Jones 1987). The Multivariate ENSO index MEI version 2 (MEIv2) dataset was extracted for the area between 32-34°S and 16-18°E for January 1962 to December 2019. MEIv2 was designed to provide a comprehensive depiction of the atmospheric and oceanic anomalies associated with ENSO events (Zhang et al. 2019). MEIv2 is constructed using five key variables from the tropical Pacific namely sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, and outgoing longwave radiation (Zhang et al. 2019). The SOI and MEIv2 indices were included in the investigation to explore the influence of ENSO on sardine growth (see Table 3.1), despite ENSO limited known impact on the Benguela Current. Rouault and Tomety (2022) identified a leading lag correlation between ENSO and SST in the Benguela upwelling system, indicating that ENSO might have a more significant impact than previously recognised. Thus, including ENSO in the analysis ensures a thorough exploration of any indirect or previously unnoticed effects on sardine growth, particularly during strong ENSO events.

Bordbar et al. (2021, 2023) reanalysed hourly sea level pressure and surface wind vectors from the European Centre for Medium-Range Weather Forecasts ERA5 available for 1979–2019, to determine the coastal upwelling driven by alongshore winds and wind-stress-curl-driven upwelling offshore was calculated in m^2s^{-1}. The daily and monthly averages were computed from hourly values. Monthly coastal upwelling indices created by (Bordbar et al. 2021, 2023) were used for Cape Columbine (32.8256° S, 17.8453° E). The monthly coastal upwelling index for Cape Columbine is represented by "UICC" parameter in Table 3.1.

The total sardine biomass time series (1984-2019) was sourced from available spawner-stock biomass estimated from annual pelagic acoustic surveys by the Department of Forestry, Fisheries and the Environment in November for 1984 to 2019 (Barange et al. 1999; van der Lingen et al. 2006a). The total sardine biomass estimates were divided to represent the proportions for the areas west of Cape Agulhas, east of Cape Agulhas and for both west and east of Cape Agulhas. However, the primary focus was on the area west of Cape Agulhas. The sardine biomass time series was log-transformed and lagged by 1 year to match with the next year, e.g. November of 2020 represents 2021 summer growth (austral summer of 20/21 was labelled as 2021 year of capture) (Morrongiello and Thresher 2015). The sardine biomass 'SarBiom' parameter is presented in Table 3.1 and used in predicting the growth of sardine in shorter time series (1984-2019).

Zooplankton samples were collected annually from 1951 to 2016 (updated from Verheye et al. 2016) in St Helena Bay on the west coast of South Africa during austral autumn (March - June) (see Verheye et al. 1998 for sampling details). However, there were gaps in the time series: specifically, data for the years 1968-1977, 1979-1983, 1985-1986, and 2012-2014 were unavailable due to the absence of zooplankton surveys done during those years; in addition, there are also no zooplankton data available to match our sardine growth data during 2017-2019. Annual zooplankton samples were collected during peak sardine and anchovy recruitment periods. The zooplankton samples were analysed on the basis of copepod abundance. The sardine growth time series was correlated (Pearson's Correlation Coefficient) with log-transformed (Log_{10} (No. m^{-2} + 1)) copepod abundances updated from Verheye et al. (2016). The copepod abundance parameter is represented by "Copepod" in Table 3.1. The environmental, sardine biomass and copepod abundances estimates were sequentially included in the sardine growth model.

3.3.4 Data Analysis

It was assumed that the translucent zone was formed during austral winter/spring while the opaque zone was formed during austral summer. A series of mixed effects models was developed to investigate increment width (Inc) response to a series of intrinsic (fish-specific) and extrinsic (environmental) sources (Morrongiello and Thresher 2015). The fixed effects in a model estimate the impact of variables that are presumed to exert a consistent influence on the outcome variable, whereas the random effects reflect variability in outcome across different groups or individuals. The fixed intrinsic effects were determined as Age and Age at Capture (AAC) (Table 3.1). The inclusion of the ACC term serves to address biases arising from sampling (such as skewed age distributions) and assesses potential biases arising from selectivity based on growth rate, aiming to correct for them (Morrongiello and Threshner 2015). Sex of the fish was not used as a covariate, as sex data were not available for the majority of the archived otoliths. Increment widths, Age, and AAC were log-transformed and mean-centred to satisfy model assumptions and facilitate model convergence (Morrongiello and Threshner 2015). Random effects were intercepts of FishID, cohort and year along with the by-FishID, by-Cohort and by-Year random slopes for the effect of Age. The FishID term accounts for the correlation between incremental measurements within a fish, considering the individual's estimated growth relative to the average. FishID deviations may arise from genetic identification and/or measurement error processes (Morrongiello and Threshner, 2015). The concept of cohort incorporates a temporal estimate derived by considering both inherent and external variations in growth, as well as systematic deviations in growth observed among groups of fish over their lifetimes (Morrongiello and Threshner, 2015). The Year random effect essentially captures the annual fluctuations in growth that may be linked to external environmental factors, once age effects have been taken into consideration.

Table 3.1. Description of parameters used in predicting the growth of South African sardine (*S. sagax*).

Parameter	**Description**	**Range**	**Mean**
Fixed effects			
Age	Age (yr) when otolith increment formed	2-7	2.071
Age-at-capture (AAC)	Final age (yr) at time of capture	2-7	3.837
Random effects			
FishID	Unique identification number for each fish		
Cohort	Group of fish spawned in the same year		
Year	Calendar year of otolith ring formation		
Environmental effects			
Copepod	Annual $\log_{10}$ total copepod abundance (1962-2016)	3.28 – 5.89	4.876
HADSST1	Monthly SST (HADSST3.1) for January (1962-2019)[a] (ºC)	-1.98 – 1.43	-0.023
HADSST6	Monthly SST (HADSST.3.1) for June (1962-2019)[a] (ºC)	-0.55 – 0.95	0.077
SOI4	Monthly Southern Oscillation Index for Apr (1962-2019)	-1.40 – 1.90	0.097
MEIAvg4-6	Monthly Multivariate ENSO index averaged Apr-Jun (1962-2019)	-1.57 – 2.53	0.293
NWSST1	Monthly SST Reynolds et al. (2002) for North West area January (1982-2019)[b] (ºC)	19.27 – 21.78	20.13
SWSST6	Monthly SST Reynolds et al. (2002) for South West area June (1982-2019)[b] (ºC)	14.42 – 16.50	15.40
UI_CCPrev11	Monthly Upwelling index at Cape Columbine lagged with 1 year for Nov (1980-2019) (m^2/s^{-1})	0.54 – 2.51	1.664
UI_CC7	Monthly Upwelling index at Cape Columbine for July (1979-2019) (m^2/s^{-1})	-1.28 – 0.714	-0.084
SarBiom	Annual November survey biomass estimates lagged by 1 year for the area West of Agulhas (1985-2019) (tons)	25457 – 1343118	364451.63

[a] HADSST were used in 1962-2019 period and;

[b] SST as described by Reynolds et al. (2002) were used in the 1984-2019 period.

The following mixed effects full model was fitted to the entire time series 1962-2019:

$$\text{Log (Inc)} \sim \text{Log(Age)} + \text{Log(AAC)} + \text{Log(Age)} \mid \text{Fish ID} + \text{Log(Age)} \mid \text{Year} + \text{Log(Age)} \mid \text{Cohort.}$$

(1),

The model includes combinations of fixed effects (Age and AAC) and random effects. The intercepts for random effects are represented by '|' and are grouped by FishID, Cohort, and Year. Additionally, random slopes for the effect of Age are also included; for example, the random slope of the effect of log(Age) by FishID is denoted as log(Age) | FishID. Variables were tested for the best combinations of explanatory variables describing increment width (Inc) as indicated in Equation 1. Akaike's Information Criterion corrected for small sample sizes (AICc) was used to select the optimal base model describing fish growth (Burnham and Anderson 2004). The best model was selected and refitted with maximum likelihood estimates to produce unbiased parameter estimates (Zuur et al. 2009) using the random effects of year to produce a best linear unbiased predictor (BLUP) of growth for each year from 1962-2019. The best linear unbiased predictor (BLUP) was extracted for the Year random effect model was derived from the Year random effect model to illustrate the variation in fish growth across different years. The conditional R^2 metric was computed for each model to evaluate the proportion of variance in fish growth explained by both fixed and random effects (Nakagawa and Schielzeth 2013).

Sequential T-test Analysis of Regime Shifts (STARS) was performed on the BLUP series of the year effect to detect the magnitude and scale of the regime shifts from the mean growth of fish (Rodionov 2004). The STARS method calculates a probability level for the mean year and regime shift year with respect to an adjusted two-tailed Student's *t*-test. The sequential analysis calculates the regime shift index (RSI), the mean value of the regimes with equal and unequal weights, regime length, and final confidence levels for the shifts and the weights of the outliers. Rodionov (2006) developed a ‘pre-whitening’ procedure to eliminate potential autocorrelation (red noise) component from the time series before carrying out the STARS analysis using “pre-whitening” method. The cut-off length, l = 10 years, was established since regime shifts are related to oceanic variability on a decadal scale. Furthermore, it was required that the results correspond with regime studies conducted by (Howard et al. 2007; Blamey et al. 2012) in the Benguela ecosystem. The cut-off length l = 7 years and l = 13 years were used by (Howard et al. 2007; Blamey et al. 2012). However, in the present study it was found that l = 7 did not detect some regime shifts, whereas l = 13 produced a result similar to l = 10, and was thus deemed unnecessary to be applied to the BLUP time series. The Huber parameter is default at H = 1 where the sensitivity analysis for the study was performed. The analyses were carried out using a significance level of 0.10 in order to detect regime shifts and to be comparable with (Howard et al. 2007; Blamey et al. 2012) that determined more shifts were identified at the 10% significance level compared to the 5% level. The alteration points were evaluated against earlier research on regime shifts to check for alignment with previous regime shift results (Table B4).

Supplementary fixed terms were included to assess the impact of extrinsic environmental predictors (SST and upwelling), copepod abundance, and sardine biomass on growth. The predictors (SST, upwelling index, SOI, MEI, sardine biomass and copepod abundance estimates) were evaluated for collinearity (Figure B5, Figure B6 and Figure B7). During this phase, the dataset was restricted to two periods 1962-2019 and 1984-2019 to align sardine growth data with the available environmental variables (SST and upwelling), copepod abundance, and sardine biomass data (see Table 3.1). To assess the possible impact of extrinsic environmental factors on the growth of fish, correlations of the extrinsic variables (Figure B5) and a set of model comparisons was carried out, considering the influence of variables such as copepod abundance estimates, sardine biomass, sea surface temperature (SST), and upwelling indices. Considering the temporal constraints of sardine biomass, upwelling indices, and SST variables, this process was carried out in two steps. In the first step, the period 1962-2019 was used to include SOI, MEIv2, HADSST and copepod abundance estimates in the set of optimal model comparisons (N=2352 increments; Groups: 808 FishID and 58 Years). However, since SOI and MEIv2 are correlated (Figure B5), only one of these variables was included in the model at a time. In the second step, the period 1984-2019 was used to include sardine biomass and the upwelling index in addition to SST described by Reynolds et al. (2002) and SOI variables (N=1424 increments; Groups: 464 FishID and 35 Years). The most suitable model was chosen as the model with the lowest AICc and with ΔAICc < 2 compared to the model with the lowest AICc, and fewer parameters (K) than the model with the lowest AICc.

All data analyses were performed in R Studio Version 1.1.463 (R Core Team, 2018), with libraries lme4 (Bates et al. 2014), AICcmodavg (Mazerolle, 2019), effects (Fox 2003; Fox and Weisberg 2019), lattice (Sarkar 2008), tidyverse (Wickham et al. 2019) and MuMIn (Bartoń 2019).

3.3 Results

The optimal base model that explained fish incremental growth 1962 – 2019 (Figure B3) comprised fixed effects for intercept, Age and AAC, alongside random effects for intercept of Year and slope of Age and FishID with the exclusion of cohort (AICc = -23.7, Conditional R^2 = 0.791, Table B1). The optimal base model explained 79% of the variation in sardine growth. Age was the most significant factor affecting growth among the tested variables, with the predicted increment widths decreasing markedly as the fish got older (Figure B4). A positive relationship between fish growth and Age-at-capture was indicated by the optimal base model (Table 3.2) for data fitted during 1962-2019 period. The random effects, demonstrated considerable inter-annual variation (Table 3.2).

To address Hypothesis 1, which tested whether annual otolith growth patterns of sardine remained stable over time (H_0) or exhibited significant temporal changes (H_1), the sardine otolith biochronology was analysed for evidence of growth shifts. The Sequential T-test Analysis of Regime Shifts (STARS) was conducted on the best linear unbiased predictor series of the year effect in order to determine the occurrence of regime shifts in the growth of the fish (Figure 3.3). Growth during the final interval (2015-2019) was considered low, despite a high confidence level. This is attributed to the shorter cut-off length of 5 years and a significantly smaller sample size (N=62) compared to other regimes in the otolith biochronology. The results demonstrated a trend of predicted growth from low growth (1962-1985) to high growth (1986-2005), then to average growth (2006-2014) and finally to low growth (2015-2019) indicated in (Figure 3.3). The shifts in the growth of fish were detected at a significance level ($p < 0.1$) with alteration points in 1986, 2006 and 2015 (RSI = 0.74, -0.27 and -0.43, respectively). STARS analysis performed on the BLUP of the year effect on fish growth indicated four regimes with three alteration points in the southern Benguela (Figure 3.3). The first alteration occurred in 1986 from low average growth to high average growth (two years after the SST alteration point (Howard et al. 2007), and the second in 2006 from high growth to average growth (1-2 year(s) after the SST alteration point (Howard et al. 2007) and the final alteration occurred in 2015 from average growth to low growth (Figure 3.3 and Table B4).

To address Hypothesis 3, which tested whether environmental variables (sea surface temperature and upwelling intensity) and biological variables (copepod abundance) significantly influence annual otolith growth patterns (H_1) or have no effect (H_0), additional variables were applied to the base model to assess the strength and direction of these associations. The addition of environmental variables (HADSST, SOI) and copepod abundance parameters to the optimal base model fitted to data during 1962 to 2019 period indicated significant effects on growth by decreasing the model AICc significantly (Table B2). The best suited model for the period 1962-2019 incorporated HADSST in June (HADSST6) and copepod abundance (Copepod). The secondary best model had the lowest AIC (AICc = 2.9, Conditional R^2 = 0.79), but differed by AIC=0.38 and had one more parameter (K) than the best suited model chosen (AICc = 3.28, Conditional R^2 = 0.79, Table B2). The secondary best model indicated a positive effect on growth of both HADSST6, SOI in April (SOI4) and copepod abundance (Table 3.2, Figure 3.4).

To address Hypotheses 2, which tested whether sardine biomass significantly influence annual otolith growth patterns (H_1) or have no effect (H_0), statistical analyses were conducted to evaluate the relationships between these predictors and growth variation in sardine. Therefore, sardine biomass predictor parameter (SWBiomLag), together with all other predictor parameters which were available from 1984 onwards and represented by SST as described by Reynolds et al. (2002) for the northwest and southwest area of the southern Benguela (NWSST and SWSST) for winter and summer months, upwelling index at Cape Columbine (UI_CC), copepod abundance (Copepod) were added to the base model to find the optimal model (Table B3). The optimal model of sardine growth 1984-2019 contained fixed effects for intercept, Age and AAC, and random effects for intercept of Year and FishID (base model) as well as June SST for southwest area (SWSST6), January SST for northwest area (NWSST1) and sardine biomass (AICc = -110.68, Conditional R^2 = 0.81, Table B3, Table 3.3). BLUP of otolith growth significantly positively correlated with the June SST for southwest area (SWSST6) and sardine biomass in the southern Benguela (Figure 3.5a). BLUP of otolith growth significantly negatively correlated with the January SST for northwest area (NWSST1) in the southern Benguela (Figure 3.5b).

Table 3.2. Variance components and estimates of random (a) and fixed (b and c) effects of the initial sardine growth model fitted to data from 1962 to 2019 (Number of observations: 2352, groups: FishID, 808; Year, 58). Random age slopes are denoted by "|". Age was log-transformed in the model. Significance level codes: <0.001 '***' <0.01 '**' <0.05 '*'.

a)

Random effects	Variance (± SD)	Correlation
FishID	0.017 (0.131)	
Age|FishID	0.021 (0.146)	0.23
Year	0.004 (0.060)	
Age|Year	0.002 (0.041)	-0.20
Residuals	0.037 (0.191)	

b)

Intrinsic effects	Estimate (SE)	*t*-value	p-value
Intercept	-2.372 (0.243)	-9.78	
Age	-0.664 (0.018)	-36.49	< 2.2e-16 ***
AAC	0.085 (0.035)	2.44	0.0043001 **

c)

Extrinsic effects	Estimate (SE)	*t*-value	p-value
Copepod Abundance	0.111 (0.028)	3.93	0.0003031 ***
HADSST6	0.072 (0.030)	2.43	0.0214654 *

Table 3.3. Variance components and estimates of random (a) and fixed (b and c) effects of the final sardine growth model fitted to data from 1984 to 2019 (Number of observations: 1424, groups: FishID, 464; fYear, 35). The model was incorporated to encompass SST, upwelling, copepod abundance and biomass estimates available from 1984. Random age slopes are denoted by “|”. Age was log-transformed in the model. Significance level codes: <0.001 ‘***’ <0.01 ‘**’ <0.05 ‘*’.

a)

<table>
<tr><th>Random effects</th><th>Variance (± SD)</th><th>Correlation</th></tr>
<tr><td>FishID</td><td>0.017 (0.131)</td><td></td></tr>
<tr><td>Age|FishID</td><td>0.022 (0.148)</td><td>0.21</td></tr>
<tr><td>fYear</td><td>0.003 (0.089)</td><td></td></tr>
<tr><td>Residuals</td><td>0.037 (0.192)</td><td></td></tr>
</table>

b)

Intrinsic effects	Estimate (SE)	*t*-value	p-value
Intercept	-2.356 (0.239)	-9.87	
Age	-0.670 (0.016)	-42.24	< 2.2e-16 ***
AAC	0.085 (0.034)	2.50	0.0075798 **

c)

Extrinsic effects	Estimate (SE)	*t*-value	p-value
SWSST6	0.082 (0.022)	3.80	0.0006157 ***
Log(SarBiom)	0.039 (0.012)	3.20	0.0026387 **
NWSST1	-0.045 (0.021)	-2.17	0.0376348 *

The predicted growth was positively affected by sardine biomass West of Agulhas (lagged by one year) (Figure 3.6b) and austral winter (June) SST for southwest area (SWSST6) but negatively affected by austral summer (January) SST described in the NW area (Figure 3.6a and c). The copepod abundance representing the entire period 1962-2019, demonstrated significant impacts on sardine growth (Figure 3.6d).

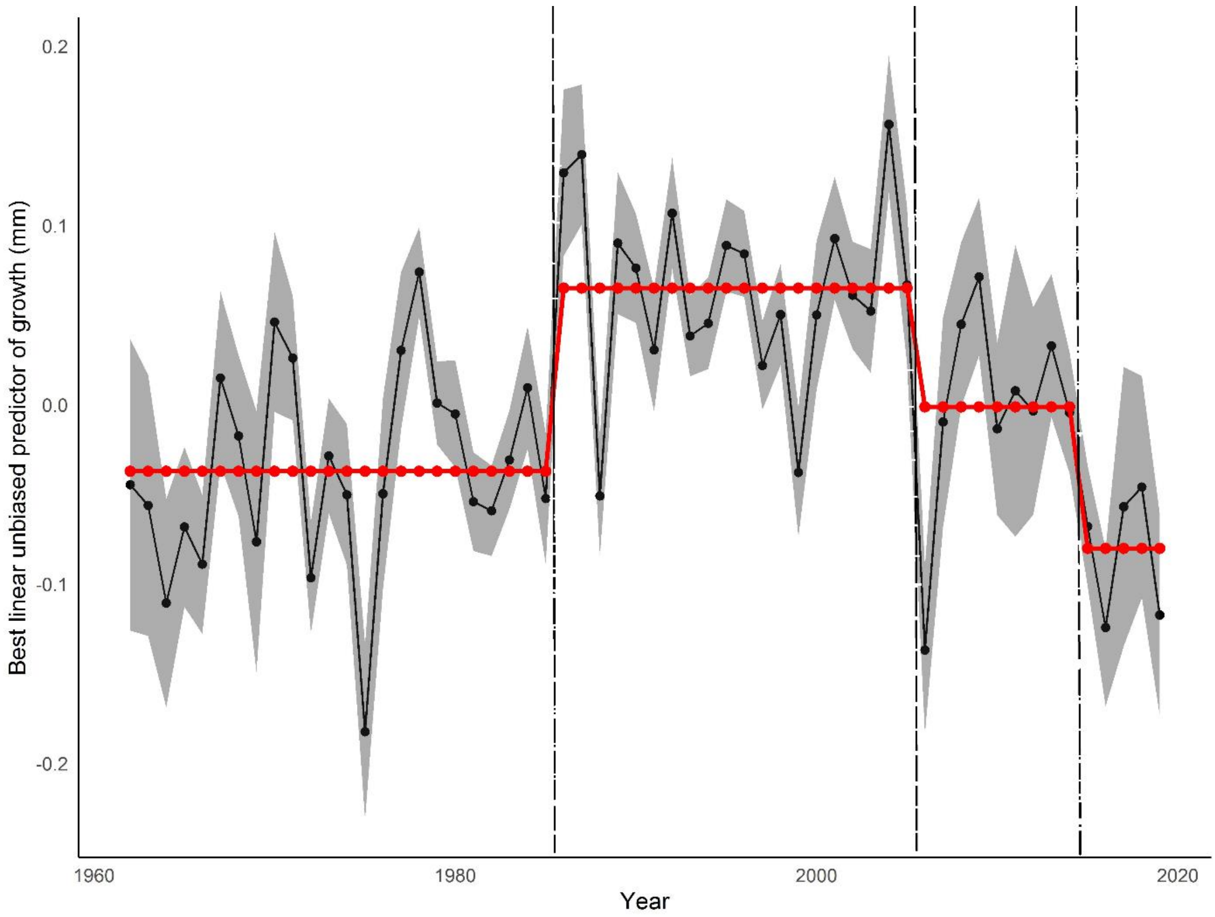


Figure 3.3. The best linear unbiased predictor (BLUP) of growth (width in mm for annual increments) against year for South African sardine caught off the west coast of South Africa with regime shifts identified through Sequential t-test of regime shifts (STARS) analysis (marked by vertical dashed lines), alongside mean growth values for each identified regime period represented by red lines with alteration points 1986, 2006 and 2015. The grey areas represent the 95% confidence intervals, while the dashed line denotes the average growth. The alteration points of SST at 30ºS and 32ºS were 1984 and 2004/2005 as identified by STARS analysis (Howard et al. 2007; Appendix Table B4).

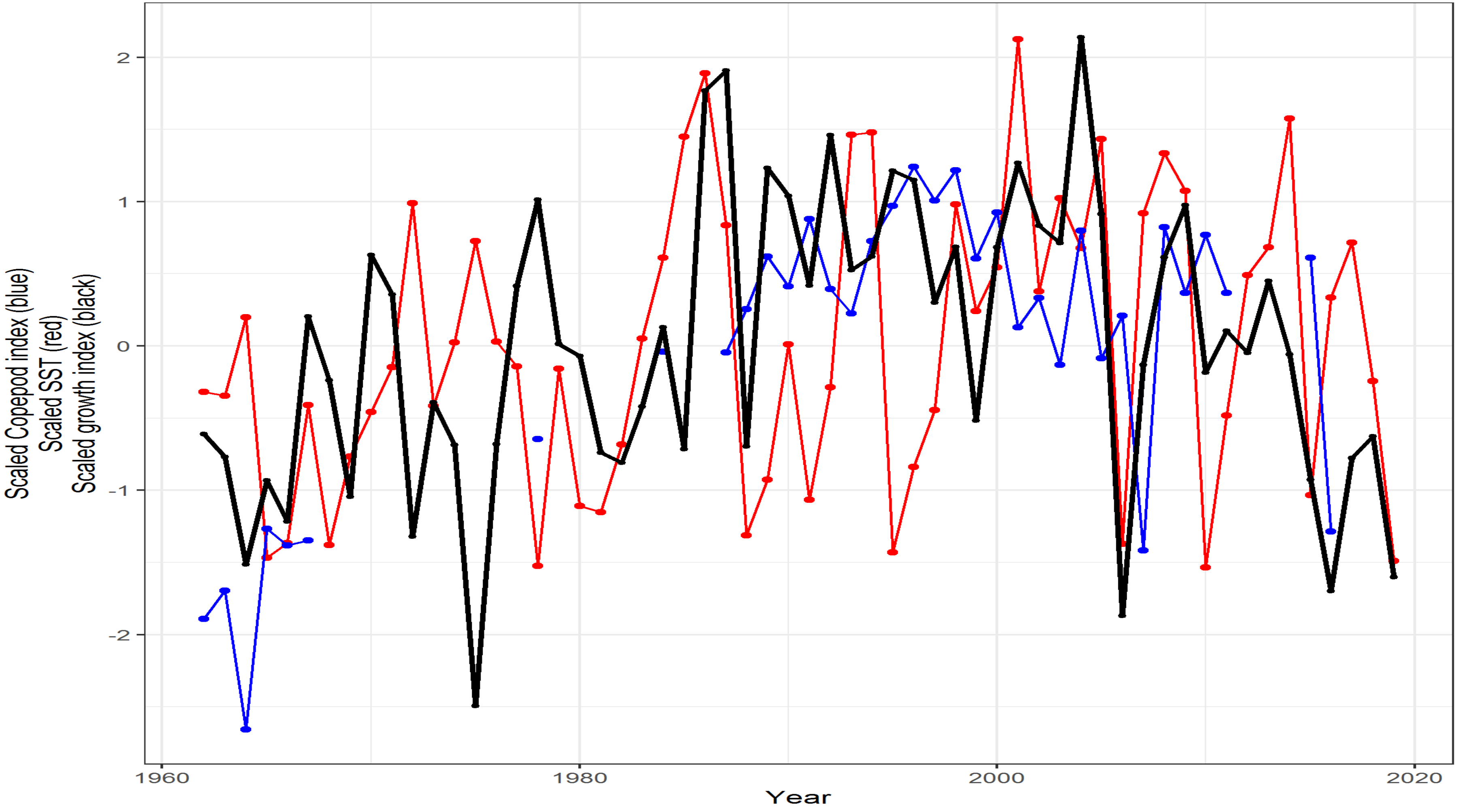


Figure 3.4. Model predictions of the best linear unbiased predictor (BLUP) of growth in black scaled with the scaled copepod abundance index that was log-transformed (Log10 (No. m-2 + 1)) in blue and the scaled June HADSST (°C) in red for the area West of Cape Agulhas from for 1962–2019.

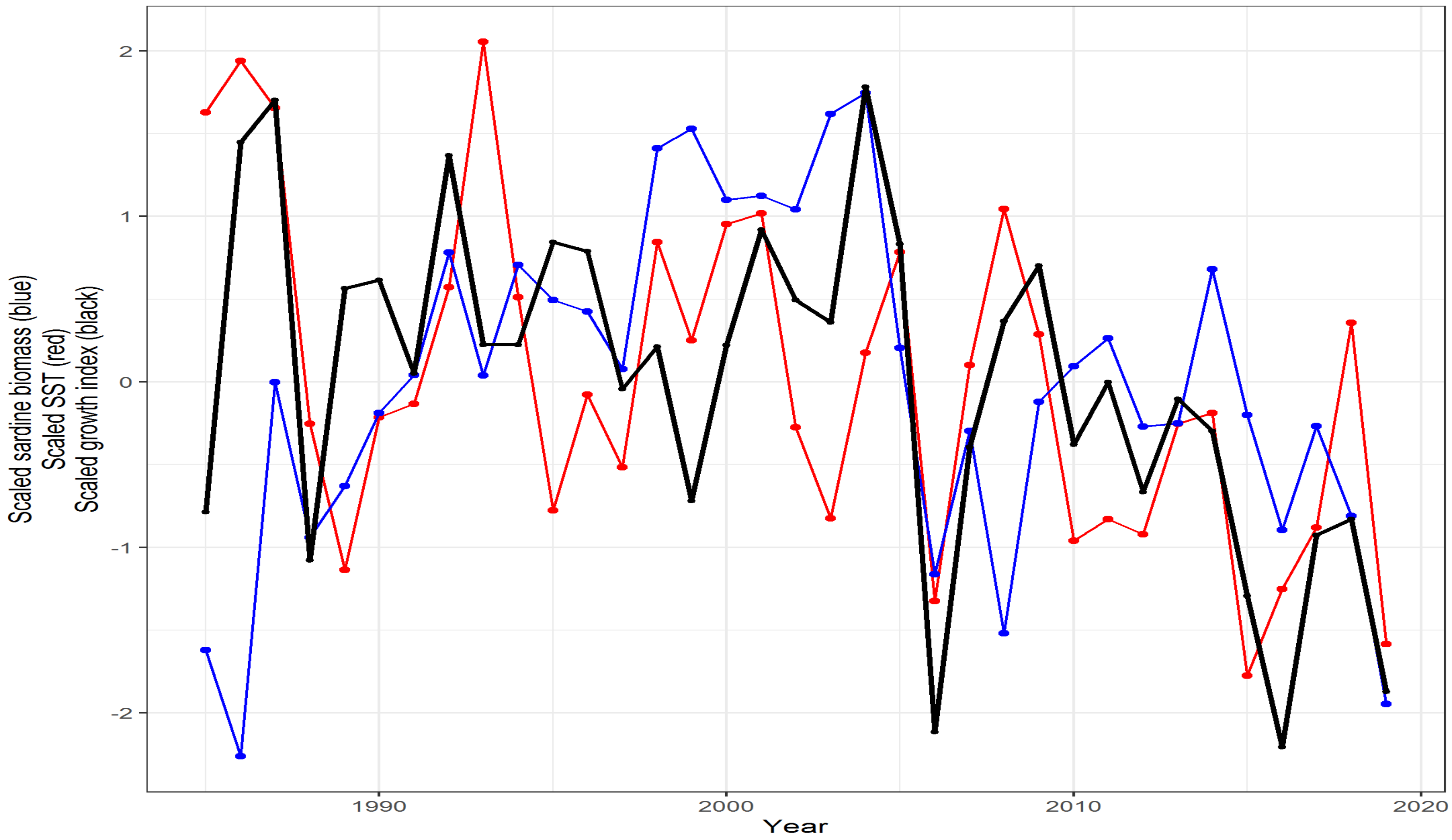


Figure 3.5a. Model predictions of the best linear unbiased predictor (BLUP) of growth in black scaled with the scaled sardine biomass (t) lagged by 1 year that was log-transformed (Log_{10}) in blue and the scaled winter (June) SWSST (°C) in red for the area West of Cape Agulhas for 1984-2019 period.

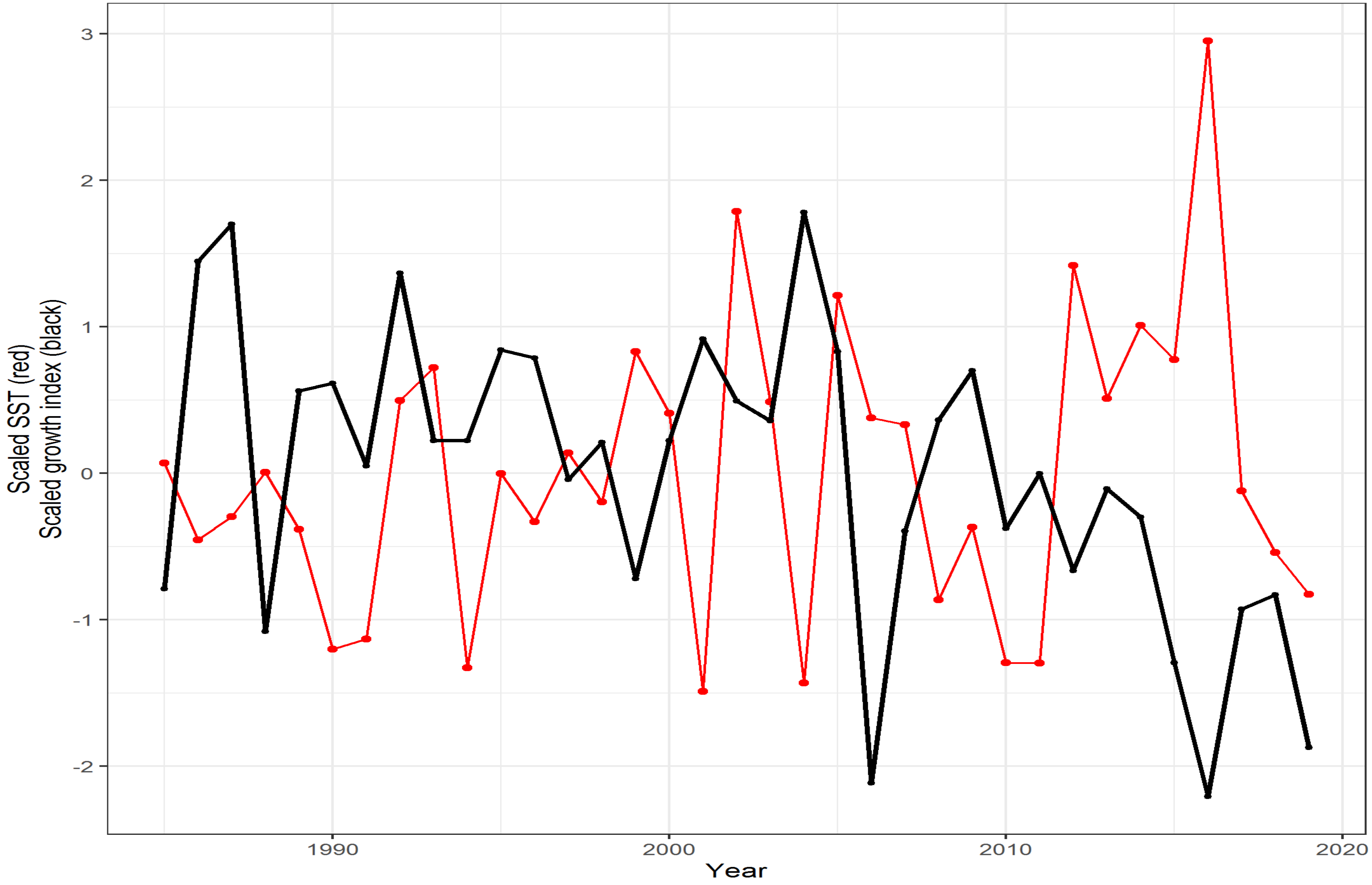


Figure 3.5b. Model predictions of the best linear unbiased predictor (BLUP) of growth in black scaled with the summer (January) NWSST (°C) in red for the area West of Cape Agulhas for 1984-2019 period.

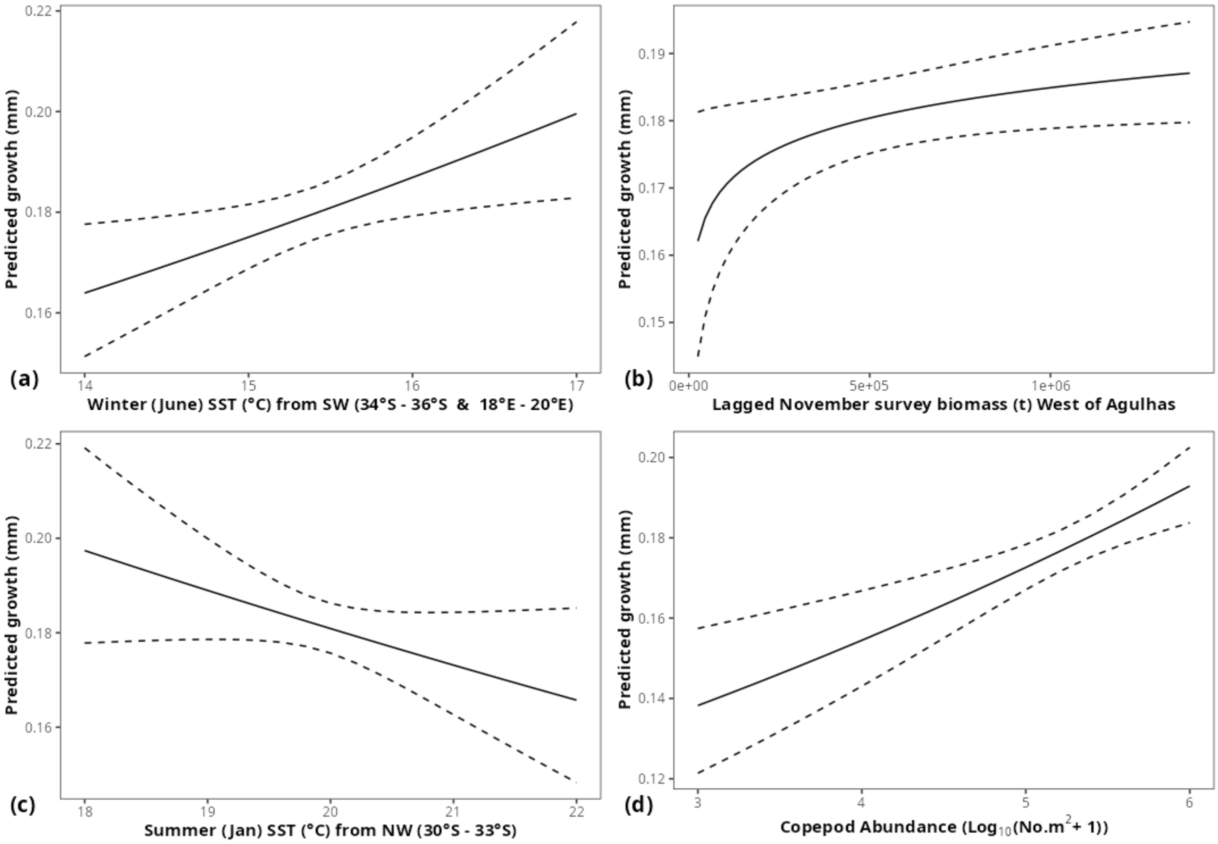


Figure 3.6. Predicted growth of sardine in relationship with (a) winter (June) SST (°C) from the SW area (34°S - 36°S and 18°E – 20°E), (b) summer (November) sardine biomass (log transformed and lagged by one year) West of Cape Agulhas, (c) summer (January) SST (°C) as described by Reynolds et al. (2002) for the NW area and (d) Copepod abundance at St. Helena Bay. Dashed ribbons are 95% confidence intervals.

3.4 Discussion

The present study provided a continuous 58-year growth biochronology derived from otolith increment measurement data for the commercially important sardine in southern Benguela off South Africa, thereby establishing the longest otolith time series available for any stock in the Benguela region. The study demonstrated that otolith biochronologies can be used as indicators for sardine growth, regime shifts, and biological responses to changing environmental conditions.

The results from the mixed effects models showed that sardine growth was most significantly influenced by Age, and to a lesser extent by Age-at-capture (AAC). Age is often considered an important factor in understanding fish growth patterns since it is closely related to the developmental stages and physiological processes that affect growth (Campana 2001). Indeed, it is commonly expected that the age of a fish has a significant and systematic influence on its growth. As fish age their growth rates tend to decrease, which is a well-known phenomenon referred to as "negative age-growth relationship" (e.g. Doubleday et al. 2015; Izzo et al. 2016; Smoliński 2019). This negative age-growth relationship occurs due to various factors. As fish grow older, they may face limitations in resource availability, such as food or habitat, which can constrain their growth potential (Enberg et al. 2012). Additionally, physiological factors, such as decreased metabolic rates or reduced energy allocation towards growth, can contribute to the observed decrease in growth rates with age (Winemiller and Rose 1992; Enberg et al. 2012). The inclusion of AAC as the second fixed effect in the growth model emphasizes its significance in elucidating fish growth trends by detecting any ecologically and evolutionarily significant growth-based selectivity within a species. Moreover, it demonstrates potential biases in the sampling process, which could otherwise undermine the analyses (Morrongiello and Threshner 2015). A positive correlation between growth and AAC suggests that the absence of fish exceeding 7 years old in the sample may have affected the results, potentially indicating an impact from either fishing practices or environmental factors (Morrongiello and Threshner 2015; Enberg et al. 2012). The inclusion of the FishID term and slope of Age suggests that there is considerable variation in growth patterns between individual fish, and there are noticeable differences in the relationship between increments (growth marks on otoliths) and age among the fish. The inclusion of a random Year effect in the optimal growth model accounted for a substantial portion of the variation observed in fish growth. Hypothesis 1 posited that annual otolith growth patterns of sardine remained stable over time (H_0), while the alternative (H_1) proposed that significant temporal changes in growth occurred across the biochronology. The results provide support for the alternative hypothesis. The inclusion of a random Year effect in the optimal growth model explained a substantial portion of the variance in individual growth patterns, indicating that growth varied significantly across years. This temporal variation implies that external, year-specific factors (likely environmental or biological in nature) exert a significant influence on growth dynamics. These may include interannual fluctuations in sea surface temperature, prey availability, or sardine biomass, all of which vary over time and can shape the observed growth trajectories. Therefore, H_0 is rejected, and H_1 is supported which implies that sardine growth patterns were not stable, but rather subject to significant year-to-year variability driven by extrinsic factors.

Sardine growth rates were primarily influenced by variations at the individual and inter-annual levels, rather than being attributed to cohort-specific differences. This trend aligns with patterns consistently observed in growth of other fish species from otolith chronologies (e.g. Morrongiello and Thresher 2015; Martino et al. 2019; Denechaud et al. 2020, Wilhelm et al. 2020). The absence of a cohort effect in sardines can be attributed to several factors. Firstly, the sardine spawning season is prolonged, occurring throughout the year (van der Lingen and

Huggett 2003) leading to a continuous presence of sardine cohorts. Additionally, the distribution of sardine eggs reveals two distinct spawning grounds: one west of Cape Agulhas within a cool temperate upwelling system characterized by higher productivity, and another east of Agulhas in a subtropical to warm temperate zone with lower productivity which results in divergent outcomes for sardines (van der Lingen and Huggett 2003; van der Lingen et al. 2021). Furthermore, sardine distribution patterns are closely linked to size (Beckley and van der Lingen 1999). Juvenile sardines primarily occur on the west coast but also sporadically along the south coast (Beckley and van der Lingen 1999). As sardines mature, they concentrate over the Agulhas Bank, especially in the inshore regions of the western Agulhas Bank (Beckley and van der Lingen 1999). Sardine adults (>18 cm total length, TL) exhibit dispersal both eastwards and westwards from the Agulhas Bank (Beckley and van der Lingen 1999). This continuous distribution and movement of sardines across different regions could have contributed to the absence of a distinct cohort effect in the biochronology.

Further support for Hypothesis 1 was provided by the results of the otolith biochronological analysis, which demonstrated the capacity to detect abrupt shifts in growth patterns over time. The first alteration identified in this study occurred in 1986, marked by a shift from low to high growth. This shift is corroborated by the present study findings, which found a positive relationship between SST in winter (June) and sardine growth for the period 1962-2019 in the area West of Agulhas. Further support for this alteration point is provided by the Benguela Niño event that took place two years earlier, in 1984, and by a previous study by Howard et al. (2007), which identified a sea surface temperature (SST) regime shift at 30°S/32°S during 1984/1985 using the STARS method, indicating a significant increase in SSTs (Howard et al. 2007). This implies that the initial point of positive regime alteration observed in 1986 was linked to elevated SST conditions, which were conducive to the growth of copepods and a low sardine biomass (after the 1960's collapse).

The study's second regime alteration point at 2006, where the otolith biochronology shifted from high to average growth, was also strongly supported by the present study findings that sardine growth was significantly negatively affected by summer SST in recent years (1984-2019) in the NW area. This supports previous STARS analysis performed by Howard et al. (2007) using SST and upwelling index at 30°S and 32°S which identified 2004/2005 as oceanographic alteration point, which was 1-2 years prior to otolith biochronology alteration point. Therefore, the second regime alteration in 2006 suggests a connection to elevated SST conditions from the mid-2000s onwards. However, in this instance, the SST was unfavourable for the sardine growth at high sardine biomass, as rising water temperatures during austral summer led to increased intra-specific competition that resulted in slower growth rates, although their survival rate remained high. Furthermore, the 2006 alteration point in the otolith biochronology coincides with the eastward distribution of sardine biomass from the west coast to the south coast where the majority of the sardine population had been concentrated since 2003 (Fairweather et al. 2006; van der Lingen et al. 2006b; Coetzee et al. 2008).

The third regime shift was detected at the alteration point in 2015 wherein the otolith biochronology shifted from average to below average growth. Growth during the final interval (2015-2019) was considered low, despite a high confidence level. The smaller sample size and shorter duration reduced data variability, making it easier to detect significant differences and thus increasing confidence in the findings. The third regime shift in 2015 coincided with the occurrence of unusual and widespread harmful algal blooms (HABs) along the south coast over the last decade, notably in 2011 and 2015 (van der Lingen 2021). The harmful algal blooms

(HABs) seemed to adversely affect sardine, while anchovy or round herring appeared unaffected. Sardine within the HAB-affected area exhibited a significant decline in body condition (van der Lingen et al. 2016). This is attributed to the hypothesis that sardine cease feeding due to potential chemical irritation caused by the entrapment of small (50µm) bloom-causing dinoflagellates on their gill rakers (van der Lingen et al. 2016), and decreased body growth rates would follow. The compromised health of sardines carries detrimental effects on their ability to successfully reproduce and replenish their populations, given their reliance on stored energy reserves for effective spawning (Ganias et al. 2014). Moreover, aside from these biological repercussions, harmful algal blooms (HABs) have been identified as a contributing factor to reduced sardine availability along the south coast, notably impacting catch yields in Gqeberha and Mossel Bay following bloom occurrences. The projected escalation of HAB incidents, attributed to climate change, poses a concerning trend, with indications of heightened frequency, severity, and expanded geographic distribution (Wells et al. 2015).

Hypothesis 2 examined whether sardine biomass significantly influences annual growth patterns, with the null hypothesis (H_0) assuming no effect and the alternative (H_1) proposing a significant relationship. The results support the alternative hypothesis. A significant positive effect of sardine biomass west of Agulhas on individual fish growth was detected, indicating that changes in population biomass are directly associated with growth variation. This observation implies that sardine population dynamics exhibit depensation, meaning that as the sardine biomass declines to low levels, the growth rate, productivity and fertility also decreases instead of increases (Rose et al. 2001). The lack of sardine recovery after heavy fishing pressure in the 1950s, the collapse sardine stocks and the low and depleted sardine population since 2019 (van der Lingen et al. 2006; Hutchings et al. 2009; DFFE 2023) is demonstrative of depensation. Depensation has a destabilizing effect on fish populations. This mechanism is particularly critical for depleted fish populations and endangered species as it accelerates further population decline and may impede recovery efforts (Myers et al. 1995; Shelton and Healey 1999; Rose et al. 2001). Various mechanisms can induce depensation, mainly reduced probability of fertilization, impaired group dynamics, environmental conditioning, and predator saturation (Liermann and Hillborn 2001). Coetzee et al. (2008) stated that the factors contributing to the lack of recovery after the sardine collapse remains uncertain, potentially stemming from disruptions to the life cycle of a segment of the population. The authors suggested decreases in biomass since 2004-2005 result from prolonged low recruitment and unexplained adult mortality not linked to fishing. Based on results from the present study, it is proposed that the depensatory population dynamics observed in sardine of southern Benguela could be elucidated by adverse environmental conditions.

Hypothesis 3 proposed that environmental and biological variables significantly influence annual sardine growth patterns, while the null hypothesis (H_0) posited no such effect. The results support the alternative hypothesis (H_1). In the present study, sea surface temperature (SST) and copepod abundance emerged as the most influential factors affecting sardine growth. In the present study, SST and copepod abundance emerged as the most influential environmental and biological variables affecting the growth of sardine. This supports the notion that although fishing effects are significant and certainly contribute to population declines, a fish's environment and alterations to that environment also play a (often more crucial) role (McFarlane et al. 2002). Sardine growth for the period 1962-2019 was positively affected by SST in winter (June) in the area West of Agulhas. This finding is supported by the first alteration point in 1986 of the otolith biochronology. Sardines spawn in autumn or spring on the Agulhas Bank on the south or west coast (Hutchings et al. 2012). Eggs and larvae either stay in the South Agulhas Bank nursery ground or move to the west coast nursery ground (offshore between

Lamberts Bay 32°S and Orange River 29°S) where pre-recruits (20-50 mm) are initially offshore and later migrate southward as juveniles (60-80 mm) towards the inshore productive region of the west coast between 29°S (Orange River) and 34°S (Cape Point) where they actively feed on phytoplankton and copepods during autumn and winter (Hutchings et al. 2012). This feeding activity allows them to grow in length and accumulate energy reserves in preparation for their spawning migration in spring, as they return to the south coast (Hutchings 1992; Hutchings et al. 1998; Hutchings et al. 2012). Therefore, based upon sardine feeding behaviour, late autumn and winter (May, June and July) should be the best predictor of fish somatic growth and it is supported by the model predictions of positive effect of SST in winter (June) in area West of Agulhas on sardine growth (1962-2019). The current findings are consistent with previous studies demonstrating that the sea surface temperature (SST) during winter exhibited a strong correlation with sardine growth during autumn and winter (du Plessis 1959; Hutchings et al. 2012).

The contrasting trend observed in projected growth during the austral winter and summer SSTs in recent decades, suggests that sardine populations optimal growth preference exhibits a relatively narrow temperature range, 17-18 °C, reflected by warmer winters and cooler summers. This temperature preference suggests that in recent decades sardine growth may have reached their thermal minimum and maximum limits during austral winter and summer due to a pronounced thermal gradient (inshore cooling and offshore warming) in the southern Benguela and supports findings of a previous study that demonstrated a significant correlation between the cross-shelf sea surface temperature gradient and the proportion of sardine biomass (Augustyn et al. 2018). Hence, when considering the crucial role of sardines in the trophic dynamics of the upwelling ecosystem, the negative effects of ocean warming and inshore cooling on sardine growth and life cycle could have significant implications for fish recruitment and the overall structure of the ecosystem (Faleiro et al. 2016). A minor rise in the thermal range of several marine species' can enhance their growth due to the availability of more energy (Vieira et al. 2020). Nonetheless, it might also reduce growth rates if the heightened metabolic needs from warmer temperatures are not matched by an increase in food availability (van der Sleen et al. 2018). Further research is necessary to fully understand thermal boundaries that affect sardine life cycles and growth.

Model predictions of sardine growth correlate positively with copepod abundance (updated from Verheye et al. 2016) for the area West of Cape Agulhas. Copepod abundance experienced a 100-fold surge from 1950 to 1995, followed by a tenfold reduction in 1996 on the west coast, coinciding with a significant ecological regime shift from larger to smaller copepod species dominance in 1995 (Verheye et al. 2016). Larger copepods, such as *Centropages brachiatus*, *Calanoides natalensis* (previously *C. carinatus*), and *Rhincalanus nasutus*, which are the preferred prey of anchovy (James 1987), were prevalent in the 1950s–1960s and in recent years (from late 2000s), while smaller copepods, such as *Oithona* spp., *Metridia lucens* and small calanoid species, the preferred prey for sardine van der Lingen (2021) increased from the late 1980s and declined in recent years (from late 2000s) (Verheye et al. 2016). This shift was likely triggered by environmental changes, such as ocean warming, and intensified by a change in predation pressure based on prey size by pelagic fish stocks along the west coast (Verheye et al. 2016). Hence, it is hypothesized that stronger upwelling conditions lead to an increase in the abundance of larger copepods benefiting anchovy and round herring, while weaker upwelling conditions are associated with a higher prevalence of smaller copepods benefiting sardine (van der Lingen 2021). The otolith biochronology demonstrated increased sardine growth rates from 1986-2005, followed by a decline from 2006-2019, coinciding with changes in copepod species dominance, recruitment strength and total biomass of sardine which may be considered as evidence of a climate change-induced reduction in the trophic environment for sardine (van der Lingen 2021).

Environmental influences that contributed to the collapse of resources or hindered the recovery of a population have been proposed by several authors. Okunishi et al. (2012) simulated global warming effects on sardines of Japan, and found potential impacts of global warming on the growth and migration patterns of sardine potentially disadvantaging recruitment under future climate conditions. Moreover, trophic modelling studies have proposed that the shifts observed in pelagic fish stocks in the southern Benguela region were predominantly driven by environmental factors (van der Lingen et al. 2006). These effects were transmitted up the food web, influencing the availability of mesozooplankton prey for anchovy and sardine (Shannon et al. 2004b; van der Lingen et al. 2006). Shannon et al. (2004a and 2008) developed a dynamic model with catch and biomass data from 1978-2002 in the southern Benguela and found fishing patterns explained only 2-3% of variability, while an environmental factor tied to phytoplankton production accounted for 4-12%. Given the moderate fishing levels in the southern Benguela ecosystem, it's unsurprising that trophic interactions, rather than fishing, are considered the main drivers of observed changes from the 1980s-2000s (van der Lingen et al. 2006b; Shannon et al. 2008). It is recommended that the interannual growth rate variability estimated in the present study be incorporated in an ecosystem model (e.g. Shannon et al. 2020).

Otolith biochronologies revealed decadal variability that indicated rapid regime shifts in the southern Benguela marine ecosystem. The utilization of preserved otoliths in this study enabled the analysis to identify prolonged shifts in sardine growth, which are influenced by a range of biological and physical factors. Sardine population display depensation that have destabilized the population after the fishery collapse. Depensatory density dependence may have been exacerbated by rising sea surface temperatures and low prey availability, negatively impacting sardine growth. This mechanism is especially crucial for depleted fish populations as it accelerates further decline and can hinder recovery efforts. The application of statistical methods to detect regime shifts with established marine biochronologies can serve as a valuable tool for identifying potential occurrences of ecosystem regime shifts or revealing significant environmental events in the past. The otolith archives found in numerous marine research facilities globally offer an exceptional chance to create extensive biochronologies, capturing biological alterations that are difficult to study, particularly since satellite and species biomass data became available only later in the 21st century, while otoliths can provide insights that extend back in time from their point of collection. Therefore, the application of an otolith biochronological approach to evaluate the responses of various populations and species to historical environmental changes may facilitate the adjustment of future management policies and the establishment of indicators at the ecosystem level, and should be made use of, especially within the Benguela and similar upwelling regions. The need to conduct such studies is underscored, especially in the current context marked by rapid global climate changes.

CHAPTER FOUR: POST-COLLAPSE SOMATIC GROWTH AND POPULATION RECOVERY FAILURE OF SARDINE (*SARDINOPS SAGAX*) IN THE NORTHERN BENGUELA FROM OTOLITH BIOCHRONOLOGIES

Abstract

The sardine (*Sardinops sagax*) population in northern Benguela off Namibia, supported high catches in the 1950s-1960s and collapsed by the late 1960s. Despite a fishing moratorium since 2018, the population has shown no signs of recovery by 2023. In this study, a 48-year (1974-2021) biochronology was developed using archived sardine otoliths. Otolith increment widths, used as a proxy for annual fish growth, were analysed using linear mixed effects models to explore intrinsic (within individual) and extrinsic (sardine biomass, sea surface temperature and upwelling) factors contributing to annual variations in fish growth. The absence of otolith data from before the population collapse in the late 1960s meant that the long-term annual sardine otolith growth post-collapse showed short-term fluctuations, but no significant long-term growth rate changes. Predicted annual sardine growth was significantly negatively linked with SST in Austral spring, and positively linked with upwelling in summer for the area 17-20ºS (northern Namibia). The results suggest environmental conditions play a dominant role in driving sardine growth, exacerbated by the extremely low sardine biomass, which may be indicative of depensation. The study provides insights on the reasons for the lack of recovery in sardine biomass. Therefore, otolith biochronologies provide a broader understanding of how small pelagic fish stocks respond to environmental changes.

4.1 Introduction

The northern Benguela system exemplifies an eastern boundary current upwelling region, noted for its significant biological productivity (Jarre et al. 2015; Roux and Shannon 2004). The northern border is defined by the Angola Benguela Front (ABF), a distinct oceanographic boundary that separates the warm tropical waters of the Angola Current from the cooler, nutrient-dense upwelled waters of the northern Benguela (Figure 4.1) (Roux and Shannon 2004). The front is located off the coast of southern Angola, moving seasonally during winter between 15° and 18°S (Meeuwis and Lutjeharms 1990; Mohrholz et al. 2001; Veitch et al. 2006). The intense year-round upwelling off Lüderitz (26 – 28°S) is characterised by intense wind stress, high turbulence, cold water, and appears to serve as an environmental barrier for most fish populations, effectively divides the northern and southern Benguela regions (Boyer et al. 2001; Roux and Shannon, 2004). This phenomenon creates a stream of newly upwelled, turbulent water moving northwest, with minimal vertical layering, which serves as a semi-permanent environmental barrier to pelagic fish migration (Boyer et al. 2001). There are upwelling cells further north included in this study, while the southern cell at Lüderitz (26–28°S) acts as a barrier, marking the boundary between the northern and southern Benguela sardine stocks.

The South Atlantic high-pressure system and its seasonal movement promote the wind patterns favourable for upwelling, which prevail year-round in the northern Benguela (Hampton and Willemse 2012). There has been a southward shift and strengthening of the ABF since 1980, linked to the southward movement of the South Atlantic subtropical anticyclone and may be connected to, but are not always synchronised with El Niño Southern Oscillation (ENSO) (Hampton and Willemse 2012). This has led to periodic southward incursions of warm, saline, nutrient-poor, and low-oxygen water onto the Namibian shelf, associated with significant southward displacement of the ABF, a phenomenon known as Benguela Niños (Rouault et al. 2007) and their cold equivalents, the Benguela Niñas (Koungue et al. 2021). Furthermore, monthly SSTs in coastal regions displayed a period of prolonged subsequent warming since the mid-1990s in the northern Benguela (Hardman-Mountford et al. 2003; Shannon et al. 1992).

The ABF shows significant variability in sea surface temperatures (SST) across various frequencies, ranging from sub-monthly to decadal timescales (Koungue et al. 2021). In a Benguela Niño (or Niña) event, sea surface temperatures (SSTs) in the ABF region may vary by as much as 3°C above (or below) the typical climatological values. These extreme events can influence the marine ecosystem, biological productivity, and fisheries in the Benguela upwelling system by altering the nutrient supply from deeper waters, as they affect both the intensity of upwelling and mixing in the upper ocean (Blamey et al. 2015; Koungue et al. 2021).

A fishery collapses when a valuable commercial species experiences significant depletion and does not swiftly replenish even after fishing efforts have ceased (Hutchings, 2000; Kirby et al. 2009). Typically, it involves a significant and enduring alteration in the composition of the marine ecosystem (Hutchings and Reynolds 2004). Overfishing reduces the population size of commercial fish species, reduces their ability to perform their functional role in the ecosystem, and can destabilise their population dynamics (Anderson et al. 2008). While overfishing can drastically reduce fish populations, environmental factors such as habitat destruction, pollution, climate change and invasive species may contribute to the collapse of fisheries (Hauge et al. 2009). In many cases, identifying the primary reasons for the depletion of fish stocks is quite challenging (Hauge et al. 2009). In this study, the causes of the collapse were not investigated, with the focus instead placed on evaluating the variability in sardine growth after the collapse, as otolith samples did not cover the period prior to the collapse.

Heavy fishing pressure in the 1950s and 1960s in northern Benguela off Namibia led to the collapse of sardine stocks in the early 1970s (Jarre et al. 2015; Roux and Shannon 2004). Despite minimal fishing pressure on the sardine stock in northern Benguela off Namibia over the past twenty years, and a recent moratorium on fishing since 2018, there is no sign of recovery. Despite scientists advocating for a sardine fishing moratorium since 1995, only a one-year moratorium was implemented in 2002, which did not succeed in recovery of the sardine population. A three-year moratorium was announced in 2018, which is still in place due the continued low levels of sardine biomass. The sardine biomass in northern Benguela off Namibia, as determined by Virtual Population Analysis, indicated a notable increase in the mid-1960s followed by a substantial decrease in the late 1960s, and subsequent years have not demonstrated any significant signs of recovery (Kirchner et al. 2009; van der Lingen et al. 2006). Although there were signs of a partial recovery of the sardine biomass in the early 1990s, the biomass declined once more following occurrences of low-oxygen and warm-water events in 1994 and 1995 (Boyer and Hampton 2001). Along with the reduction in biomass, there have been significant alterations in the stock structure of sardines (Kreiner et al. 2011). The average total length of sardines has decreased by over 4 cm from the 1950s to the 2000s, and the length at which 50% of sardines reach maturity has dropped by more than 3 cm from the 1980s to the 2000s (Kreiner et al. 2011). The near-complete removal of sardine from the northern BCLME in the 1970s and 1980s due to overfishing has led to a shift toward a less efficient and less environmentally stable regime (Hampton and Willemse 2012).

The ABF serves as a significant habitat for pelagic fish feeding and spawning, while also acting as an ecological barrier that delineates the northern extent of crucial Namibian fish stocks (Beckley and van der Lingen 1999). Therefore, the sardine collapse in northern Benguela off

Namibia could be attributed in part to the substantial catches recorded during the 1960s, but it was also influenced by continuously low recruitment rates over an extended duration (Boyer et al. 2001). Despite a period of high recruitment during the first half of the 1960s, subsequent years saw consistently low recruitment levels despite a significant spawner biomass (Boyer et al. 2001). It suggests that environmental conditions might play a dominant role in determining recruitment success, surpassing the influence of spawner biomass (Boyer et al. 2001). Recruitment of sardines in the northern Benguela region demonstrates significant year-to-year fluctuations impacting the fishing industry due to its direct influence on both biomass size and the subsequent determination of the total allowable catch (TAC) (Boyer et al. 2001).

The somatic growth of fish serves as an excellent proxy that reflects responses to both environmental shifts and fishing pressure. Changes in growth, whether in space or time, have been linked to various environmental factors, including temperature (Campana et al. 1995; Denechaud et al. 2020), prey availability (Graeb et al. 2004) and population effects including density-dependence (Lorenzen and Enberg 2002) and harvesting (Enberg et al. 2009). A significant characteristic of fish ear stones (otoliths) is that incremental growth is typically closely linked to the overall somatic growth of fish (Denechaud et al. 2020; Doubleday et al. 2015). Hence, assessing the annual growth increments in otoliths and the resulting biochronologies can offer extended, continuous, and yearly detailed time series depicting variations in growth. These data can be employed for further analysis of patterns and trends in somatic growth, along with understanding the factors influencing them (e.g. Black et al. 2011; Smoliński 2019; van der Sleen et al. 2016).

The overall objective of this study was to develop a sardine otolith biochronology for the northern Benguela, to evaluate intrinsic (between-individual and within-individual) and extrinsic (environmental) factors that may influence the growth of sardine. The otolith biochronology is based on measurements of fish otolith increments made from samples collected from archived scientific surveys and commercial catches from 1977-2021 in the northern Benguela. The sardine otolith biochronology methodology allowed for a rigorous statistical assessment of the factors influencing sardine growth in the northern Benguela. Additionally, a cross-wavelet coherence analysis was performed to examine changes in fish growth patterns and their relationships with environmental time series, exploring these dynamics across time, frequency, and spatial domains.

Furthermore, this chapter addresses the following hypotheses:

a) H_0: Annual otolith growth patterns of sardine in the northern Benguela remained stable over time, with no abrupt shifts in the biochronology.

   H_1: There are significant temporal changes in the annual otolith growth patterns of sardine in the northern Benguela.

b) H_0: Population biomass does not significantly affect the annual growth patterns of sardine.

   H_1: Population biomass significantly influences the annual growth patterns of sardine.

c) H_0: Environmental factors (sea surface temperature, upwelling intensity) do not significantly affect the annual growth patterns of sardine.

   H_1: The environmental variables (sea surface temperature, upwelling intensity) have a significant effect on growth patterns of sardine.

4.2 Materials and Methods

4.2.1 Study area, sample selection and otolith measurements

The study area (Figure 4.1) is located in northern Benguela extends from the north of Lüderitz at 25°S to the Kunene River (or even into Angola 16°-17°S) in Namibia (Figure 4.1a). Otoliths from 1977 to 2021 were selected from survey stations spanning between 25°-17° S (Figure 4.1b). The northern Benguela region was divided into the ABF region also known as the Kunene region (20-17°S) and the central Namibia region (20-24°S).

Annual biomass surveys for sardine were conducted by the Ministry of Fisheries and Marine Resources (MFMR), therefore an extensive archive of otoliths and biological data are available from 1990 to 2021. Otoliths dating back to 1982 and 1985 present in the archives of the MFMR were also used.

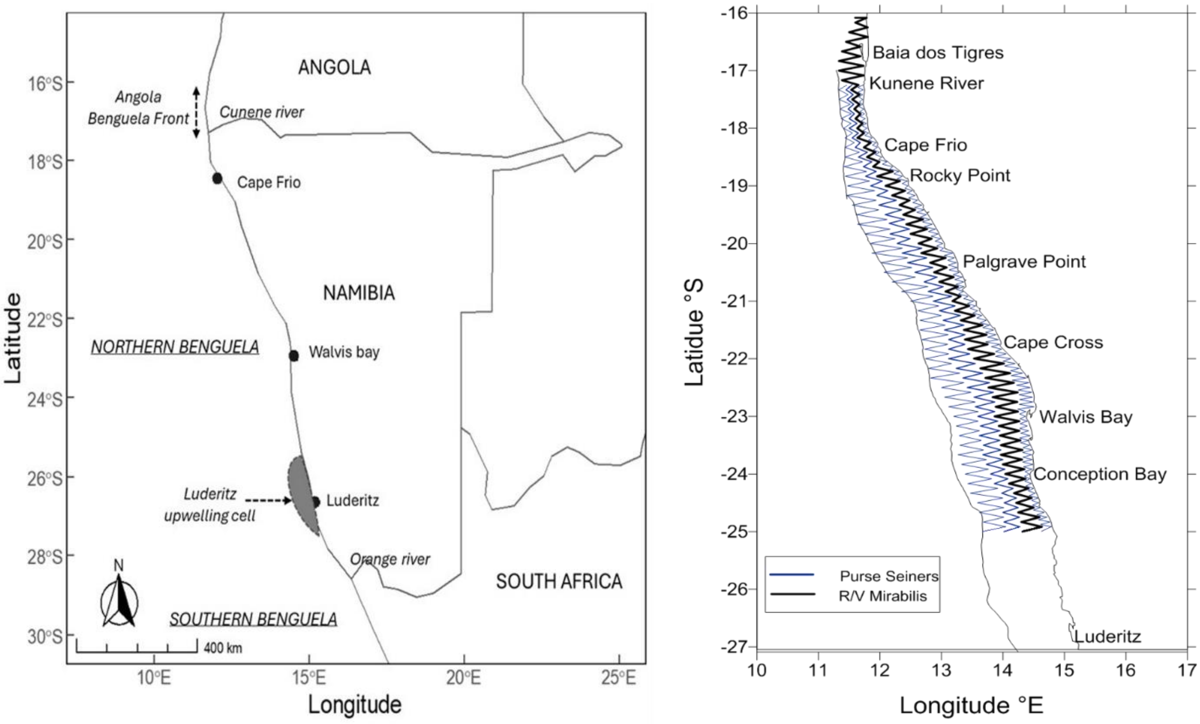


Figure 4.1. Geographical map showing (a) the northern Benguela, (b) the sardine biomass survey design in black (R/V Mirabilis) and commercial design (Purse Seiners) within the northern Benguela off Namibia.

Smoliński et al. (2020) demonstrated that a minimum of ten individuals per year for a period of 100 years in short-lived species can improve the precision of environmental parameter estimates in the mixed effects model. Therefore, a minimum of 20 otoliths per year for a period of 50 years were considered sufficient to ensure a robust mixed effects model. A random subsample of a minimum of 20 sagittal otoliths from available years of capture of fish at least 2 years old (> 18 cm total length) were selected in order to successfully validate chronologies (time series). Thus, the analysis incorporated measurements on a total of 700 otoliths equalling 2,862 increments spanning ages 2 to 9 years (Figure C1).

Whole otoliths from the years 1982–2021 were individually cleaned and immersed in distilled water (LabQ water) in a petri dish, following the NOAA Fisheries (2024) method. Calibrated images of the sardine otoliths were taken under reflected light against a black background using a Zeiss Stemi 508 stereo microscope fitted with a Carl Zeiss Axiocam 208 colour camera, at 32× magnification. The optimal orientation for analysis is with the distal surface facing upward and the proximal surface facing downward. The assumption that otolith growth is directly proportional to somatic growth was tested by correlating fish length with otolith radius and found a significant relationship between fish length and otolith radius ($r=0.676$, $p<0.05$, Figure C2).

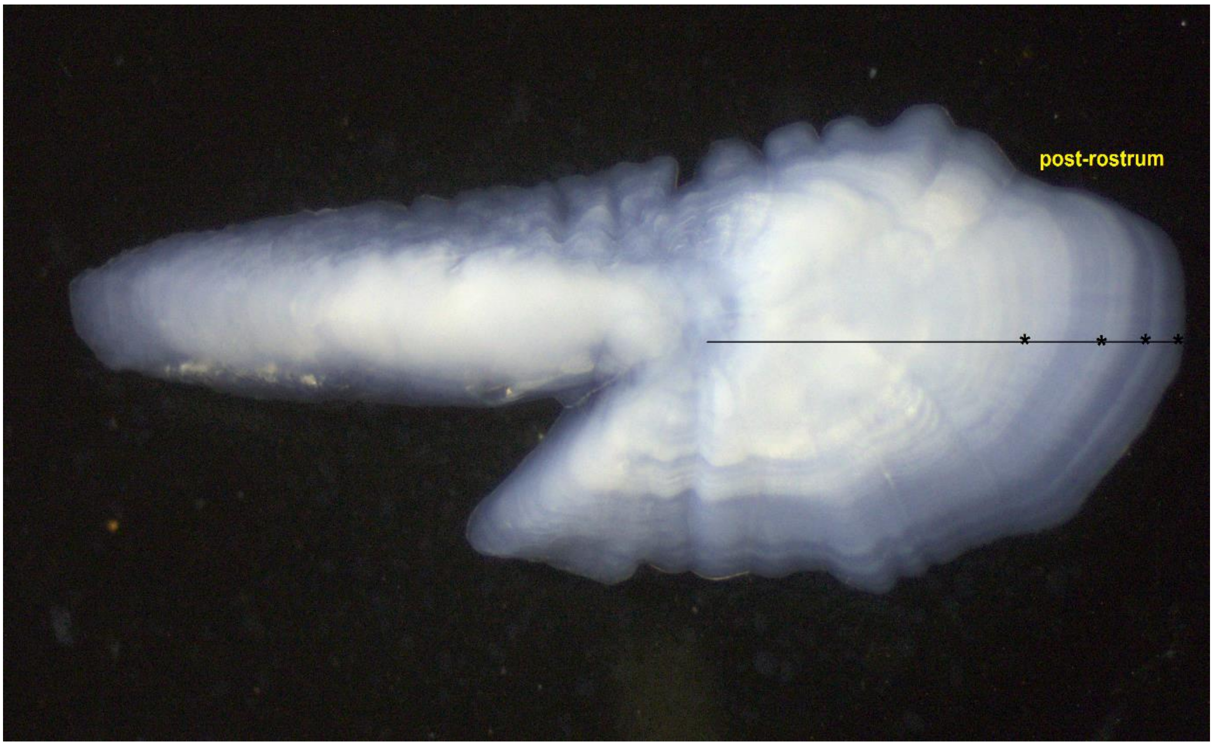


Figure 4.2. Sardine (Sardinops sagax) whole otolith from a 4-year old caught in December 1992 in Namibia. The annual increments (black asterisks) along the horizontal line were annotated and measured from the nucleus along a horizontal black line to the posterior edge. All otolith samples were viewed under reflected light at 32x magnification.

The otolith images were analysed using ObjectJ which is an ImageJ plugin. For each otolith, the length of each annual increment was measured along the post-rostrum axis of the otolith from the nucleus to posterior edge (Figure 4.2). The otolith increment widths were recorded together with its year when the increment was formed (calendar year), and age at the time of increment formation (Age in years) for each fish. The cohort was assigned as the Year-class of fish born in the same spawning year. The age-at-capture (AAC) defined as the age (in years) at time of capture was assigned for each fish. One increment consisted of the relatively broad opaque zone and the relatively narrow translucent zone (Figure 4.2). The sardines date of birth was set as 1 January (FAO 2002). The translucent zones were assumed to start forming mainly between (austral winter and spring) (Waldron 1998; Thomas 1983; Kerstan 1995) and the opaque zone was assumed to form during austral summer (October to April), which spans two calendar years.

4.2.2 Extrinsic Environmental Predictors

A summary explanation of all environmental (SST and upwelling) and sardine biomass variables used in the growth model are provided in Table 4.1. The "ERSSTv5" is a global SST dataset derived from the International Comprehensive Ocean–Atmosphere Dataset (ICOADS) (Huang et al. 2017) and is available from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC). Average monthly SST values were extracted from the Extended Reconstructed sea surface temperature version 5 (ERSSTv5) dataset for the Kunene area (11-15°E; 20-24°S) and central area (11-15°E; 20-17°S) from 1974-2021.

The Southern Oscillation Index (SOI) is a standardised index derived from observed sea level pressure (SLP) variations between Tahiti and Darwin, Australia. It acts as a gauge for significant alterations in air pressure across the tropical Pacific, delineating the condition of the Southern Oscillation during El Niño and La Niña occurrences (Ropelewski and Jones 1987). The average monthly Southern Oscillation Index (SOI) which is a normalised index derived from the observed sea level pressure (SLP) variations between Tahiti and Darwin Australia was extracted for 1974-2021 from the KNMI Climate Explorer webpage.

The MEI dataset is formulated to offer a holistic representation of the atmospheric and oceanic irregularities linked to ENSO events, surpassing the coverage of single-variable time series like the SOI indices. MEI version 2 (MEIv2) is created using five essential variables from the tropical Pacific: sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, sea surface temperature (S), and outgoing longwave radiation (OLR). The MEIv2 index was extracted for the years 1982-2021 from the KNMI Climate Explorer webpage. The combination of the Southern Oscillation dataset and the El Niño dataset is commonly referred to as ENSO, which denotes a cyclic variation (occurring every 2–7 years) in sea surface temperature (El Niño) and the atmospheric air pressure (Southern Oscillation) over the equatorial Pacific Ocean. The MEIv2 indices were included in the investigation to explore the influence of ENSO on sardine growth especially since the Benguela Niño/Niña (warming/cooling) events, were found to be linked to ENSO events in the Pacific (Rouault and Tomety 2022).

Bordbar et al. (2021, 2023) reanalysed the European Centre for Medium-Range Weather Forecasts ERA5 dataset, specifically focusing on hourly sea level pressure and surface wind vectors spanning from 1979 to 2021. This analysis aimed to assess the coastal upwelling induced by alongshore winds and the wind-stress-curl-driven upwelling offshore, with the results expressed in m^2/s^{-1}. Daily and monthly averages were derived from the hourly values (Bordbar et al. 2023). Monthly coastal and offshore upwelling indices for Walvis Bay (22.9584° S, 14.5058° E) and Kunene River Mouth (-17.2556ºS ,11.7522ºE) were created and updated from Bordbar et al. (2023) from 1979-2021.

The total sardine survey-estimated biomass time series (1990-2013) was sourced from the Ministry of Fisheries and Marine Resources (MFMR) in Namibia. After Namibia's independence in 1990, spawner-stock biomass was estimated from annual pelagic hydroacoustic surveys conducted by the Ministry of Fisheries and Marine Resources (Boyer et al. 2001; Fossen et al. 2001). The MFMR were unable to determine the sardine biomass during the 1996 acoustic pelagic survey due to very low sardine abundances, thought to be caused by adverse environmental conditions of the Benguela Niño and overfishing during the early 1990s

(Boyer et al. 2001). Since 2014 the biomass of sardine could not be assessed acoustically due to the very low abundances. Sardine catches were very low and the stock assessment models estimated the sardine biomass to be close to zero (well below the limit reference point).

4.2.3 Data Analysis

Prior to the analysis, the increment widths (referred to as growth), Age, and AAC were log-transformed and mean-centred (Morrongiello and Thresher 2015). Hierarchical linear mixed effects models were produced using log-transformed and mean-centred data to examine how increment width (Inc) responds to various intrinsic (fish-specific) and extrinsic (environmental) factors (Morrongiello and Thresher 2015). Within a mixed effects model, the fixed effects are used to address the consistent or foreseeable variation, while the random effects are employed to address the unpredictable or stochastic variation. The fixed effects represent the influence of variables expected to consistently affect the outcome variable, while the random effects indicate the impact of variables that demonstrate a varying effect on the outcome variable among different groups or individuals. The fixed intrinsic effects were determined as Age and Age at Capture (AAC) (Table 4.1). Incorporating the ACC term aims to rectify biases stemming from sampling issues, such as imbalanced age distributions, and to evaluate potential biases resulting from selectivity based on growth rate, with the intention of correcting these biases (Morrongiello and Thresher 2015). Sex was not included as an intrinsic fixed effect, as sex data were not available for the majority of the archived otoliths.

The random effects were FishID, cohort and year. The FishID term accommodates the correlation among incremental measurements within a fish, taking into consideration the individual's estimated growth in comparison to the average. Deviations in FishID can result from processes related to genetic identification and/or measurement errors (Morrongiello and

Thresher 2015). The concept of cohort incorporates a temporal estimate derived by considering both inherent and external variations in growth, as well as systematic deviations in growth observed among groups of fish born in the same year (Morrongiello and Thresher 2015).

Equation 1 demonstrates the full mixed effects base model fitted to the entire time series 1974-2021:

$$\text{Log (Inc)} \sim \text{Log(Age)} + \text{Log(AAC)} + \text{Log(Age)} \mid \text{Fish ID} + \text{Log(Age)} \mid \text{Year} + \text{Log(Age)} \mid \text{Cohort} \qquad (1),$$

where the combinations of fixed effects (Age and AAC) and random effects, intercept (denoted by “|” in by-FishID, by-Cohort and by-Year) and slope for random effects (random slopes of the effect of Age is denoted by e.g. log (Age) | FishID.

The selection of the optimal base model describing fish growth was determined using Akaike’s Information Criterion (AICc) corrected for small sample sizes (Burnham and Anderson 2004). The optimal model was chosen and adjusted using maximum likelihood estimates to generate unbiased parameter estimates (Zuur et al. 2009) using the random effects of year to produce a best linear unbiased predictor (BLUP) of growth for each year from 1974 to 2021 (Number of observations= 2862, groups: FishID= 700; Year = 47; Cohort = 43). The conditional R^2 metric was computed for each model to evaluate the proportion of variance in fish growth explained by both fixed and random effects (Nakagawa and Schielzeth 2013).

Prior to use in the mixed effects models (see Table 4.1), the variables SST, upwelling index, SOI, and sardine biomass were assessed for collinearity (Figure C5, Figure C6 and Figure C7).

Table 4.1. Description of parameters used in the predicting the growth of sardine (*Sardinops sagax*) in northern Benguela (Namibia).

Parameter	Description
Fixed effects	
Age	Age (yr) when otolith increment formed
Age-at-capture (AAC)	Final age (yr) at time of capture
Random effects	
FishID	Unique identification number for each fish
Cohort	Group of fish spawned in the same year
Year	Calendar year of otolith ring formation
Environmental effects	
SST8-10_N	SST averaged Aug-Oct at northern region 17-20º S (1974-2021)
SST8.9_C	SST averaged Aug-Sep at central region 20-24º S (1974-2021)
SOI4	Monthly Southern Oscillation Index for Apr (1974-2021)
UI_WB12-1	Monthly Upwelling index at Walvis Bay averaged lagged Dec-Jan (1979-2021)
KUIprev12	Monthly Upwelling index at Kunene for Dec lagged 1 year (1979-2021)
Sarbiom	Annual sardine biomass estimates (1990-2013)

Additional fixed terms were incorporated to evaluate if and how extrinsic environmental predictors (e.g. SOI, SST and upwelling) or sardine biomass influenced annual sardine body growth. The SST datasets (ERSSTv5) and the SOI were available from 1974-2021. The upwelling indices were available from 1979-2021. The MEIv2 was available from 1982-2021. However, SOI and MEIv2 are collinear (Figure C5), and therefore only SOI was used in the analysis. The sardine biomass was available from 1990-2013 (Table 4.1).

To evaluate the potential influence of external environmental factors on sardine growth, a series of model comparisons were conducted, considering the time limitations related to sardine biomass, upwelling indices, and sea surface temperature variables. Consequently, this procedure was applied across three distinct time periods: 1974-2021, 1981-2021, and 1990-2013. These periods were selected to align sardine growth data with the available environmental variables (SST and upwelling) and sardine biomass data (Table 4.1). Sardine growth was assessed independently for each time period to ensure that any overlapping intervals were excluded from each individual evaluation. During the first time period, the SST and SOI variables were included in a set of optimal model comparisons for the entire time period 1974-2021 (Number of observations = 2862, groups: FishID = 700; Yea r= 47; Cohort = 43). In the second time period, SOI, SST and upwelling index were included in the model comparisons for the period 1979 to 2021 (Number of observations = 2679, groups: FishID = 656; Year = 40; Cohort = 38). Finally, SST, SOI, upwelling indices and sardine biomass estimates were included in model comparisons for the period 1990 to 2013 (Number of observations = 1972, groups: FishID = 552; Year = 23; Cohort = 29). The best model was chosen as the model with the lowest AICc and with ΔAICc < 2 compared to the model with the lowest AICc, and fewer parameters (K) than the model with the lowest AICc.

Finally, the Year random effect (BLUP) time series, along with the environmental time series (upwelling index and SST), were utilised in the cross-wavelet coherence analysis. Wavelet coherence analysis converts two time series into a time–frequency space with varying time resolution, allowing for the identification of the localised correlation coefficient and how these modes change over time (Grinsted et al. 2004; Ng and Chan 2004). This method enables the identification of periodic patterns in shared variability by accounting for both nonstationary temporal changes and inherent noise elements (Jenouvrier et al. 2005; Smoliński 2019). The analysis utilised the Morlet wavelet function, applying a 5% significance level with 1000 Monte Carlo simulations (Grinsted et al. 2004) for further details on wavelet coherence analysis.

All data analyses and plots were executed in R Studio Version 1.1.463 (R Core Team 2018), utilising the libraries lme4 (Bates et al. 2014), AICcmodavg (Mazerolle 2019), effects (Fox 2003; Fox and Weisberg 2019), and lattice (Sarkar 2008), tidyverse (Wickham et al. 2019) and MuMIn (Bartoń 2019) for visualisation.

4.3 Results

To address Hypothesis 1, which tested whether annual otolith growth patterns of sardine remained stable over time (H_0) or exhibited significant temporal changes (H_1), the sardine otolith biochronology was analysed for evidence of growth shifts. The annual increments of 700 sardine otoliths were assessed and resulted in a 48-year long biochronology spanning from 1974 to 2021 (Figure C3). The optimal base model of the growth structure contained fixed effects for Intercept, Age and AAC, and random effects for Cohort intercept, intercept and age slopes for FishID and Year (AICc = -1987.24, Conditional $R^2 = 0.864$ Table C1). The optimal base model accounted for 86.4% of the variability in fish growth. An analysis of variance for the components employed in the random structure revealed that a substantial portion of the inter-annual variability in otolith increments could be explained by the effects of FishID, Age|FishID, and Age|Year (Table C2). However, a notable amount of unexplained variance was observed in the residuals (Table 4.2). There was a notable decrease in increment width with age, consistent with the typical pattern observed in fish otoliths, signifying that growth exhibited age-dependent characteristics (Figure C4). A positive correlation was observed between fish growth and Age-at-capture.

The growth time series obtained from the BLUP for the Year random effect demonstrated significant year-to-year fluctuations with no directional trend in sardine growth within the northern Benguela region (Figure 4.3a). The year-to-year fluctuations in sardine growth from the BLUP of the Year have very similar range (± 0.12 mm), these fluctuations have a more-or-less similar frequency (6 – 8 years). In Figure 4.3b, the cohort BLUP for the Year, the year-to-year fluctuations can be described as: cohorts from 1974-1990 are characterised by higher cohort-specific variation in growth, from 1990-onwards cohorts had more similar growth, with the exception of year class 2003, which was characterised by very poor growth. The cohort-specific growth time series (BLUP for the Cohort random effect) generally displayed a less significant yet consistent pattern of year-to-year fluctuations and shifts across the entire time period (Figure 4.3b).

To address Hypothesis 3, which tested whether environmental variables (sea surface temperature and upwelling intensity) significantly influence annual otolith growth patterns (H_1) or have no effect (H_0), statistical models were applied to assess the strength and direction of these associations. Thus, the addition of SST and Southern Oscillation Index (SOI) variables to the optimal base model fitted for the otolith growth time series for the entire period (1974-2021) indicated significant SST effects on sardine growth by decreasing the model AICc significantly (Table C3). The best model incorporated SST averaged for August-October in the northern region 17-20ºS (SST8-10_N), which is representative of the Angola-Benguela Front (ABF) off northern Namibia and indicated a negative effect of austral winter-spring SST on growth (AICc = -2010, Conditional R^2 = 0.79, Table 4.2).

The addition of SST, upwelling index, and SOI in the model selection during the shorter time period (1980-2021) indicated a significant negative effect of August-October SST (SST8.10_N) on sardine growth (Figure 4.4a and c) and it scatter plot and a significant positive effect of the Kunene upwelling index in December of the previous year (KUIprev12) on the growth of sardine (Figure 4.4b and d) (AICc = -1852.51, Conditional R^2 = 0.86; Table 4.2, Table C4).

To address Hypotheses 2, which tested whether sardine biomass significantly influence annual otolith growth patterns (H_1) or have no effect (H_0), statistical analyses were conducted to evaluate the relationships between these predictors and growth variation in sardine. Therefore, sardine biomass ‘Sarbiom’ predictor variable together with all environmental predictor variables (sea surface temperature and upwelling intensity) were available for the shortest time period (1990-2013) (Table C5). The most parsiomonious model for the period 1990-2013 included a negative relationship with August-October SST (SST8-10_N) and sardine growth (AICc = -1289.11, Conditional R^2 = 0.86; Figure 4.4a; Table 4.2). Predicted sardine growth was positively affected by the Kunene upwelling index in December of the previous year (KUIprev12) (Figure 4.5a and b).

A cross-wavelet coherence analysis was performed to examine changes in fish growth patterns and their relationships with environmental time series across time, frequency, and spatial domains, in order to test Hypothesis 3. Thus, the wavelet analysis identified a consistent band of coherence of sardine growth and upwelling at an 8-year period throughout this entire time range (1980-2021) in Figure 4.6a. The coherence in the sardine growth and the upwelling time series were not significant prior to 1996 however from 1996 to 2021 the coherence is significant. Beyond 2010, there was a shift to a shorter coherence period of 2-4 years, corresponding with observed changes in sardine growth. However, the 8-year period is the most prominent and significant from 1996 to 2021 (Figure 4.6a). The observed in-phase relationships are consistent with the positive coefficients estimated for upwelling index by the linear mixed models (Table 4.2b). The sardine growth coherence with the SST time series (Figure 4.6b) indicated significant short-term coherence at 2-4-year periods from 1980-2005. However, from 2002-2021 significant longer-term coherence at 12-14-year periods were observed indicating a strong anti-phase relationship between SST and sardine growth consistent with the linear mixed effects model (Figure 4.6b).

Table 4.2. Variance and correlation components of random effects and parameter estimates with standard error and significance of fixed effects of the optimal model that describes sardine growth model for the period (a) from 1974 to 2021 (Number of observations: 2862, groups: FishID, 700; Year, 47; Cohort, 43), (b) from 1981 to 2021 (Number of observations: 2679, groups: FishID, 656; Year, 40; Cohort, 38) and (c) 1990 to 2013 (Number of observations: 1972, groups: FishID, 552; Year, 23; Cohort, 29). The model was incorporated to include SST and upwelling estimates that are available from 1981-2021. Random age slopes are denoted by "|". Age was log-transformed in the model. Significance level codes: < 0.001 '***' <0.01 '**' <0.05 '*'.

a) Entire period (1974-2021)			
Random effects	**Variance (± SD)**	**Correlation**	
FishID	0.019 (0.137)		
Age|FishID	0.010 (0.098)	0.49	
Year	0.003 (0.057)		
Age|Year	0.010 (0.099)	0.93	
Cohort	0.004 (0.061)		
Residuals	0.017 (0.129)		
Fixed effects	**Estimate (SE)**	**t-value**	**p-value**
Intercept	-1.988 (0.015)	-132.46	
Age	-0.487 (0.017)	-29.36	2.2e-16 ***
AAC	0.156 (0.025)	6.26	1.762e-09 ***
SST8-10_17-20S	-0.039 (0.010)	-2.87	0.00755 **
b) Shorter period (1981-2021)			
Random effects	**Variance (± SD**	**Correlation**	
FishID	0.018 (0.136)		
Age|FishID	0.008 (0.092)	0.48	
Year	0.002 (0.04)		
Age|Year	0.008 (0.09)	0.96	
Cohort	0.004 (0.061)		
Residuals	0.017 (0.129)		
Fixed effects	**Estimate (SE)**	**t-value**	**p-value**
Intercept	-1.525 (0.190)	-8.02	
Age	-0.491 (0.016)	-30.28	< 2.2e-16 ***
AAC	0.157 (0.025)	6.26	6.483e-10 ***
SST8-10_17-20S	-0.035 (0.012)	-2.90	0.007238 **
KUIprev12	0.016 (0.007)	2.44	0.025613 *
c) Shortest period (1990-2013)			
Random effects	**Variance (± SD)**	**Correlation**	
FishID	0.021 (0.146)		
Age|FishID	0.009 (0.095)	0.50	
Year	0.002 (0.040)		
Age|Year	0.006 (0.075)	0.99	
Cohort	0.004 (0.068)		
Residuals	0.018 (0.132)		
Fixed effects	**Estimate (SE)**	**t-value**	**p-value**
Intercept	-1.211 (0.236)	-4.69	
Age	-0.499 (0.017)	-28.97	< 2.2e-16 ***
AAC	0.183 (0.029)	6.34	4.308e-10 ***
SST8-10_17-20S	-0.059 (0.015	-3.85	0.001843 **

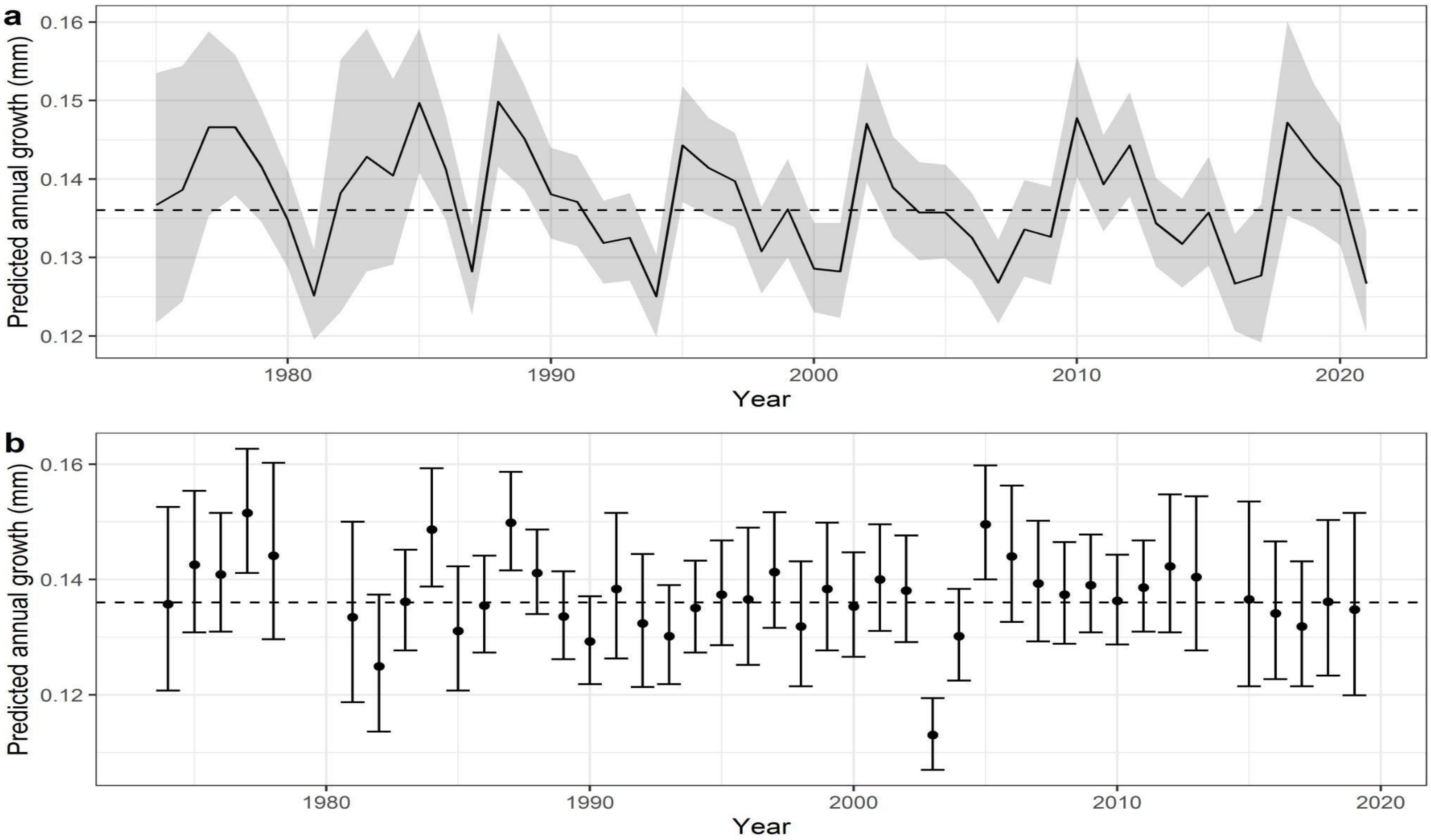


Figure 4.3. The best linear unbiased predictor (BLUP) of growth (dots and solid lines) against year for sardine caught in northern Benguela (Namibia). The grey areas represent the 95% confidence intervals, while the dashed line denotes the average growth. (a) time series and (b) BLUP for the Cohort random effect.

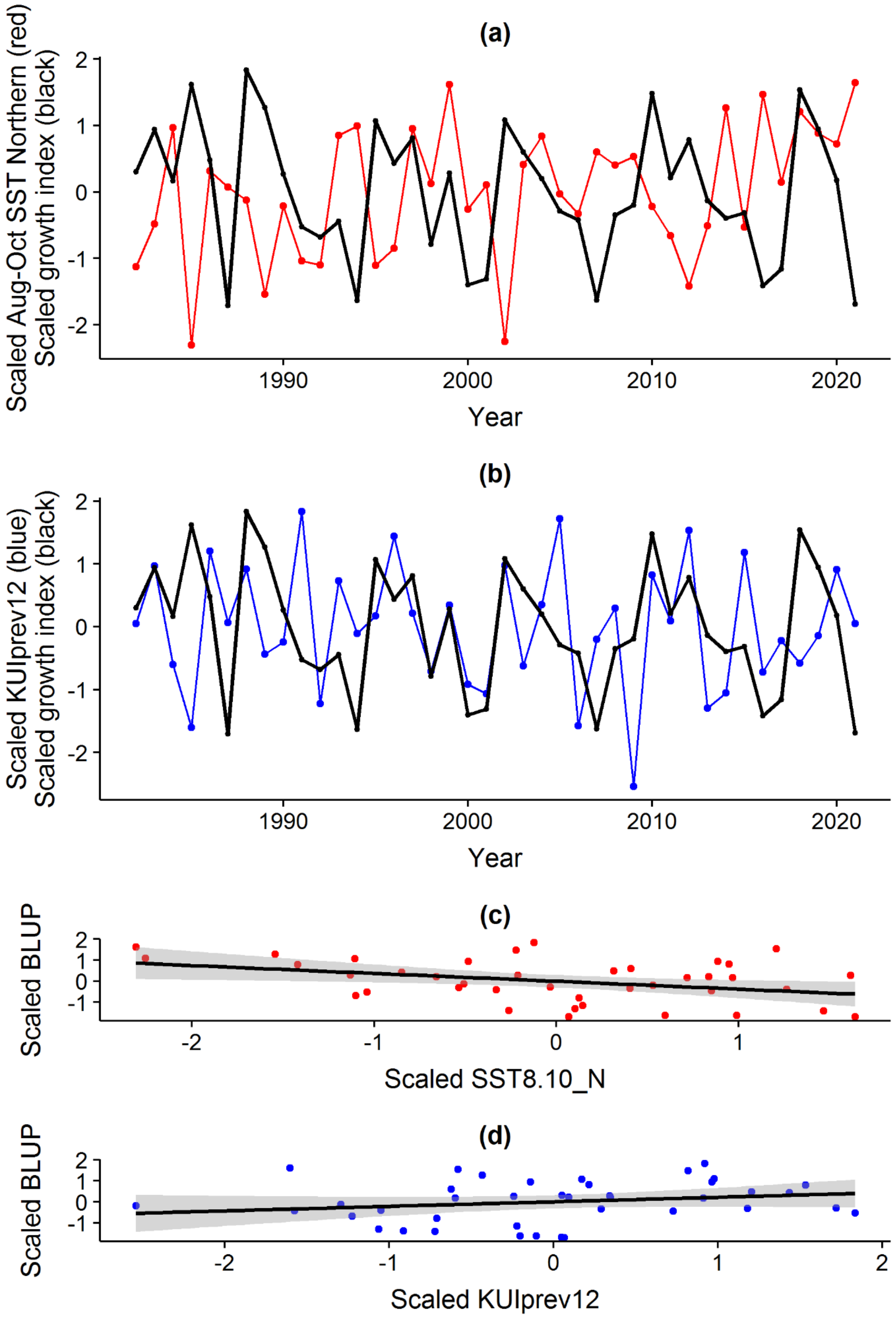


Figure 4.4. Model predictions of the best linear unbiased predictor (BLUP) of growth in black scaled with (a) the scaled spring Aug-Oct SST (°C) namely SST8-10_N in red for northern region 17-20 ºS (b) the scaled Kunene upwelling index in December of the previous year (KUIprev12) (c) scatter plot with regression line of BLUP of Year with SST8-10_N and (d) scatter plot with regression line of BLUP of Year with Kunene upwelling index in December of the previous year (KUIprev12) within the northern Benguela (Namibia) for the shorter time period 1980-2021.

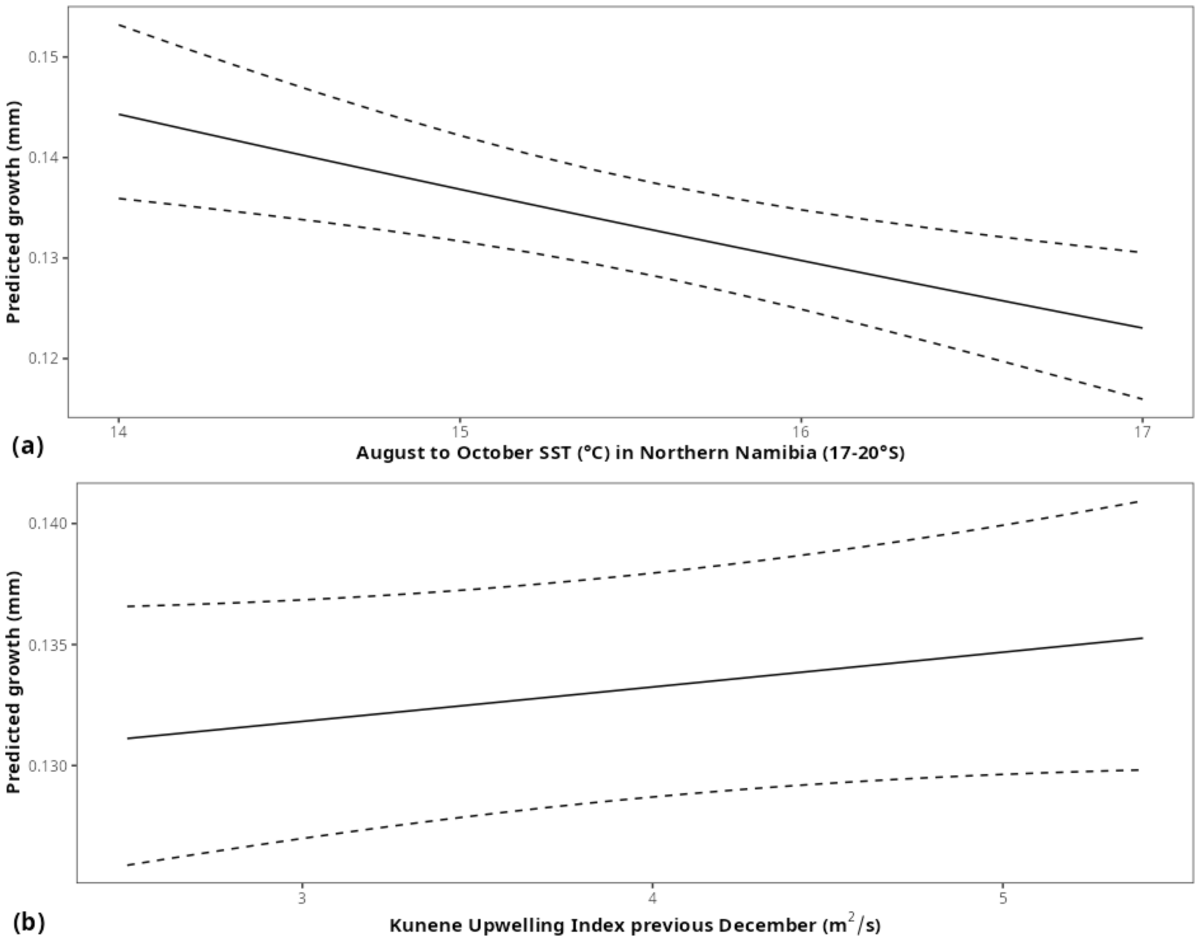
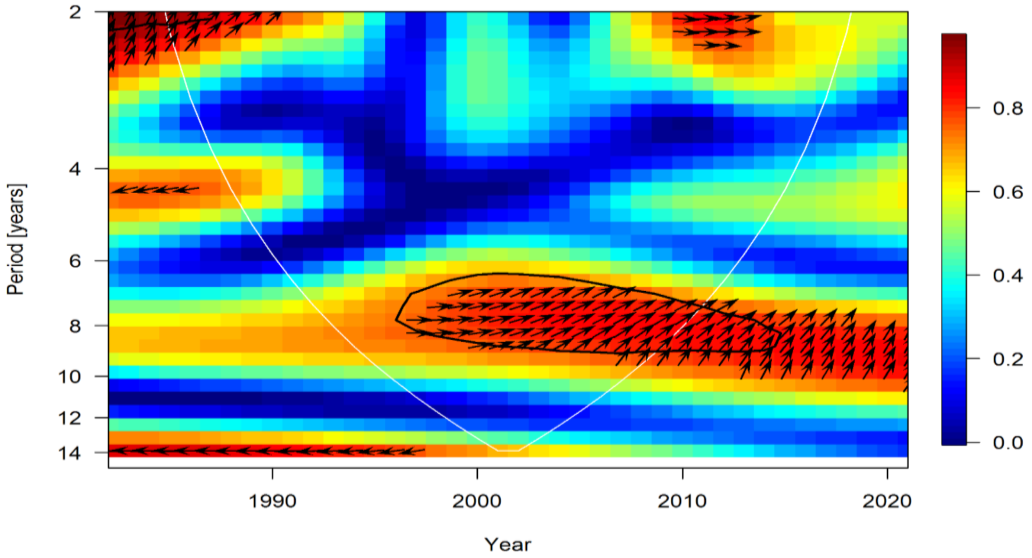


Figure 4.5. Predicted growth of sardine against relationship with 95% confidence interval (a) spring (Aug-Oct) SST (°C) from northern Namibia (17°S - 20°S) during 1974-2021, (b) summer Coastal Upwelling Index (m2 s-1) lagged with 1 year at Kunene (17 ºS) during 1979-2021.

(a) Upwelling index



(b) SST

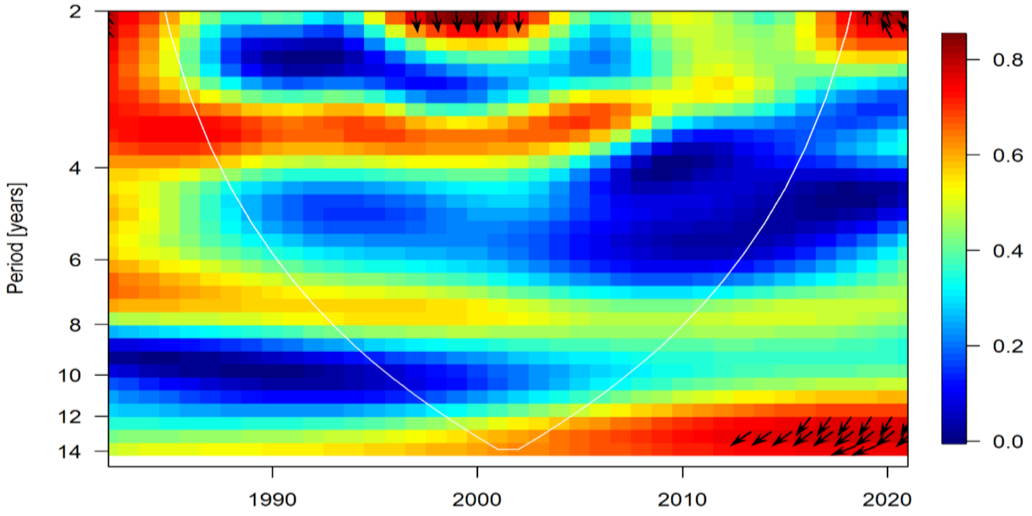


Figure 4.6. The wavelet coherence and phase plot between sardine growth year random effect time series obtained from the (1981-2021) model and (a) Kunene upwelling index (b) spring Aug-Oct SST (°C), for the northern Benguela (17-20 ºS) for the period 1979-2021. The wavelet coherence plot visualizes the relationship between two time series across different periods (scales) and over time. The X-Axis (Year): represents time, spanning from around 1981 to 2021. The Y-Axis (Period [years]): represents the different periodicities (or scales) of the data. For example, a period of 4 years indicates cycles that repeat every 4 years. The colour scale shows the magnitude of the wavelet coherence, ranging from 0 (blue) to 1 (red). Therefore, high coherence (red/yellow areas): indicates a strong correlation between the two time series at a specific period and time. Low coherence (blue areas): indicates little to no correlation. The 5% significance level of coherence from the 1000 Monte Carlo randomizations is shown with the thick black contour. The relative phase relationship is indicated with arrows (with the anti-phase pointing left, in-phase pointing right, and the sardine growth time series leads the second time series by 90 degrees if arrows points down. Cut-off value for plotting phase arrows was set to R^2=0.75. The white line represents the cone of influence, which indicates the region of the plot where edge effects might distort the analysis.

4.4 Discussion

A 48-year uninterrupted and annually detailed growth history of the sardine population in the northern Benguela was developed using an otolith-based approach, representing the most extended biological time series available for this fish species in the northern Benguela. The results indicated that variations in sardine growth are significantly impacted by both intrinsic factors (Age, and to a lesser degree, Age-at-Capture, AAC) and extrinsic environmental conditions, specifically sea surface temperature and upwelling in northern Namibia. Hypothesis 1 in this chapter investigated whether sardine otolith growth in the northern Benguela remained stable over time (H_0), or whether there were significant temporal changes throughout the biochronology (H_1). The base model identified fish age as the most influential intrinsic fixed effect, confirming a biologically expected pattern of decreasing growth rates with increasing age — a trend consistent with ontogenetic development and widely supported in the literature (e.g., Doubleday et al. 2015; Izzo et al. 2016; Smoliński 2019). However, when year-to-year variability was accounted for via the inclusion of the Year random effect, the resulting BLUP time series demonstrated substantial interannual fluctuations in growth, with no clear directional trend. This temporal variability provides support for the alternative hypothesis (H_1), indicating that sardine growth in the northern Benguela is influenced by external year-specific factors. Notably, no significant shifts in growth were detected following the stock collapse, suggesting that while annual fluctuations are present; these did not result in regime-like transitions over the study period (1974–2021). Overall, H_1 is supported: sardine growth in the northern Benguela is not temporally stable, but subject to considerable interannual variation likely driven by environmental and ecological dynamics. The positive correlation observed between otolith increment width and the AAC implies that faster-growing sardines were more prone to capture at older ages compared to their slower-growing counterparts. The reason may be attributed to the lack of fish older than nine years in our samples, which could have influenced the results or might reflect an impact from fishing activities or environmental factors in an area with a history of significant commercial fishing (Morrongiello and Thresher 2015). It is crucial to incorporate an "AAC" term in biochronology analyses because it allows for the detection of ecologically and evolutionarily significant growth-based selectivity in a species (Morrongiello and Thresher 2015). Additionally, the AAC term corrects for potential biases in the sampling regime that could otherwise undermine the accuracy of the analyses (Morrongiello and Thresher 2015).

Sudden environmental shifts influencing growth patterns, resource overexploitation, and a combination of these factors are all likely contributors to variations in species growth over time (Möllmann and Diekmann 2012). Hypothesis 3 addressed whether environmental variables significantly influence annual sardine growth patterns in the northern Benguela (H_1), or whether such variables exert no effect (H_0). The findings provide clear support for the alternative hypothesis (H_1). Among the tested variables, average sea surface temperature (SST) from August to October in northern Namibia emerged as the most influential driver of sardine growth. Cooler summer temperatures during this period were associated with enhanced growth, suggesting that interannual fluctuations in SST play a critical role in determining individual growth outcomes. The majority of the year-to-year variability in SST is linked to changes in upwelling intensity, which is influenced by local and/or distant wind-stress fluctuations (Bartholomae and van der Plas 2007). During years when upwelling weakens for extended periods in the summer (such as 1984, 1988, 1995, 1999, 2001, 2002, and 2003), warm-water events tend to occur. Conversely, when upwelling is more vigorous in the summer (such as in 1982, 1983, 1987, 1992, 1997, and 2004), cooler conditions prevail (Bartholomae and van der Plas 2007). These Benguela Niño/Niña (warming/cooling) events involve the irregular intrusion of warm, nutrient-deficient, and oxygen-poor water from southern Angola into the northern Namibia region evident in a southward movement of the ABF (Angola-Benguela Front), during late summer and early autumn (Hampton and Willemse 2012). Additionally, a general warming trend has been observed across the northern Benguela system (Monteiro et al. 2008), along with a rise in the frequency of warm water events at the ABF since the late 1990s (Bartholomae and van der Plas 2007) leading to fewer years with cooler conditions (Kirchner et al. 2009). The addition of the wavelet analysis revealed a significant coherence at a 2-4-year period during 1980-2005 short-term fluctuations in SST was strongly correlated with sardine growth during 1980-2005. The significant coherence in this period indicates that changes in SST likely had a notable impact on sardine growth in cycles of 2-4 years. This coherence suggests that the relationship between SST and sardine growth could have potentially been utilized to make accurate year-to-year projections at that time period. Another significant coherence is observed at a 12-14-year period from 2002 to 2021 indicating a strong anti-phase relationship between SST and sardine growth. This indicates that during this period, there was a longer-term correlation between SST and sardine growth. The significant coherence in this longer cycle suggests that SST changes influenced sardine growth over a more extended timeframe.

In further support of H_1, upwelling was identified as the second most significant environmental factor affecting sardine growth. Specifically, the Kunene upwelling index in December of the previous year showed a significant positive relationship with growth. This indicates that intensified upwelling events during early developmental stages (likely enhancing nutrient availability and boosting food web productivity) has a delayed but measurable effect on growth outcomes. These combined results reinforce the conclusion that sardine growth is closely tied to interannual variability in both temperature and upwelling intensity, thus validating the alternative hypothesis. Furthermore, our findings showed that sardine growth and upwelling followed a synchronized pattern, with peaks and troughs occurring roughly every seven years, and the pattern more pronounced in recent decades after the 1990s. Thus, the sensitivity of sardine growth to upwelling variability may have undergone changes over time, exhibiting a more pronounced association with upwelling indices in recent decades (1990s-2000s) compared to earlier periods (1980s). This pattern aligned with variations in the three-month averages of offshore Ekman volume transport, a proxy for upwelling-favourable wind stress, at Cape Columbine during 1957 to 1992 (Johnson and Nelson 1999). Their averages indicated that upwelling at this site is consistent over this timescale, with peaks and troughs approximately every seven years. However, there was a significant decrease in upwelling following the 1983 El Niño, which only resumed increasing in 1990 (Johnson and Nelson 1999). According to Johnson and Nelson (1999) an explanation for this is found in polar events rather than in the tropical Pacific (El Niño). Furthermore, the sensitivity of sardine growth to upwelling variability may have undergone changes over time, exhibiting a more pronounced association with upwelling indices in recent decades (1990s-2000s) compared to earlier periods (1980s). Furthermore, our results indicated that sardine growth was most significant during December at the Kunene region. In the northern Benguela, upwelling tends to be weaker during the austral summer (December to February) and stronger during the austral winter (June to August). Historically, sardines in the northern Benguela spawn in two main periods: during the winter-spring (September–November) and late summer-autumn (February–April) (Boyer et al. 2001). Thus, our results revealed that sardine growth accelerated (i.e., the opaque zone developed) during the summer following the spring spawning season (September–November), which is consistent with previous studies (Thomas 1983; Kerstan 1995; Waldron 1998). In summer, when sardine growth speeds up and upwelling is weaker, there needs to be ample phytoplankton and zooplankton available to support the feeding of larvae, recruits, and adults. Therefore, optimal growth are likely to occur when upwelling in the central Namibian region is above average and the ABF shifts northward, signalling cooler conditions usually linked to stronger upwelling in northern Namibia (Kunene region) (Bartholomae and van der Plas 2007; Kirchner et al. 2009). An additional wavelet analysis indicated that a significant coherence between sardine growth and upwelling time series at a higher frequency with an approximately 8-year cycle from 1996 to 2005. After this period, there was a shift to a shorter frequency with coherence period of 2-4 years post-2010, corresponding with observed changes in the otolith biochronology of sardine growth. The observed in-phase relationships are consistent with the positive coefficients estimated by the linear mixed models. The results suggest that the strength of relationship between growth and upwelling can vary over time, and thus influence SST and the food-web structure (Bartholomae and van der Plas 2007)

The relationship between sardine growth and biomass was evaluated through model comparisons for the period 1990 to 2013 using AIC values. Hypothesis 2 proposed that sardine biomass significantly affects annual growth patterns (H_1), as opposed to exerting no influence (H_0). The results provide partial support for the alternative hypothesis. Model comparisons conducted for the period 1990–2013 demonstrated that the inclusion of sardine biomass, alongside environmental variables such as upwelling and sea surface temperature (SST), lowered the AIC, suggesting improved model fit. However, the model that included sardine biomass had more parameters and, although within ΔAICc < 2 of the best-fitting model, was not selected due to its increased complexity (Table C5). Furthermore, sardine biomass in Namibian waters fell from millions of tons in the 1950s-1960s to hundreds of thousands by the 1980s, with rising fishing pressure leading to a moratorium in 2018. The ban remains due to the stock's poor recovery. Therefore, the otolith biochronology for the northern Benguela sardine population post-collapse revealed short-term fluctuations in growth but no clear long-term shifts corresponding with the prolonged period of low biomass. This pattern indicates that while sardine biomass may contribute to explaining variation in growth, its effect is likely secondary to environmental drivers. The apparent lack of strong density-dependent responses in growth at low biomass levels supports the concept of growth depensation, wherein environmental variability dominates over intraspecific competition or food limitation, even when population density is low. These findings suggest that sardine growth is only weakly influenced by biomass levels in the northern Benguela, providing limited but notable support for the alternative hypothesis. However, the depensation mechanism is especially important for depleted populations and endangered species, as it speeds up further population decline and can hinder recovery efforts (Rose et al. 2001). Several mechanisms can lead to depensation, including a lower likelihood of fertilisation, disrupted group dynamics, environmental factors, and predator saturation (Liermann and Hilborn 2001). It is proposed that the depensatory population dynamics observed in sardines of the northern Benguela could be elucidated by a reduced probability of fertilisation (recruitment) due to adverse environmental factors with a very low sardine spawner biomass. Boyer and Hampton (2001) linked the sardine collapse to heavy fishing in the 1960s and prolonged low recruitment. Despite high recruitment early in the 1960s, subsequent years saw consistently low levels, even with substantial spawner biomass (Boyer et al. 2001; Boyer and Hampton 2001). This indicates that environmental conditions may play a more dominant role in determining recruitment success, overshadowing the impact of spawner biomass (Boyer et al. 2001). Furthermore, the sardine population dynamics in the southern Benguela indicate a depensation effect, contributing to instability post-collapse. Sardine growth has been largely shaped by sea surface temperature (SST) and copepod abundance, likely influenced by depensatory population dynamics (Chapter 3; Brinkman et al. 2025a). The biochronology of fish growth in the southern Benguela indicated four regimes with three alteration points in 1986, 2006, and 2015 that correspond with periods of low, high, average and low biomass, respectively; i.e. high growth rates occurred during the high biomass period and vice versa (Chapter 3; Brinkman et al. 2025a).

Further support for alternative Hypothesis 1, which posited that there are significant temporal changes in the annual otolith growth patterns of sardine, was found in the cohort-level analysis. In addition to the interannual variability captured by the BLUP of the year random effect, growth also varied consistently among year-classes, indicating that fish born in the same spawning season exhibited similar growth trajectories. This cohort-specific variation underscores the role of early life environmental conditions in shaping subsequent growth outcomes. Such patterns are a key component of temporal growth fluctuations and suggest systematic differences in how individual cohorts respond to environmental drivers (Morrongiello & Thresher 2015; Denechaud et al. 2020). These findings reinforce the conclusion that sardine growth in the northern Benguela is temporally dynamic and influenced by both year-specific and cohort-specific extrinsic factors, thereby supporting the alternative hypothesis. This is frequently linked to carry-over effects (Murphy et al. 2013), where early conditions can impact the growth trajectory. For instance, individuals born in a year-class with unfavourable (or favourable) environmental conditions may experience lasting effects on their future growth. The recruitment of sardines in the northern Benguela exhibits significant year-to-year fluctuations, which directly impact the fishing industry by affecting both the size of biomass and the subsequent determination of the total allowable catch (Boyer et al. 2001). A significant feature of cohort-specific growth, as determined by the BLUP for each random effect, was the greater variability observed before 1990, followed by reduced variability after 1990. Concurrently, the average proportion of 0-group fish (recruits) in the population was higher post-1990, at least a 50% increase proportion of recruits, compared to earlier periods, suggesting a decrease in longevity (Fossen et al. 2001). While the proportion of sardine recruits in the stock remained stable in the fishery's early years (pre-collapse during early 1970s), it began to experience significant fluctuations following the stock's collapse in the mid-1970s (Fossen et al. 2001). After the collapse, fishing mortality rose and became a major contributor to overall mortality until 1990 (Fossen et al. 2001). Throughout this time, a considerable number of juvenile sardines were captured in the growing anchovy (*Engraulis capensis*) fishery, and the combined sardine catches likely led to both growth and recruitment overfishing (Fossen et al. 2001). Therefore, the greater variability observed in the cohort-specific differences in growth as determined in the present study was mainly due to the sardine biomass reduction caused by excessive fishing and recruitment failure after the stock collapse in the 1960s. Historically, spawning primarily occurred in two key regions: central Namibia near Walvis Bay (23°S), where older fish spawned in early summer, and northern Namibia near Palgrave Point (20°30′ S), where younger adults spawned later in the season during late summer and autumn (Kirchner et al. 2009). However, spawning locations have shifted from the less favourable northern regions in the early 1980s to areas further south by the 2000s (Kreiner et al. 2011). Sardine spawning occurred off the coast of Walvis Bay during warmer years in the 1980s, while in cooler years, spawning of both species was restricted to regions north of 22°S (Kreiner et al. 2011). The shift toward more southern spawning areas since the 1980s was anticipated due to the overall warming of the northern Benguela system (Kreiner et al. 2011). Therefore, the sardine cohort-specific growth rate differences before 1990 indicates greater variability in the optimal environmental conditions necessary for larval survival and feeding.

Furthermore, the results showed reduced growth for the 2003 sardine cohort. (i.e. recruits born between September 2002 and August 2003). The Benguela Niño in 2001 may have influenced the growth of the 2003 sardine cohort, which emerged a year following the warming event. One possible explanation for the poor growth in the 2002-2003 cohort could be reduced primary production and widespread hypoxic conditions. The seasonal rise in temperatures aligns with the second half of the spawning season for most pelagic fish species (Bartholomae and van der Plas 2007). Short-term fluctuations in temperature, whether warming or cooling, can impact fish behaviour, potentially influencing their migration and spawning patterns. Furthermore, such temperature changes can also affect the survival of fish eggs and larvae if alterations occur in retention or food concentration resulting from these short-term events (Bakun 1997; Cury and Roy 1989). Consequently, the subsequent rise in SST over northern Namibia in 2001 likely could have hindered primary production, leading to lower survival rates for fish larvae given that weak upwelling reduces the size of the upwelling area and creates conditions that allow nutrient- and oxygen-depleted Angolan waters to enter the region (Kirchner et al. 2009). Another potential explanation for the very low growth in the 2003 cohort could be that the Benguela Niño event in 2001 triggered changes in zooplankton composition, shifting from large-species dominance in the 1970s–1980s, when zooplankton biomass was lower, to smaller species dominating in the 2000s, when zooplankton biomass was higher (Verheye et al. 2016). Large to medium species, such as *C. carinatus*, *M. lucens*, and *C. brachiatus*, were more common in the 1980s (collectively making up 25–60%) compared to the early 2000s (<10%). However, their dominance increased again from 2005 onward (Verheye et al. 2016). In contrast, the smallest species, which are the preferred prey for sardine (van der Lingen 2021), the cyclopoid Oithona spp., rose in prevalence from less than 25% of total copepod abundance in the 1980s to 30–70% in the early 2000s, before declining again (Verheye et al. 2016). These shifts in zooplankton communities are likely to have significant impacts on biogeochemical processes, the structure of the food web, and the overall functioning of the northern Benguela ecosystem (Verheye et al. 2016). The warming event in 2001 was similar to the Benguela Niños of 1984 and 1995, though it was less intense and shorter in duration (Rouault et al. 2007). Although warm water events occurred in 1984 and 1995 (Rouault and Lutjeharms 2003), their effects were not clearly reflected in the otolith biochronology, supporting the hypothesis that changes in zooplankton composition may have influenced sardine growth. However, a clear relationship between sardine growth and zooplankton abundance could not be established in the study. Similarly, Hampton (2012) found no definitive predator-prey relationship between pelagic fish and zooplankton in the northern Benguela. While top-down control of zooplankton populations may have been significant prior to the collapse of pelagic fish stocks in the 1970s, its impact in recent decades is likely minimal due to the consistently low levels of planktivorous pelagic fish off Namibia (Verheye et al. 2016).

We recommend that future research focus on synchronies, as combining otolith chronologies from various populations and different basins provides a deeper insight into how species respond to environmental changes. This insight can be integrated into overarching management strategies to enhance their effectiveness, as highlighted by studies (Izzo et al. 2016; van der Sleen et al. 2018). Furthermore, other species' otolith biochronologies in the northern Benguela demonstrated a significant negative correlation between sea surface temperature (SST) and the growth of *Merluccius paradoxus* (Wilhelm et al. 2020) and *Argyrosomus inodorus* (Jagger 2024; Jagger et al. 2025).

CHAPTER FIVE: UNRAVELLING THE IMPACT OF CLIMATE CHANGE AND FISHING ON OTOLITH GROWTH OF CAPE HORSE MACKEREL (*TRACHURUS CAPENSIS*) IN THE NORTHERN BENGUELA

Abstract

Assessing how fish populations reacted to previous environmental changes is valuable for predicting their future behaviour. However, this process is often constrained by the limited availability of long-term biological data. Cape horse mackerel (*Trachurus capensis*) is the most abundant commercial fish species in Namibia and has been heavily exploited since the early 1970s. In this study a 50-year Cape horse mackerel biochronology was developed using archived otoliths of the northern Benguela (Namibia). Otolith increment widths, indicating alterations in fish growth, were analysed using linear mixed effects models to explore intrinsic (within individual) and extrinsic (fish biomass, sea surface temperature and upwelling index) factors contributing to variations in fish growth with the assumption that otolith growth is a proxy for somatic growth. Sequential t-test analysis of regime shifts (STARS) performed on the Cape horse mackerel biochronology of fish growth indicated three regimes with two alteration points in 1980 and 1990 for Cape horse mackerel. The predicted annual growth of Cape horse mackerel in the northern Benguela did not show a significant response to any environmental or biological factors. These results suggest that other variables associated with year random effect play a dominant role in the variation observed in Cape horse mackerel growth. Biochronologies revealed decadal variability that indicated rapid regime shifts in the northern Benguela marine ecosystem supporting previous regime shifts identified in literature. The utilization of preserved otoliths in this study enabled the analysis to identify prolonged shifts in sardine growth, which are influenced by a range of biological and physical factors.

5.1 Introduction

The Cape horse mackerel (*Trachurus capensis*) is the most commercially abundant species in the northern Benguela region, with annual catches surpassing 300,000 tons since the 1970s (Bauleth-D'Almeida et al. 2001; Axelsen et al. 2003). Cape horse mackerel is distributed continuously from Port Alfred on South Africa's south-eastern coast to Tombwa in southern Angola, at the northern boundary of the Benguela (Axelsen et al. 2004). Historically, it was believed that the Cape horse mackerel (*Trachurus capensis*) populations along the northern and southern Benguela were distinct stocks. However, genetic examination has exposed their identical characteristics, leading to the inference that they are one stock separated by the strong perennial Lüderitz upwelling cell (Karaiskou et al. 2004; Naish 1990). The Namibian and South African governments assess the stocks and manage fisheries on the stock independently (Hecht 1990; Naish et al. 1991; Healy et al. 2020). Krakstad and Kanandjembo (2001) reported that the highest concentrations of Cape horse mackerel are located between 17°00'S and 20°00'S in Namibia (Figure 5.1).

Cape horse mackerel size distribution in the northern Benguela (Namibia) varies with both latitude and depth. Smaller fish are more commonly found in the northern areas near the Kunene River at depths of less than 200 meters (Bauleth-D'Almeida et al. 2001). In contrast, adult fish are located farther offshore, typically at depths between 200 and 500 meters (Bauleth-D'Almeida et al. 2001; Krakstad et al. 2002; Kanandjembo et al. 2004). The biomass of Cape horse mackerel fluctuated between 0.5 and 1.8 million tonnes from 1990-2021 with the lowest estimates of approximately 0.5 million tonnes occurring in 2006 and 2007. The recent increase in Cape horse mackerel biomass occurred after a previous decline from about 3 million tonnes in the early 1960s (Kirchner 2012). Before Namibia's independence in 1990, resource management was overseen by the International Commission of South East Atlantic Fisheries

(ICSEAF). Following independence, this responsibility shifted to the Ministry of Fisheries and Marine Resources (MFMR) in Namibia. Kirchner (2012) reported shifts in life history parameters and the size structure of catches of the Cape horse mackerel in northern Benguela off Namibia, such that the length at 50% maturity of Cape horse mackerel dropped from 25.9 cm total length (TL) in the 1990s to 18.9 cm TL during the 2000s. Moreover, the modal TL of commercial catches shifted from about 29 cm in the 1980s to an average of approximately 23 cm over the period from 2003 to 2012. This is a typical effect of fisheries-induced evolutionary changes, which occur as a result of continuously removing the larger mature individuals in a population (Enberg at al. 2012). Somatic growth rates of horse mackerel are therefore likely to decrease as investment into pre-mature somatic growth is usually paired with reduced length at maturity and reduced mean length of the catches (Enberg et al. 2012). An example of this fisheries-induced evolutionary reaction was also demonstrated to have occurred for the deepwater hake (*Merluccius paradoxus*) in Namibia (Wilhelm et al. 2020).

A persistent upwelling cell near Lüderitz, Namibia (around 26ºS), is the border between the northern and southern Benguela, and is thought to act as a barrier, limiting the north–south movement of certain fish species, including Cape horse mackerel (Cury and Shannon 2004). The Angola–Benguela Front (ABF) is a distinct thermal boundary that marks the northern boundary of the northern Benguela and divides the Angola and Benguela systems (Shannon 1985). Typically, the location of the ABF shifts with the seasons, ranging from around 14°S in austral winter to 17°S (Figure 5.1) during austral summer/autumn (Meeuwis and Lutjeharms 1990; Mohrholz et al. 2001; Veitch et al. 2006). The ABF serves as a key feeding and spawning ground for pelagic fish and acts as an ecological barrier that defines the northern limit for several important fish stocks in Namibia (Crawford 1987, Beckley and van der Lingen 1999). The Benguela ecosystem experiences significant natural variability, influenced by environmental factors across both space and time (Hampton 2012). Since the mid-1980s, the ABF has shifted southward and strengthened, influenced by the southward movement of the South Atlantic subtropical anticyclone, potentially linked to the El Niño Southern Oscillation (ENSO), though not always in sync (Hampton and Willemse 2012). This has resulted in periodic intrusions of warm, salty, nutrient-poor, and low-oxygen water onto the Namibian shelf, coinciding with significant southward shifts of the ABF. These events, known as Benguela Niños, have colder counterparts referred to as Benguela Niñas (Rouault et al. 2007; Koungue et al. 2021). Copepods are key components of the zooplankton community and an essential food source for many species such as Cape horse mackerel (Verheye et al. 1998; Verheye 2000; Hutchings et al. 2006). Copepods are highly sensitive to environmental changes due to their short life spans. This sensitivity makes them valuable indicators of shifts within marine ecosystems (e.g. Verheye et al. 1998; Verheye 2000; Hutchings et al. 2006).

Cape horse mackerel are predominantly found in the northern Namibian continental shelf, with their most significant concentrations located between 17°S and 20°S, making this region their primary distribution area in Namibia (Axelsen et al. 2004). However, lesser and more dispersed groupings have been discovered to the south, spanning between 19°S and 23°S, with limited amounts of mature fish located in deep waters south of 23°S (Krakstad and Kanandjembo 2001; Axelsen et al. 2004; Ndjaula et al. 2013). This overall distribution pattern undergoes seasonal variations, exhibiting more sporadic and concentrated groupings during the summer months (December–February) compared to the winter months (June–August) (Ndjaula et al. 2013). Consequently, somatic growth of Cape horse mackerel would be negatively affectedby rising sea surface temperatures, the frequent southward shift and strengthening of the ABF, and Benguela Niño events, all exacerbated by the possibly already existing fisheries-induced evolutionary changes.

Identifying the impacts of climate change (e.g. rising sea surface temperatures) on marine ecosystems is difficult due to the complex responses that occur at various levels, including individuals, populations, species, and communities (Parmesan et al. 2011). The challenge is compounded by the limited availability of long-term data sets (Morrongiello et al. 2012) and the lack of detailed studies on certain marine species, such as large deep-sea fish (Morrongiello and Thresher 2015). Long-term data on individual fish growth rates can serve as proxies for tracking changes in fish somatic growth over time, offering a unique opportunity to examine somatic growth variability on an unprecedented scale (Morrongiello and Thresher 2015). Biochronological approaches using such data have been successfully applied to detect fish responses to environmental factors across a variety of species and regions (e.g., Black et al. 2011; Morrongiello et al. 2014; Izzo et al. 2016; Smoliński and Mirny 2017; Martino et al. 2019; Tanner et al. 2019; Vieira et al. 2020; Wilhelm et al. 2020; Brinkman et al. 2025a). Otolith biochronologies offer a valuable and distinctive method for reconstructing historical climate conditions (Reynolds et al. 2017), predicting future effects of environmental changes on otolith growth and body size (Rountrey et al. 2014), and detecting rapid regime shifts in ecosystems (Smoliński and Mirny 2017).

In this study, the objectives were to: (1) develop a multi-decadal growth chronology for Cape horse mackerel using otoliths, (2) to examine how intrinsic factors (such as age, age-at-capture, and sex) influence Cape horse mackerel otolith growth; (3) to examine the fishing-induced factors (fish biomass) influence the species' annual growth, and (4) to examine environmental (such as sea surface temperature, upwelling indices) or biological (zooplankton abundance) factors given recent changes in the environment and visible, possibly fisheries-induced, changes in the stock’s life history traits.

This chapter addresses the following hypotheses:

a) H_0: Annual otolith growth patterns of Cape horse mackerel in the northern Benguela remained stable over time, with no abrupt shifts in the biochronology.

   H_1: There are significant temporal changes in the annual otolith growth patterns of Cape horse mackerel in the northern Benguela.

b) H_0: Population biomass does not significantly affect the annual growth patterns of Cape horse mackerel in the northern Benguela.

   H_1: Population biomass significantly influences the annual growth patterns of Cape horse mackerel in the northern Benguela.

c) H_0: Environmental factors (sea surface temperature, upwelling intensity) and copepod abundance do not significantly affect the annual growth patterns of Cape horse mackerel in the northern Benguela.

   H_1: These environmental and biological variables have a significant effect on growth patterns of Cape horse mackerel in the northern Benguela.

5.2 Materials and Methods

5.2.1 Sample selection, study area and otolith measurements

A comprehensive archive of otoliths and biological data, available from 1991 to 2021 at the MFMR (Namibia), were used in the present study (Table 5.1). Surveys were conducted by the *R.V. Dr. Fridtjof Nansen* from 1991 to 1998, by the *R.V. Welwitchia* from 1999 to 2001 and by the *R.V. Mirabilis* since 2002. Additionally, the MFMR collected otoliths from port samples taken from commercial fishing vessels during the same period. Otoliths from 1977 were sourced from the archives of the Polish Department of Fisheries Resources (National Marine Fisheries Research Institute) during the ICSEAF era, were made available for analysis. In order to ensure representative sampling for a mixed-effects modelling approach (Smoliński et al. 2020), at least 20 otoliths per year over a period of 30 years (Table 5.1), which resulted in a total of 614 otoliths (individual fish) analysed.

The study area was situated in the northern Benguela, extending from north of Lüderitz at 25°00' S to the Kunene River at 17°15' S in Namibia (Figure 5.1). Samples were collected from a depth range from nearshore waters (around 20 m) to the offshore boundary of the stock, which generally extends to about 500 m depth south of approximately 18°30' S and up to 2000 m depth north of this latitude. Otoliths from 1977 to 2022 were selected from survey stations along the course track of the survey design (Figure 5.1).

In order to ensure representative sampling for a mixed-effects modelling approach (Smoliński et al. 2020), at least 20 otoliths per year over a period of 30 years (Table 5.1), which resulted in a total of 614 otoliths (individual fish) analysed.

Table 5.1. Otolith sample selection of Cape horse mackerel (Trachurus capensis) from the northern Benguela, Namibia. The institute, type of sampling (research survey or commercial catches), collection years, sample sizes (N) and fish size range in total length (TL) are indicated.

Institute	**Type**	**Years**	**N**	**Fish size range TL (cm)**
National Marine Fisheries Research Institute, Poland	Survey	1977-1978	50	20 – 37
Ministry of Fisheries and Marine Resources, (MFMR) Namibia	Survey	1991-1994 1996-1998 2000-2006 2009-2018 2022	509	13 – 48
Ministry of Fisheries and Marine Resources, (MFMR) Namibia	Commercial	2001 2004 2006	55	15 – 33
TOTAL	**N = 614**			

Whole otoliths were individually cleaned and immersed in distilled water following the ICES (2015) protocol as well as the method used at the Ministry of Fisheries and Marine Resources in Namibia (Shivute 2016). Calibrated images of the Cape horse mackerel otoliths were captured against a black background using two setups: (1) a Zeiss Stemi 508 stereo microscope with a Carl Zeiss Axiocam 208 colour camera (in Namibia), and (2) a Nikon SMZ1270 microscope with a DS-Fi3 camera (in Poland) at 10x magnification. The z-stack technique, which combines multiple images along the vertical axis for improved focus on different parts, was used to capture the images in Poland (N = 55, Table 5.1). The optimal orientation for analysis is with the distal surface facing upward and the proximal surface facing downward. Subsequently, the otolith images were analysed using ObjectJ, an ImageJ plugin. For each otolith, the length of each annual growth increment was measured along the posterior axis, from the nucleus to the edge (Figure 5.2). The analysis included a total of 614 otoliths, representing 3067 increments from fish aged 2 to 16 years (Figure D1).

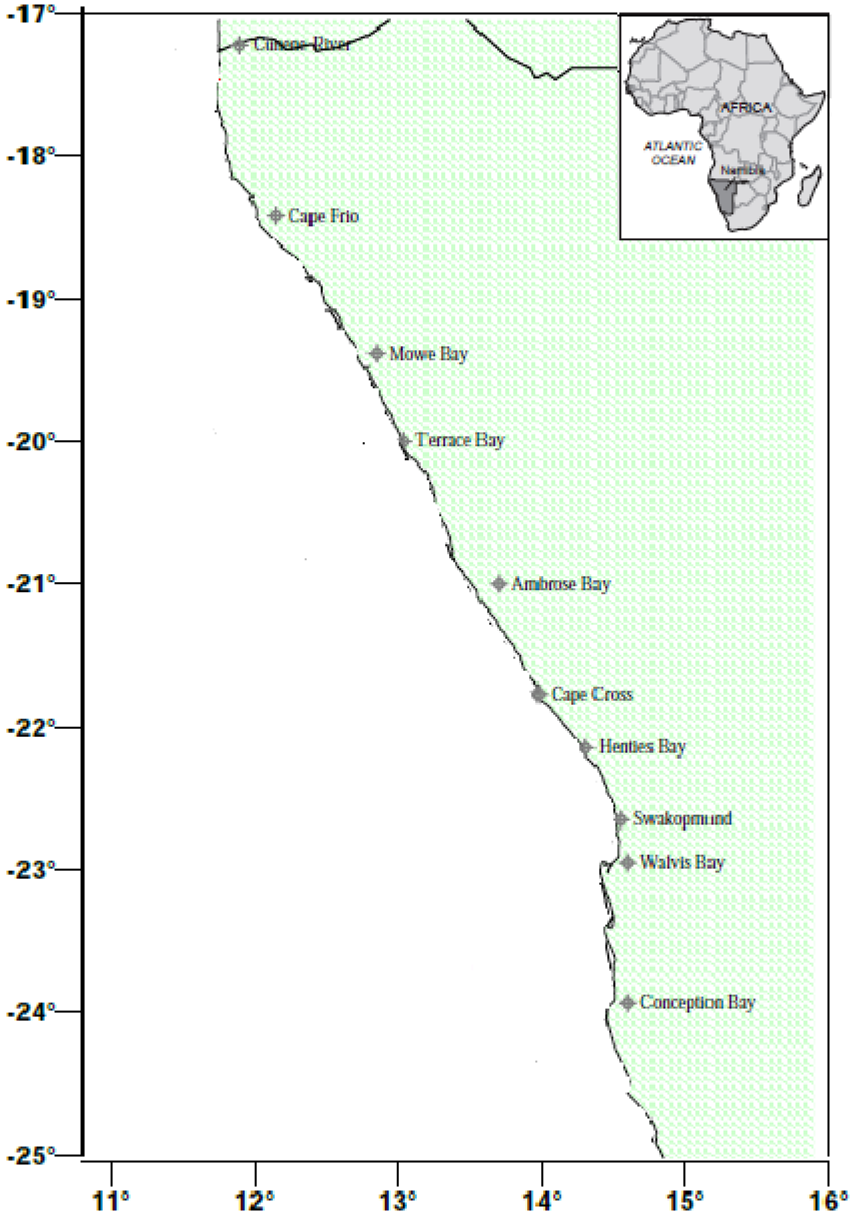


Figure 5.1. The geographical map of the Namibia showing the northern Benguela. The Cape horse mackerel (*Trachurus capensis*) distribution covers the area from 17°15’ S to 25° 00’ S.

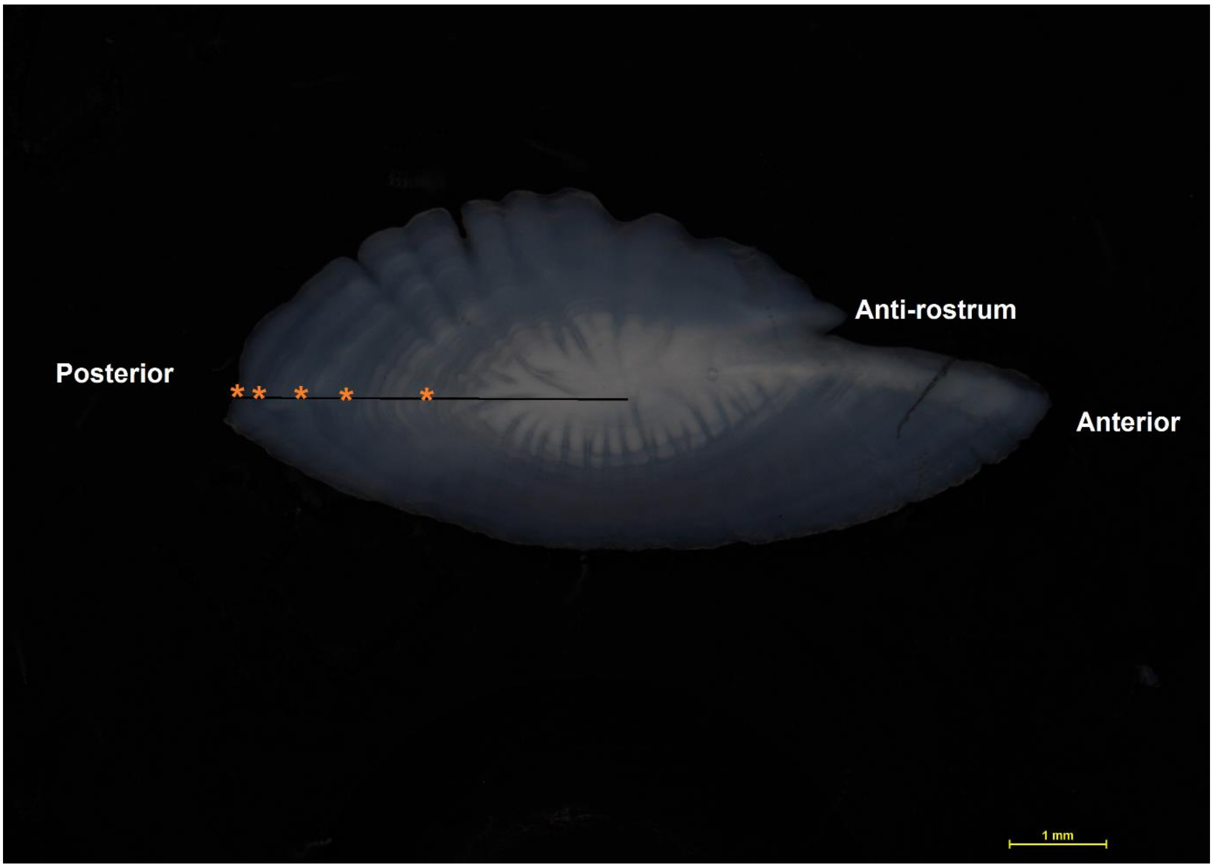


Figure 5.2. Cape horse mackerel whole otolith from a 5-year old caught in December 1977 in Namibia. The annual increments (orange asterisks) along the horizontal line were annotated and measured from the nucleus along a horizontal black line to the posterior edge. All otolith samples were viewed under reflected light at 10 x magnification. Photograph by: Faye Brinkman.

Typically, each increment consists of a pair of zones: one translucent and one opaque. The translucent zone is believed to form during periods of slow growth, while the opaque zone forms during faster growth, usually aligning with more productive times. The assumption that otolith growth is proportional to somatic growth was evaluated by correlating fish length with otolith radius, revealing a significant relationship between fish length and otolith radius ($r=0.744$, $p<0.05$, Figure D2). As a result, the width of the annual increment of Cape horse mackerel generally represents the fish's period of rapid growth each year (Figure 5.2). Date of birth was set as 1 January.

The otolith increment widths were recorded along with the calendar year in which each increment was formed and the fish's age at the time of formation. Additionally, the age-at-capture (AAC), defined as the fish's age in years at the time of capture, was assigned to each specimen. The cohort was assigned as the birth year (year of capture – AAC) of each individual.

5.2.2 Environmental Data

Monthly average sea surface temperature (SST) values were obtained from the Extended Reconstructed Sea Surface Temperature version 5 (ERSSTv5) dataset for the Kunene region (11-15° E; 20-24° S) and central region (11-15° E; 20-17° S) for the period 1970 to 2021 (Table 5.2). The "ERSSTv5" is a global SST dataset derived from the International Comprehensive Ocean–Atmosphere Dataset (ICOADS) (Huang et al. 2017).

The average monthly Southern Oscillation Index (SOI), which is a normalised index derived from the observed sea level pressure (SLP) variations between Tahiti and Darwin Australia, was extracted from the KNMI Climate Explorer (https://climexp.knmi.nl/start.cgi) for 1970-2021 (Table 5.2). The Southern Oscillation Index (SOI) is a standardized measure based on differences in sea level pressure (SLP) between Tahiti and Darwin, Australia. It serves as an indicator of major changes in air pressure across the tropical Pacific, reflecting the state of the Southern Oscillation during El Niño and La Niña events (Ropelewski and Jones 1987). The Southern Oscillation dataset and the El Niño dataset together are often referred to as ENSO, which represents a recurring cycle (occurring every 2–7 years) involving changes in sea surface temperature (El Niño) and atmospheric pressure (Southern Oscillation) across the equatorial Pacific Ocean. The SOI indices were incorporated into the study to examine the impact of ENSO on horse mackerel growth, particularly because Benguela Niño/Niña (warming/cooling) events have been associated with ENSO occurrences in the Pacific (Rouault and Tomety 2022).

Monthly coastal and offshore upwelling indices for waters off Walvis Bay (22.9584 S, 14.5058 E), the Kunene River Mouth (17.2556 S, 11.7522 E) and Lüderitz (26.6477 S, 15.1534 E) were developed and updated from Bordbar et al. (2023) for the period 1979 to 2021 (Table 5.2). Bordbar et al. (2021, 2023) conducted a reanalysis of the ERA5 dataset from the European Centre for Medium-Range Weather Forecasts, concentrating on hourly sea level pressure and surface wind vectors from 1979 to 2021. The goal of this analysis was to evaluate the coastal upwelling caused by alongshore winds as well as the upwelling occurring offshore due to wind stress curl, with results presented in m^2/s^{-1}. Monthly averages were calculated from the hourly data (Bordbar et al. 2023).

5.2.3 Zooplankton data

Zooplankton samples were collected annually from 1978 to 1989 as part of the SWAPELS programme (South West African Pelagic Egg and Larval Surveys) (see Verheye et al. 1998, 2016 for sampling details) and from 2000 to 2018 by the Ministry of Fisheries and Marine Resources (MFMR) as part of their monthly Oceanographic Monitoring program. This enabled the reconstruction of a multi-decadal time series by combining data from the SWAPELS collection (1978–1989) with data from MFMR's ongoing Monthly Oceanographic Monitoring program, covering the period from 2000 to 2018 along an across-shelf transect off Walvis Bay at 23°S. The samples were analysed on the basis of copepod community abundance per m^2 of area log-transformed (Log_{10} (No. m^{-2} + 1)) (Table 5.2).

5.2.4 Horse mackerel biomass data

The horse mackerel biomass time series from 1961 to 2021, derived from stock assessment models (Boyer et al. 2001; Fossen et al. 2001), was obtained from MFMR.

5.2.5 Data Analysis

A set of mixed-effects models was created to examine how increment width (Inc) responds to various intrinsic (fish-specific) and extrinsic (environmental or biological) factors (Morrongiello and Thresher 2015). The fixed effects in a mixed-effects model estimate the influence of variables that are assumed to have a consistent impact on the outcome variable, while the random effects capture the variation in the outcome across different groups or individuals. The fixed intrinsic effects were identified as Age, Age at Capture (AAC) (Table 5.2). The AAC term was incorporated to adjust for biases related to sampling, such as skewed age distributions, and to assess potential biases linked to growth-rate-based selectivity (Morrongiello and Thresher 2015). Fish sex could not be used as an intrinsic effect as sex information was not available for fish captured before 1999. The random effects included intercepts for FishID, cohort, and year, as well as random effects slopes for Age within FishID, cohort, and year (Table 5.2). The FishID term accounts for the correlation among incremental measurements within a fish, considering the individual's estimated growth relative to the average (Morrongiello and Thresher 2015). Cohort effect addresses cohort-specific density dependence and/or the experiences of juveniles (Morrongiello and Thresher 2015).

The full mixed effects base model fitted to the entire time series 1970-2021 was as follows:

Log (Inc) ~ Log(Age) + Log(AAC) + Log(Age) | Fish ID + Log(Age) | Year + Log(Age) |Cohort (1)

Where the combinations are fixed effects (Age and AAC) and random effects, intercept (denoted by "|" in by-FishID, by-Cohort and by-Year) and slope for random effects (random slopes of the effect of Age is denoted by e.g. log(Age) | FishID).

The otolith increment widths (representing annual fish growth, Inc), Age, and AAC were log-transformed and mean-centred before the analysis in the mixed effects models (Morrongiello and Thresher 2015). It was assumed that the translucent zone developed over a relatively short period from February to May, with a peak in April/May and the opaque zone deposition occurs from June to January, with a peak in December/January (Hecht 1990). The variables SST, upwelling index, SOI, Copepod abundance and Cape horse mackerel biomass (derived from stock assessment models (Table 5.2) were checked for collinearity (Figure D5, Figure D6 and Figure D7) before being included in the mixed-effects models.

Variables were evaluated for the optimal combinations of explanatory factors that describe annual otolith increment width (Inc), as shown in Equation 1. The optimal base model for describing fish growth was selected based on the Akaike Information Criterion (AICc), adjusted for small sample sizes (Burnham and Anderson 2004). The optimal model was selected and refined using maximum likelihood estimates to yield unbiased parameter estimates (Zuur et al. 2009). This involved utilising the random effects of year to produce a Best Linear Unbiased Predictor (BLUP) of growth for each year represented by otolith increment width measurements, covering the periods 1970–1977 and 1980–2022. The dataset includes a total of 3,066 observations (Inc) across 608 individuals (FishIDs) over 50 years (Figure D3). The conditional R^2 was calculated for each model to assess the proportion of variance in fish growth accounted for by both fixed and random effects (Nakagawa and Schielzeth 2013). After initial testing, the cohort random effects variable was removed due to its influence on the year effects (see Table D1 and Figure D8 in Appendix D).

In a second step of model selection, additional fixed term predictors were added to the best-fit base model predictors to assess the impact of environmental predictors (SST, upwelling, SOI), copepod abundance and horse mackerel biomass on annual otolith growth. To do this, a series of mixed-effects model comparisons were performed, considering the time constraints associated with the different variables in two steps, a full time series (1970-2021) and a truncated time series (1980-2018) (Table 5.2). The SST datasets (ERSSTv5), SOI and horse mackerel biomass estimates from stock assessment models were available from 1970-2021. The upwelling indices were available from 1979-2021 (Table 5.2). The copepod abundance estimates were available from 1980 to 2018 (Table 5.2). Therefore, the two periods from 1970 to 2021 and 1980 to 2018, respectively were chosen to match Cape horse mackerel growth data from 1970-1977, 1980-2021 with the available extrinsic predictor variable (Table 5.2). In the time period 1970-2021, the SST, SOI and horse mackerel biomass variables were incorporated (with a total of 3,066 observations, 608 FishIDs, and 50 years). In the time period 1980-2018, the SST, upwelling index, copepod abundance, and horse mackerel biomass were included with a total of 2780 observations across, 558 FishIDs and 39 years. In each step, the best model was selected as the one with the lowest AICc value and a ΔAICc of less than 2 compared to the model with the lowest AICc, along with having fewer parameters (K) than that model. The ages of the individual specimens in this study ranged from 2 to 16 years.

To identify the magnitude and timing of regime shifts in the mean fish growth, the Sequential T-test Analysis of Regime Shifts (STARS) was applied to the BLUP series of the random year effect (Rodionov 2004) excluding environmental predictors, 1970-1977, 1980-2021. The STARS method calculates a probability level for both the mean and regime shift years based on an adjusted two-tailed Student's t-test. This sequential analysis computes the regime shift index (RSI), regime mean values with equal and unequal weights, regime duration, final confidence levels for shifts, and outlier weights. Rodionov (2006) introduced a ‘pre-whitening’ technique to remove autocorrelation (red noise) from the time series before conducting the

STARS analysis. A cut-off length of 10 years (l = 10) was set, aligning with decadal oceanic variability. Additionally, this approach ensured alignment with regime studies in the Benguela ecosystem (Howard et al. 2007; Blamey et al. 2012; Brinkman et al. 2025a).

All data analyses and plots were executed in R Studio Version 1.1.463 (R Core Team 2018), utilising the libraries lme4 (Bates et al. 2014), AICcmodavg (Mazerolle 2019), effects (Fox 2003; Fox and Weisberg 2019), and lattice (Sarkar 2008), tidyverse (Wickham et al. 2019) and MuMIn (Bartoń 2019).

Table 5.2. Description of the parameters utilised in predicting the growth (otolith increment width) of Cape horse mackerel (*Trachurus capensis*) in northern Benguela off Namibia.

Parameter	Description
Fixed effects	
Age	Age (yr) when otolith increment formed
Age-at-capture (AAC)	Final age (yr) at time of capture
Random effects	
FishID	Unique identification number for each fish
Cohort	Group of fish spawned in the same year
Year	Calendar year of otolith ring formation
Environmental / biological effects (fixed)	
SST2_C	ERSSTv5 for February at central region 20-24º S (1970-2021)
SST1_N	ERSSTv5 for January at northern region 17-20º S (1970-2021)
SOI2	Monthly Southern Oscillation Index for February (1970-2021)
WBUI10-2	Monthly Upwelling index at Walvis Bay averaged for October-February (1979-2021)
KUI11-12	Monthly Upwelling index at Kunene for Nov-Dec (1979-2021)
Biomass	Annual horse mackerel biomass estimates from stock assessment models (1970-2021)
Copepod abundance	Annual log10 total copepod abundance in numbers per m^2 (1980-2018)

5.3 Results

The optimal base model explained 90.4% of the variation in fish growth and included fixed effects for Intercept and Age, as well as random effects for intercept and age slopes for both FishID and Year (AICc = -3107.97, Conditional $R^2 = 0.904$; Table D2). Age was the most influential factor impacting growth among the variables tested, with predicted increment widths showing a significant decline as the fish aged (Figure D4).

To address Hypothesis 1, which tested whether annual otolith growth patterns of Cape horse mackerel remained stable over time (H_0) or exhibited significant temporal changes (H_1), the Cape horse mackerel otolith biochronology was analysed for evidence of growth shifts. Therefore, STARS analysis conducted on the best linear unbiased predictor (BLUP) of the year effect on fish growth revealed three regimes with two shifts in the northern Benguela (Figure 5.3). Predicted horse mackerel growth transitioned from average growth (1970-1979) to high (above average) growth (1980-1990), followed by low (below average) growth (1990-2021) (Figure 5.3). Regime shifts in fish growth were identified at a significance level of $p < 0.01$, with change points occurring in 1980 and 1990, indicated by RSI values of 1.08 and -1.55, respectively, representing relative changes in normalised growth.

To address Hypothesis 2 (regarding Cape horse mackerel biomass) and Hypothesis 3 (regarding environmental and biological predictor variables), which tested whether these factors significantly influence annual otolith growth patterns (H_1) or have no effect (H_0), statistical analyses were conducted to evaluate the relationships between these predictors and growth variation in Cape horse mackerel. Therefore, incorporating SST, SOI, and horse mackerel biomass as predictor (fixed effect) variables into the optimal base model for the otolith growth time series (1970–2021) revealed no significant effects of any of the variables on sardine growth, as there was no reduction > 2.0 in the model's AICc (Table D2). Incorporating sea surface temperature (SST), upwelling index, copepod abundance, Cape horse mackerel biomass and the Southern Oscillation Index (SOI) into the optimal base model selection for the shorter timeframe (1980-2021) also revealed no significant impact of any of the variables on Cape horse mackerel growth as demonstrated by no significant decrease in the model's AICc of > 2.0 with additional variables (AICc = -2878.44, Conditional $R^2 = 0.90$; Figure 5.5 and 5.6; Table 5.3; Table D3). However, plotting predicted Cape horse mackerel growth against February SST from northern Namibia revealed a negative (albeit not significant) relationship (Figure 5.4). Horse mackerel biomass and horse mackerel predicted growth appeared to be postivively related on the large scale (above average growth pre-collapse and below average growth post-collapse; and negatively related post collapse (Figure 5.6).

Table 5.3. The optimal Cape horse mackerel growth models including variance and correlation components of random effects, along with parameter estimates, standard errors, and significance levels (p-vlues) of the fixed effects for the base model: (a) from 1970-1977, 1980 to 2021 (Number of observations: 3066 groups: FishID = 608; Year = 50). Random age slopes are denoted by “|”. Age was log-transformed in the model. Significance level codes: <0.0001 ‘****’

a) Entire period (1970-1977, 1980-2021)

Random effects	**Variance (± SD)**	**Correlation**	
FishID	0.018 (0.133)		
Age|FishID	0.016 (0.128)	0.48	
Year	0.007 (0.084)		
Age|Year	0.026 (0.161)	0.96	
Residuals	0.011 (0.102)		
Fixed effects	**Estimate (SE)**	**t-value**	**p-value**
Intercept	-0.378 (0.014)	-67.59	<0.0001****
Age	-0.344 (0.024)	-14.07	<0.0001****

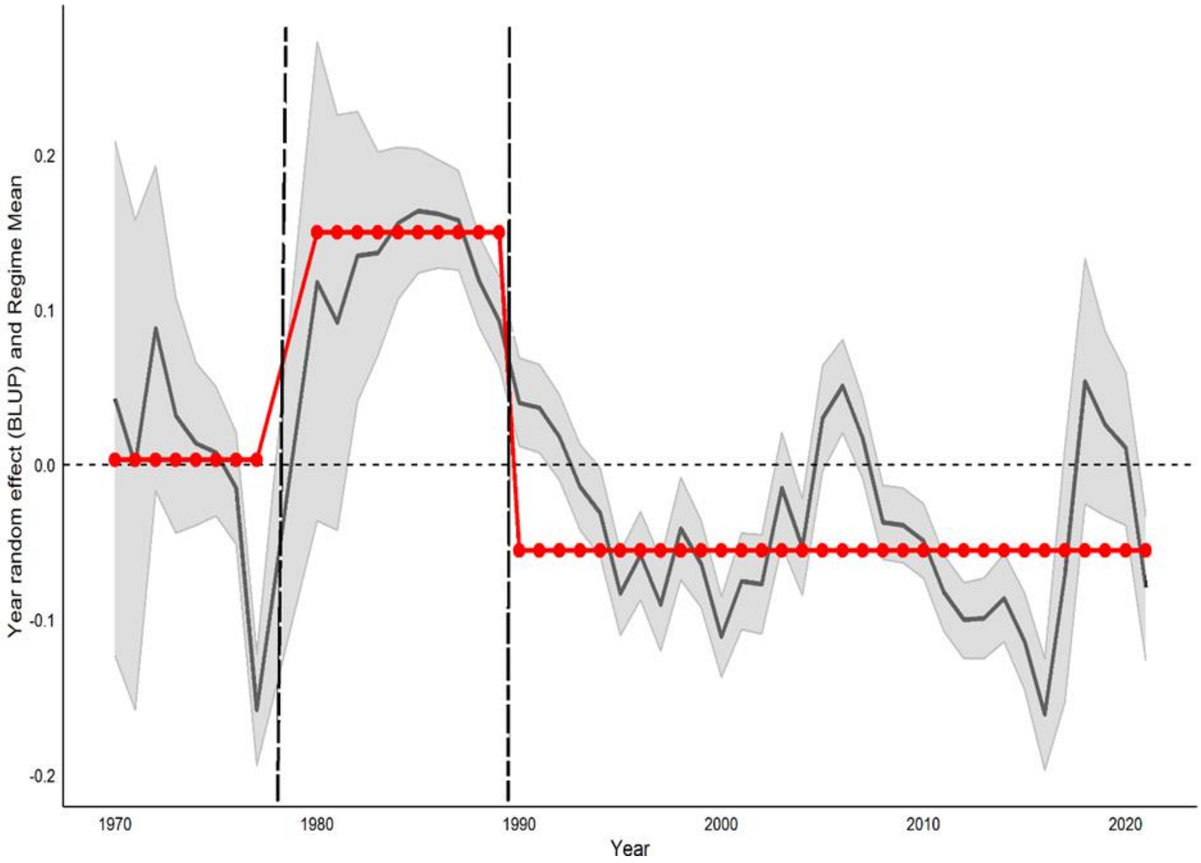


Figure 5.3. The best linear unbiased predictor (BLUP) of growth (measured in mm for annual increments) over the years for Cape horse mackerel of northern Benguela caught in Namibia is shown, with regime shifts identified using the Sequential t-test of regime shifts (STARS) analysis indicated by vertical dashed lines. The mean growth values for each identified regime period are represented by red lines, highlighting the change points in 1980 and 1990. The grey areas illustrate the 95% confidence intervals around the estimated growth valuesand the dashed line represents the average growth.

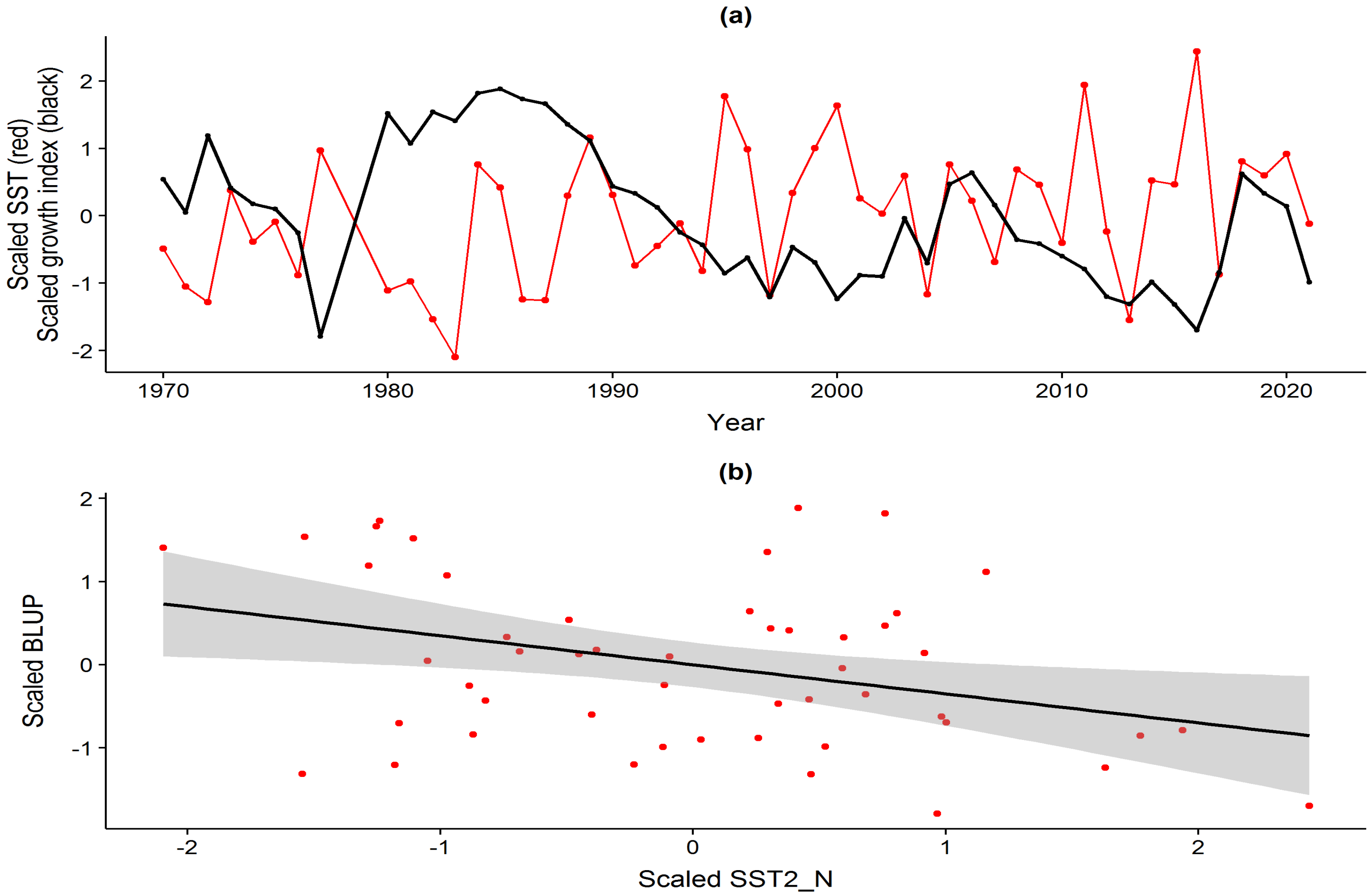


Figure 5.4. Model predictions of the scaled best linear unbiased predictor (BLUP) of growth of Cape horse mackerel (in black) with the scaled SST for February in northern Namibia for the 1970-2021 period.

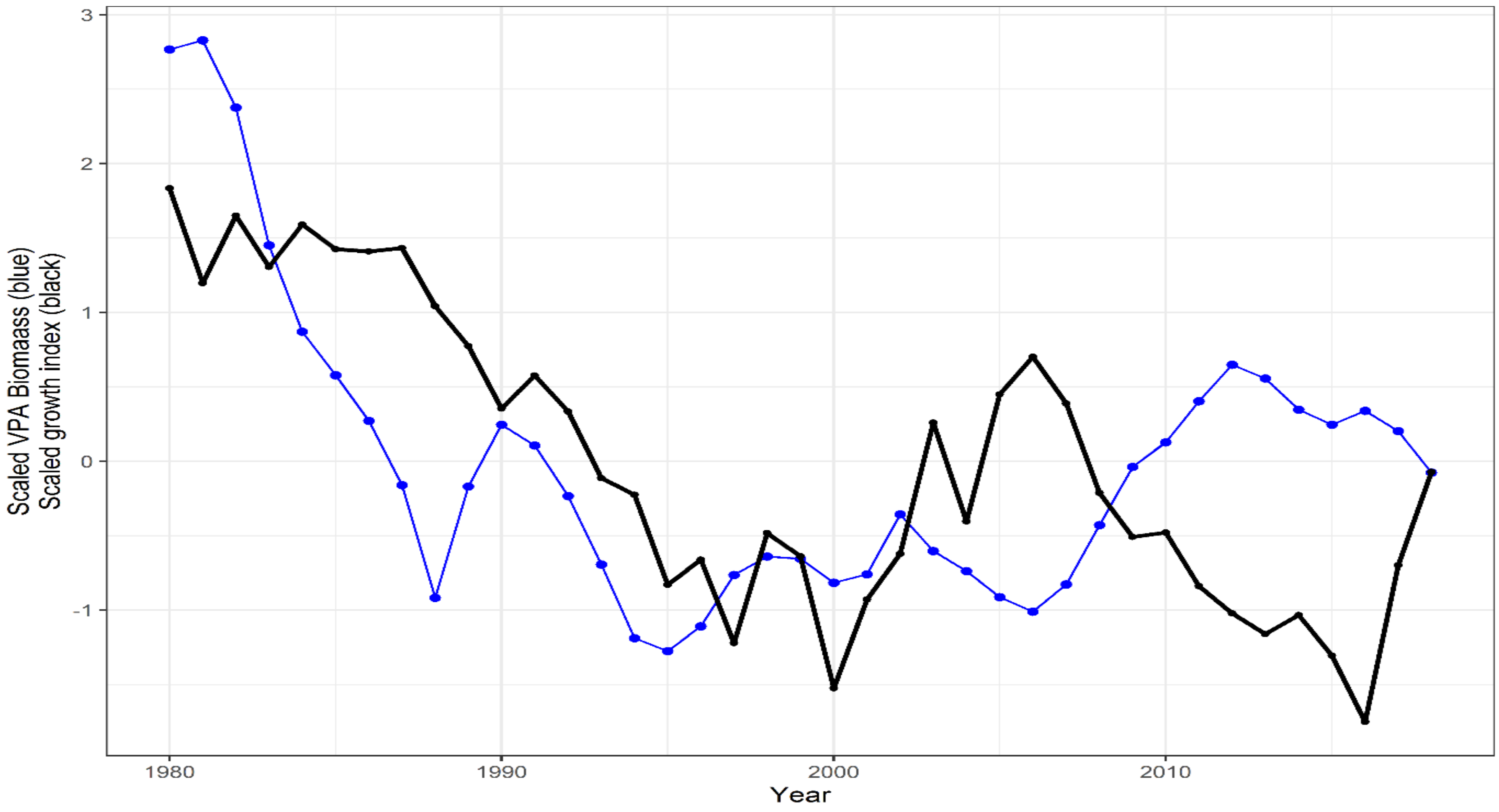


Figure 5.5. Predicted growth (in black) and biomass (in blue) of Cape horse mackerel in northern Benguela.

5.4 Discussion

The otolith increment-width-based biochronology established in this study spans 50 years, offering a long-term, annually detailed record of growth variation for one of the most commercially significant species in the northern Benguela (Namibia). The study demonstrated that otolith biochronologies can serve as indicators of Cape horse mackerel growth, regime shifts, and biological responses to environmental changes. Cape horse mackerel growth was strongly influenced by intrinsic factors (Age) and external environmental conditions linked to the year of growth, as determined by the random year effect, but not well explained by particularly sea surface temperature, upwelling, Cape horse mackerel biomass or copepod abundance in northern Benguela The influence of Age on growth was the primary factor driving variation in growth rates, adhering to a common pattern seen in fish species, where growth declines as individuals' age.

Alternative Hypothesis 1, which posited that there are significant temporal changes in the annual otolith growth patterns of Cape horse mackerel, is supported by the inclusion of a random Year effect in the optimal growth model. This component accounted for a significant proportion of the variation observed in fish growth, indicating that year-specific extrinsic factors strongly influenced growth trajectories. These findings suggest that temporal variability, likely driven by environmental conditions or ecosystem dynamics unique to each year, plays an important role in shaping otolith growth patterns in Cape horse mackerel within the northern Benguela region.

With regard to Hypotheses 2 and 3, which posited that (2) population biomass and (3) environmental factors such as sea surface temperature and prey availability significantly influence annual growth patterns in Cape horse mackerel, the results did not provide statistical support for the alternative hypotheses. When included as fixed effects in the optimal model, none of the tested environmental neither (physical or biological) variables nor biomass showed a significant effect on fish growth. This absence of clear associations does not necessarily imply that these factors are irrelevant, but rather suggests that their influence may vary in strength and direction across the time series. The relative importance of different environmental drivers may have shifted over time, potentially due to ecosystem variability or changes in species interactions. As such, consistent patterns could not be detected when evaluated across the full temporal extent of the study, and therefore, the null hypotheses for both Hypotheses 2 and 3 cannot be rejected.

Further support for Alternative Hypothesis 1, which posited that there are significant temporal changes in the annual otolith growth patterns of Cape horse mackerel, was provided by the otolith biochronological analysis. This analysis identified three distinct growth regimes, marked by two alteration points. These regime shifts indicate abrupt, time-specific changes in somatic growth, further emphasizing that horse mackerel growth patterns are not temporally stable but are instead shaped by episodic environmental or ecological shifts over the studied period. The first regime shift identified in this study took place in 1980, characterised by a transition from average to above-average annual growth and the second regime shift identified took place in 1990 with above-average annual growth switching to below-average growth rates. This suggests that shifts in climate patterns may have influenced the Cape horse mackerel population by altering their growth rates in this region, but with no obvious links with the tested variables. Prior to 1988, the northern Benguela was in a prolonged cool phase, marked by exceptionally cool years in 1982, 1983, and 1987, when the 20°C isotherm moved 1 to 3 degrees further north than typical. From the 1990s onward, warm-water events became more common, including notable instances in 1995, 2001, and the Benguela Niño, with only a single cooler event recorded in 1996–1997 (Bartholomae and van der Plas 2007). This result is also reflected by mean summer SSTs used in the present study. A warming water temperature trend has also been noted across the northern Benguela system by Monteiro et al. (2008), accompanied by an increase in the frequency of warm-water events at the ABF since the 1990s (Bartholomae and van der Plas 2007), resulting in fewer occurrences of cooler conditions (Kirchner et al. 2009). This trend is consistent with our results, indicating that Cape horse mackerel growth peaked during the cooler years of the 1980s, marking the beginning of a regime shift from average to high growth. However, since the 1990s, somatic growth has significantly declined and has remained low, signalling the onset of a second regime shift from high growth to low growth.

Furthermore, the first regime of average horse mackerel growth in the present study (1970-1980) is related to high Cape horse mackerel biomass, coinciding with the peak of fishery exploitation, when annual catches exceeded 600,000 tons under the management of the International Commission for South East Atlantic Fisheries (ICSEAF). Following this peak in catches, biomass declined until stabilizing around 1990, upon Independence of Namibia when the Ministry of Fisheries and Marine Resources (MFMR) took over management of the fishery, with biomass fluctuating between 0.5 and 1.8 million tons annually until 2021. This last low biomass period coincides with the third regime of below avaerge horse mackerel otolith growth.

The results of the present study support reults by Heymans and Tomczak (2016), who identified three distinct regimes in the northern Benguela marine ecosystem. The first regime, from 1956 to the early 1970s, had increasing fish catches and a Benguela Niño in 1963 (with minimal impact on fish populations such that the event did not lead to significant declines or disruptions in fish abundance, distribution, or overall health). This first regime of Heymans and Tomczak (2016) is not covered by the otolith biochronology of the present study. The second regime identified by Heymans and Tomczak (2016) from the early 1970s to mid-1980s, experienced high catches in all offshore fisheries, with stable biomass levels and coincided with the first and second regime of average and above average horse mackerel otolith growth, respectively in the present study (1970-1980-1990). The third regime, identified by Heymans and Tomczak (2016), after the 1990s, is marked by a reduction in catches and a decline in the biomass of many commercially significant species and coincided with the third regime of below average horse mackerel growth in the present study (1991-2021).

In conclusion, the Cape horse mackerel otolith biochronology results in the present study revealed three distinct regimes, with the first shift occurring in 1980, driven by SST changes and fisheries exploitation, and the second shift in 1990, primarily influenced by SST. SST and stock biomass were identified as the key factors affecting Cape horse mackerel growth. The northern Benguela region is expected to undergo significant oceanographic changes due to climate change, including rising sea surface temperatures, potential shifts in upwelling intensity, increased hypoxia, and ocean acidification, all of which could have cascading impacts on the marine ecosystem and fisheries (Jarre et al. 2015). By integrating otolith chronologies from multiple populations and regions, we can gain a broader understanding of species' responses to environmental changes. This knowledge can be incorporated into management strategies to improve their effectiveness, as emphasized by previous research (e.g. Izzo et al. 2016; van der Sleen et al. 2018).

CHAPTER SIX: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The study of long-term changes in fish growth can provide important insights into the impacts of fishing and environmental variability. Growth is the phenotypic manifestation of the relationship between the individual (intrinsic) and the environmental or ecological (extrinsic) components that influences the energy budgeting within an individual (Enberg et al. 2012). In data-limited fisheries (where consistent long-term data on biomass, catch, and environmental or biological indicators are lacking) understanding population dynamics becomes particularly challenging. Traditional approaches that exclusively rely on population-level data, such as size-at-capture, might not adequately capture the ongoing processes that trigger individual responses because growth is a multifaceted biological response influenced by numerous processes (Enberg et al. 2012; Morrongiello and Thresher 2015). Hence, the aim of the study was to understand how individual-level annual growth rates of sardine (*Sardinops sagax*) from the southern and northern Benguela and Cape horse mackerel (*Trachurus capensis*) from the northern Benguela are affected by environmental variability, long-term environmental changes and human exploitation (in terms of the specific population’s biomass) within the Benguela region. For this purpose, the study was designed to utilise mixed-effects modelling in examining the chronology of annual otolith growth of sardine (*Sardinops sagax*) and Cape horse mackerel (*Trachurus capensis*) in the Benguela in relation to intrinsic (between-individual and within-individual) and extrinsic (environmental and biological) factors. The study demonstrated that otolith biochronologies can be used as indicators for sardine and Cape horse mackerel growth, biological responses to changing environmental conditions and regime shifts. The main research findings in relation to the research objectives and questions, their significance and contribution are as follows.

The first objective of this dissertation was to develop otolith biochronologies for sardine (*Sardinops sagax*) in both the southern and northern Benguela, and Cape horse mackerel (*Trachurus capensis*) in the northern Benguela, and to determine whether abrupt alterations in annual otolith growth patterns occurred in response to regime shifts within the Benguela marine ecosystem. In the southern Benguela, the 58-year sardine growth biochronology revealed four distinct growth regimes, with alteration points in 1986, 2006, and 2015. These transitions corresponded closely with known periods of biomass fluctuation, providing strong evidence that ecosystem-level change, potentially driven by environmental variability and fishing pressure, manifest clearly in fish somatic growth patterns. In the northern Benguela, the 48-year sardine biochronology exhibited short-term fluctuations in growth but lacked evidence of long-term regime shifts—likely due to the absence of otolith data preceding the collapse of the sardine stock in the late 1960s. Nevertheless, significant interannual variability in the Year random effect, as well as consistent growth patterns among year-classes (cohorts), provide strong support for temporal structuring of growth in response to environmental variability. Similar to the southern Benguela sardine population, in the northern Benguela Cape horse mackerel population, the 50-year growth biochronology revealed three distinct growth regimes with abrupt shifts in 1980 and 1990, representing transitions from average to above-average growth and then from above-average to below-average growth. This regime structure likely reflects broader ecosystem reorganisations during these decades.

The intrinsic factors emerged as key drivers of individual growth variation across all three stocks (sardine in southern and northern Benguela and Cape horse mackerel in northern Benguela), with fish age being the most consistently influential predictor. This ‘negative age-growth relationship’, a well-documented phenomenon, reflects the natural decline in growth rate as fish mature and allocate more energy to reproduction and maintenance rather than somatic growth (e.g. Doubleday et al. 2015; Izzo et al. 2016; Smoliński 2019). The consistency of this finding across species and regions suggests that age-related physiological constraints shape growth trajectories irrespective of broader environmental or ecological context, reinforcing the need to account for ontogeny in ecosystem-scale growth assessments. Furthermore, age at capture (AAC) in sardines of Benguela also contributed significantly to explaining growth variation. The positive association between AAC and growth, coupled with the near absence of older individuals in recent samples, points to potential demographic truncation likely driven by fishing pressure. This pattern (evident in sardine of both northern and southern Benguela) highlights the impact of selective removal of older, larger individuals on observed growth patterns (Morrongiello and Threshner 2015; Enberg et al. 2012). In contrast, AAC did not explain growth variation in Cape horse mackerel, likely due to collinearity with age or because random effects already captured this variability (Zuur et al. 2009; Harrison et al. 2018). This contrast illustrates species-specific sensitivities to intrinsic covariates, potentially linked to life history differences, habitat use, or population structure.

The inclusion of a random Year effect in all the species' growth models highlighted the significant role of interannual variability, likely driven by environmental and ecological changes, in shaping fish' growth across the Benguela ecosystem. While fixed environmental variables such as sea surface temperature and upwelling did not significantly explain growth variation in Cape horse mackerel, this may reflect either unmeasured extrinsic drivers or species-specific differences in sensitivity to short-term environmental fluctuations compared to sardine. Furthermore, across all three case studies, alternative Hypothesis 1 (which posited significant temporal changes in annual otolith growth patterns) was accepted. This finding holds broad implications for our understanding of fish responses to shifting environmental and ecological pressures across the Benguela system. The consistent support for alternative

Hypothesis 1 across species and regions highlights the importance of biochronologies as sensitive indicators of environmental change. Temporal growth variability, particularly when characterised by abrupt shifts, can reflect ecosystem transitions and reorganisations not always captured by traditional fisheries metrics. These findings reinforce the utility of otolith biochronologies as a tool for ecological monitoring and suggest that both environmental drivers and anthropogenic pressures (e.g., fishing) leave detectable signatures in fish growth records. Integrating these patterns across species enhances our ability to detect ecosystem-level change and better understand the biological responses underpinning fisheries productivity in the Benguela.

Furthermore, the contrasting growth dynamics observed between sardine populations in the northern and southern Benguela ecosystems have important ecological and management implications. In the southern Benguela, sardine otolith growth rates were primarily driven by interannual (year-to-year) and individual-level variability, with minimal contribution from cohort-specific effects. This suggests that sardine in this region exhibit flexible growth responses to changing environmental conditions that vary from year to year, rather than persistent effects linked to specific spawning events. Such flexibility may buffer the population against long-term growth impacts from short-lived environmental perturbations, as each year-class adjusts independently to prevailing conditions. In contrast, sardine growth in the northern Benguela was significantly influenced by cohort-specific variability, indicating that fish born during the same spawning season shared similar growth trajectories. This pattern points to the presence of carry-over effects, where early-life environmental conditions exert lasting influence on individual growth potential. According to Morrongiello and Thresher (2015), and Denechaud et al. (2020), such cohort effects reflect systematic differences in how groups of fish respond to environmental variability, and may be linked to early developmental plasticity or maternal effects. For example, fish born into particularly poor or favourable conditions may continue to experience the consequences of that early exposure throughout their lives (Murphy et al. 2013).

This difference in temporal growth structuring between regions reflect contrasting oceanographic regimes of the northern and southern Benguela, spawning dynamics, and environmental predictability across the Benguela system. The stronger cohort signal in the northern Benguela suggests that growth in this region may be more vulnerable to early-life environmental disruptions, such as changes in upwelling timing, temperature anomalies, or food availability during spawning and early larval stages. Conversely, the dominance of year-to-year variation in the south implies a population less constrained by cohort history, possibly due to more stable or compensatory environmental conditions during early development. From a fisheries perspective, these findings highlight the need for species and region-specific management strategies. In the northern Benguela, the sensitivity of growth to cohort-specific conditions suggests that protecting favourable spawning environments and ensuring consistent recruitment success are critical for sustaining population productivity. In the southern Benguela, management may focus more on monitoring and responding to short-term environmental fluctuations that directly influence annual growth variability. Overall, the otolith biochronologies developed in this study reveal species- and region-specific growth-environment relationships, underscoring the complexity of fish growth responses in the Benguela ecosystem. Integrating these findings enhances our broader understanding of how sardine populations navigate environmental and fishing pressures across this dynamic marine system.

The second objective of this study was to evaluate the influence of population biomass on the annual otolith growth patterns of sardine in the southern and northern Benguela, as well as Cape horse mackerel in the northern Benguela. This was framed within the context of Hypothesis 2, which posited that density-dependent effects, particularly related to population biomass, significantly affect growth dynamics. For sardine in the southern Benguela (South Africa), there was full support for the alternative Hypothesis 2. Sardine biomass west of Agulhas exhibited a significant positive effect on sardine growth, consistent with density-dependent processes impacting growth rates. This finding aligns with the concept of depensation, where extremely low biomass levels lead to decreased growth rates, productivity, and fertility rather than the compensatory increase expected under classical density dependence (Rose et al. 2001). The long-term lack of sardine stock recovery in the southern Benguela following heavy exploitation in the 1950s, and persistently low biomass since 2019 (van der Lingen et al. 2006; Hutchings et al. 2009; DFFE 2023), exemplifies the profound implications of depensation. These results underscore the urgent need for conservation strategies that prevent further biomass depletion to avoid accelerating declines. Similarly, in the northern Benguela (Namibia), sardine biomass also showed a significant positive effect on growth, providing notable support for the alternative Hypothesis 2. Although sardine biomass has dramatically declined from millions of tons in the mid-20th century to a moratorium-imposed depleted stock since 2018, the linkage between biomass and growth suggests depensatory dynamics are also present in this region. The mechanism here may differ from the southern Benguela, with adverse environmental conditions and reduced spawning biomass leading to decreased recruitment success and fertilization probability (Liermann and Hilborn 2001). The persistence of these conditions has hindered sardine stock recovery, emphasizing the combined role of environmental and biomass-related pressures in population dynamics. For Cape horse mackerel in the northern Benguela, the null Hypothesis 2 was aceepted, as population biomass showed no significant positive effect on predicted growth of Cape horse mackerel in the mixed-effects models. Instead, there was evidence of a negative correlation between biomass and growth at depleted population sizes, consistent with classical density-dependent growth processes expected in heavily fished stocks (Enberg et al. 2012). However, the observed reduction in growth may also be influenced by disrupted group dynamics linked to unfavourable environmental conditions—particularly ocean warming—combined with low stock biomass and increased predation pressure following the collapse of the sardine population. The absence of sardine, a key forage species, may have redirected predation toward other pelagic species such as Cape horse mackerel. This supports the broader understanding that while fishing pressure contributes to population declines, environmental changes and ecological interactions can exert equally or even more significant influences on fish growth (McFarlane et al. 2002). These findings highlight the need for fisheries assessments and management strategies to account for both density-dependent processes and the complex interplay between climate-driven variability and ecosystem dynamics.

The third objective of this study sought to examine the influence of environmental variability (specifically sea surface temperature (SST), upwelling intensity) and biological variability (zooplankton abundance) on the growth of sardine in the southern and northern Benguela systems, as well as Cape horse mackerel in the northern Benguela. This analysis was designed to test Hypothesis 3, which proposed that environmental and biological factors have a significant influence on growth patterns. The results offer strong support for the alternative hypothesis for both sardine stocks in the southern and northern Benguela, while the null hypothesis could not be rejected for Cape horse mackerel in the northern Benguela. For sardine in the southern Benguela, the results clearly support alternative Hypothesis 3, demonstrating that environmental and biological factors play a central role in driving annual growth variability. Among the environmental variables tested, winter SSTs (June) and copepod abundance emerged as the most influential. Sardine growth from 1962 to 2019 was positively associated with warmer winter SSTs in the region west of Cape Agulhas. This is consistent with previous findings that highlighted a strong correlation between winter SST and sardine growth during autumn and winter months (du Plessis 1959; Hutchings et al. 2012). The analysis also revealed a divergent trend in sardine growth responses to winter versus summer SSTs in recent decades, suggesting that sardine in the southern Benguela exhibit a narrow thermal preference between 17–18 °C. Warmer winters and cooler summers appear to support optimal growth, whereas deviation from this range likely imposes thermal stress. This narrow thermal window was consistent with findings for silver kob (*Argyrosomus inodorus*) in the northern Benguela (Jagger et al. 2025), suggesting that small and large pelagic species alike may be highly vulnerable to the increasingly steep thermal gradients associated with climate change in the southern Benguela (i.e., offshore warming and inshore cooling). These patterns reinforce the work of Augustyn et al. (2018), who identified a significant correlation between the cross-shelf SST gradient and the spatial distribution of sardine biomass. In addition, copepod abundance had a positive relationship with sardine growth in the southern Benguela, emphasizing the importance of lower trophic productivity. Copepod biomass west of Cape Agulhas increased nearly 100-fold from the 1950s to 1995, but then underwent a tenfold decline in 1996 — coinciding with a regime shift from larger to smaller copepod species (Verheye et al. 2016). The sardine otolith biochronology in the southern Benguela revealed increased growth during 1986–2005, followed by a sharp decline from 2006–2019, aligning with ecological regime changes in prey availability, recruitment strength, and biomass trends. These findings strongly suggest a climate-driven deterioration in the trophic environment for southern Benguela sardine, supporting the hypothesis that environmental degradation, rather than fishing alone, underpins long-term growth and productivity declines (van der Lingen 2021).

For sardine in the northern Benguela, support for the alternative Hypothesis 3 also emerged, albeit via different environmental pathways. Here, summer SST (August–October) and summer upwelling intensity (measured via the Kunene upwelling index in December of the previous year) were the main drivers of sardine growth variability. Cooler summer SSTs and stronger summer upwelling were associated with enhanced growth, consistent with the sardine's dependence on productive, well-oxygenated waters for feeding and development. These findings align with previous work indicating that upwelling intensity and SST in the northern Benguela are primarily controlled by both local and distant wind-stress fluctuations (Bartholomae and van der Plas 2007). During years of weakened upwelling, warm-water events—often linked to Benguela Niño conditions—bring warm, nutrient-poor, oxygen-deficient water from the Angola region into northern Namibia, adversely affecting sardine growth. These conditions are associated with a southward shift of the Angola-Benguela Front (ABF) and are more frequent today than in the past (Hampton and Willemse 2012). Since the late 1990s, the northern Benguela has experienced a general warming trend and increased frequency of Benguela Niño events, leading to a decline in the number of cooler, productive years (Monteiro et al. 2008; Kirchner et al. 2009). These patterns offer a compelling environmental explanation for the observed reduction in northern Benguela sardine growth rates, and support the broader concern that climate variability and oceanographic change are increasingly limiting the productivity of this once-abundant stock.

These findings are further corroborated by wavelet coherence analysis, which revealed a dynamic, time-varying relationship between sardine growth and upwelling in the northern Benguela. A strong in-phase coherence with upwelling indices at a frequency of approximately 8 years was evident from 1996–2005, followed by a shift to higher frequency oscillations (2–4 years) after 2010. This shift in frequency corresponds with changes in the otolith biochronology and suggests that northern Benguela sardine growth has become increasingly sensitive to interannual variability in upwelling since the 1990s. These patterns mirror the ~7-year cycles in offshore Ekman transport observed at Cape Columbine from 1957–1992 (Johnson and Nelson 1999), underscoring the influence of wind-stress-driven upwelling on sardine growth dynamics in Namibia. Importantly, this recurring coherence between growth and upwelling was not observed in the other species examined, emphasizing a unique link between environmental forcing and growth in northern Benguela sardine.

In contrast, for Cape horse mackerel in the northern Benguela, the null Hypothesis 3 was accepted. While some environmental variables were explored, no significant associations were detected between growth and SST, upwelling, or copepod abundance. This result suggests that Cape horse mackerel growth is less responsive to short-term environmental fluctuations, or that their broader ecological niche and more opportunistic foraging behavior buffer them from the direct impacts of environmental variability. Alternatively, other unmeasured factors (e.g. oxygen minimum zones, spatial habitat compression, or ontogenetic dietary shifts) may play a more dominant role in shaping growth trends. Nevertheless, when interpreted alongside the weak biomass-growth relationship discussed under Objective 2, these findings highlight the relative complexity and lower environmental sensitivity of Cape horse mackerel growth dynamics compared to sardine.

6.2 Limitations and significance

This study successfully reconstructed long-term growth histories for sardine (*Sardinops sagax*) and Cape horse mackerel (*Trachurus capensis*) populations in the Benguela Current Large Marine Ecosystem (BCLME) by applying sclerochronological methods to archived otoliths, some of which had been preserved for over six decades. The use of these historical biological archives enabled the detection of temporal growth trends across multiple decades, offering valuable insight into how environmental variability and anthropogenic pressures—particularly fishing — have shaped fish population dynamics over time.

However, certain limitations warrant discussion. A key limitation in the case of the northern Benguela sardine is the absence of data from before the population collapse, unlike the situation in South Africa. As a result, the available data reflect an already fishing-altered population state, which limits the ability to assess how growth might have responded under unexploited conditions. This constrains the analysis to modelling environmental responses within a system that has already been significantly impacted by historical fishing pressure, making it difficult to disentangle the relative influence of environmental versus anthropogenic drivers on growth variability.

One major constraint was the incomplete biological metadata available in some cases, especially pertaining to fish length and sex. While fish length data were salvaged from physical records (vial labels, storage envelopes, or Perspex plates), these data were not uniformly available or digitized. Consequently, incomplete length data led to the exclusion of some samples from otolith-somatic growth relationship analyses. Additionally, fish sex was not incorporated into the sardine biochronologies as a descriptor variable for either Namibia or South Africa due to its absence in historical records. This omission is relevant, given that sex-specific growth patterns are known to exist in many fish species, including sardine and would have resulted in some variability of the model remaining unexplained. These limitations highlight a need for improved biological data management and storage protocols, particularly for long-term monitoring and the preservation of essential contextual data alongside otolith collections.

Another constraint was the restricted availability of long-term environmental and biological indices. While the study effectively used SST, upwelling indices and stock biomass as proxies for extrinsic drivers of growth, other potentially influential factors (such as dissolved oxygen concentrations, primary productivity, zooplankton abundance and chlorophyll-*a*) were unavailable for the full study period or spatial scale. Oxygen stress in particular is an important consideration in the northern Benguela region, where hypoxia events are recurrent and have known biological impacts. Despite these data gaps, the selected variables were sufficient to elucidate key environmental-growth relationships and to differentiate regional and species-specific responses, particularly for sardine populations.

From a broader scientific and applied perspective, the study holds several important contributions to fisheries science and ecosystem-based management. Firstly, by reconstructing decadal-scale growth trajectories from otolith microstructure, this study demonstrated the utility of archived otoliths in understanding long-term ecological and population dynamics — an approach still underutilized in African marine science. The research contributes directly to the field of fish sclerochronology, filling a geographic and ecological gap in long-term growth studies within eastern boundary upwelling systems.

Secondly, the study provided strong evidence linking climate variability and fishing pressure to long-term changes in growth. While depensation (most probably as a result of overfishing) was identified as the dominant driver of growth declines, the depletion of fish biomass likely magnified the sensitivity of growth to environmental variability — particularly in the northern Benguela sardine population (e.g. Morrongiello et al. 2019; Wilhelm et al. 2020; Brinkman et al. 2025b). This shift in relative influence underscores the interactive nature of fishing and climate stressors, reinforcing the need for adaptive management strategies that are responsive to both anthropogenic and environmental change.

The study’s relevance is also reflected in its uptake by large-scale international research initiatives. Findings were incorporated into key reports produced under the EU Horizon 2020 Triatlas project, including Deliverables D5.2 and D7.2, which address pelagic ecosystem status and ecosystem tipping points in the South Atlantic ((TRIATLAS Project, 2021a; 2021b). These outputs enhance the study’s credibility and impact, positioning it as a contributor to global discussions on marine ecosystem resilience and climate-informed fisheries governance.

Importantly, the present study also identified critical policy and data needs. The absence of regularly updated age-length keys for sardine and Cape horse mackerel in Namibia and South Africa severely constrains the quality of stock assessments. This study provides a compelling case for the integration of age-based data and environmental indicators into routine assessment frameworks. By linking growth anomalies to environmental trends, the research supports the adoption of an ecosystem-based management (EBM) paradigm in the Benguela — a shift that aligns with international best practices and regional priorities.

Morover, the study highlights the importance of adaptive management strategies in response to depleted stocks and shifting ecological baselines. Notably: In Namibia, adaptation may involve maintaining the sardine fishing moratorium while drawing lessons from South Africa, such as the importation of frozen sardines, and diversifying product lines to sustain local processing industries (van der Lingen 2021). In South Africa, strategies such as experimental mesopelagic fisheries, product innovation with anchovy and round herring, and the use of alternative fishing gears have been explored to mitigate the impacts of sardine depletion (van der Lingen 2021). Thereby the study contributes to ongoing efforts to build resilience and sustainability in small pelagic fisheries by identifying and contextualising these adaptive responses, under conditions of ecological uncertainty and climate change.

Finally, the study raises a broader methodological and institutional challenge: the sustainability of biological archives and metadata in long-term research. It is clear that without proper digitization and metadata curation, valuable historical material may remain underutilized. This study serves as both a model and a call to action for enhanced archiving, data recovery, and inter-institutional collaboration in support of long-term ecosystem monitoring.

6.3 Recommendations

This study underscores the utility of otolith biochronologies as powerful indicators of historical and ongoing changes in fish growth, particularly in relation to environmental variability and fishing pressure within the Benguela ecosystem. The findings offer valuable insight into the biological responses of key small pelagic species sardine and Cape horse mackerel to regime shifts and climate variability, and support the development of more integrated and adaptive fisheries management strategies. The following recommendations are proposed for future research, monitoring, and management:

1) Incorporate time-varying otolith growth rates into stock assessments: The study demonstrated that time-varying growth patterns in sardines of the Benguela are influenced by both environmental and biological drivers. Despite their relevance, such growth indices are rarely included in stock assessments. It is therefore recommended that the time-varying growth indices generated from otolith biochronologies in this study be integrated into existing single-species assessment models, similar to the method used by Lee (2017), to improve parameter estimation and management outcomes. This is especially important in ecosystems with high environmental autocorrelation and variance.

2) This study identified key environmental factors (such as upwelling intensity, SST anomalies, and zooplankton biomass) as influential drivers of sardine and Cape horse mackerel growth. These variables are often excluded from traditional stock assessment frameworks. To improve the prediction of stock dynamics under changing climate conditions, it is recommended to develop integrated assessment models that combine both biological and environmental variables (e.g., Denechaud et al. 2020; Smoliński 2019; van der Lingen 2021).

3) The findings revealed that single-species approaches may miss important ecosystem-level interactions. For instance, changes in sardine growth in the southern Benguela were found to coincide with both regime shifts and biomass depletion. It is recommended that ecosystem-based management frameworks be adopted that incorporate growth variability and ecosystem indicators, such as sardine growth anomalies, into ecosystem models (e.g. Ecosim forcing functions, as explored by Coll et al. 2023). This approach can improve the realism and responsiveness of management strategies.

4) Improve data preservation and archival standards for biological samples: A limitation identified in this study was the incomplete and inconsistent availability of biological metadata, including fish length and sex. This highlights the need for more rigorous standards for storing biological samples and associated data. Future otolith archiving efforts should ensure that key biological information is digitised and preserved to enable accurate long-term analyses.

5) Results suggest that multiple fish species within the Benguela Current system respond similarly to environmental changes, such as SST anomalies and upwelling variability. It is recommended to pursue comparative studies of otolith biochronologies across species and regions (e.g. Izzo et al. 2016; Morrongiello et al. 2021), to uncover shared growth responses and potential ecosystem-wide indicators. Notably, synchronised negative SST–growth relationships have been observed in other species such as *Merluccius paradoxus* (Wilhelm et al. 2020), *Argyrosomus inodorus* (Jagger et al. 2025), and *Sardinops sagax* in the northern Benguela (Brinkman et al. 2025b; present study) supporting the value of such integrative research.

6) This study successfully utilised otoliths collected over several decades, demonstrating the untapped value of archived material. It is recommended that fisheries institutions expand and maintain otolith archives, alongside complete metadata, to enable retrospective analyses of growth and environmental change over time.

7) Given the lack of recovery in the northern Benguela sardine stock despite minimal fishing pressure over the past two decades and a moratorium since 2018, it is recommended that the current moratorium be maintained until there is clear scientific evidence of stock recovery. In the interim, Namibia's small pelagic sector could adopt adaptation strategies similar to those implemented in the southern Benguela and other countries facing comparable challenges. These include importing frozen sardines to support domestic processing industries and diversifying product lines to reduce dependence on sardines alone. Lessons can be drawn from South Africa's proactive response, which included experimental fishing of alternative species such as lanternfish (*Lampanyctodes hectoris*), developing anchovy-based consumer products, and increasing exploitation of underutilized species such as round herring. Investing in alternative fishing gear (e.g., pelagic or midwater trawls) and processing infrastructure could also support diversification. Importantly, an integrated research strategy should be formulated to improve climate-related stock predictions and support long-term resilience of the pelagic fishery.

CHAPTER SEVEN: REFERENCES

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APPENDICES

APPENDIX A

(A1) Research permission letter from the director of postgraduate studies.

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RESEARCH PERMISSION LETTER

Student Name: FAYE BRINKMAN

Student Number: 9617027

Programme: DOCTOR OF PHILOSOPHY IN FISHERIES AND AQUATIC SCIENCES (17DPFA).

Approved Research Title: ASSESSEMTN OF CLIMATE CHANGE AND FISHERIES EFFECTS ON SARDINE (SARDINOPS SAGAX) AND CAPE HORSE MACKEREL (TRANCHURUS CAPENSIS) OTOLITH GROWTH RATES AND TROPIC SHIFTS IN THE BENGUELA REGION.

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.

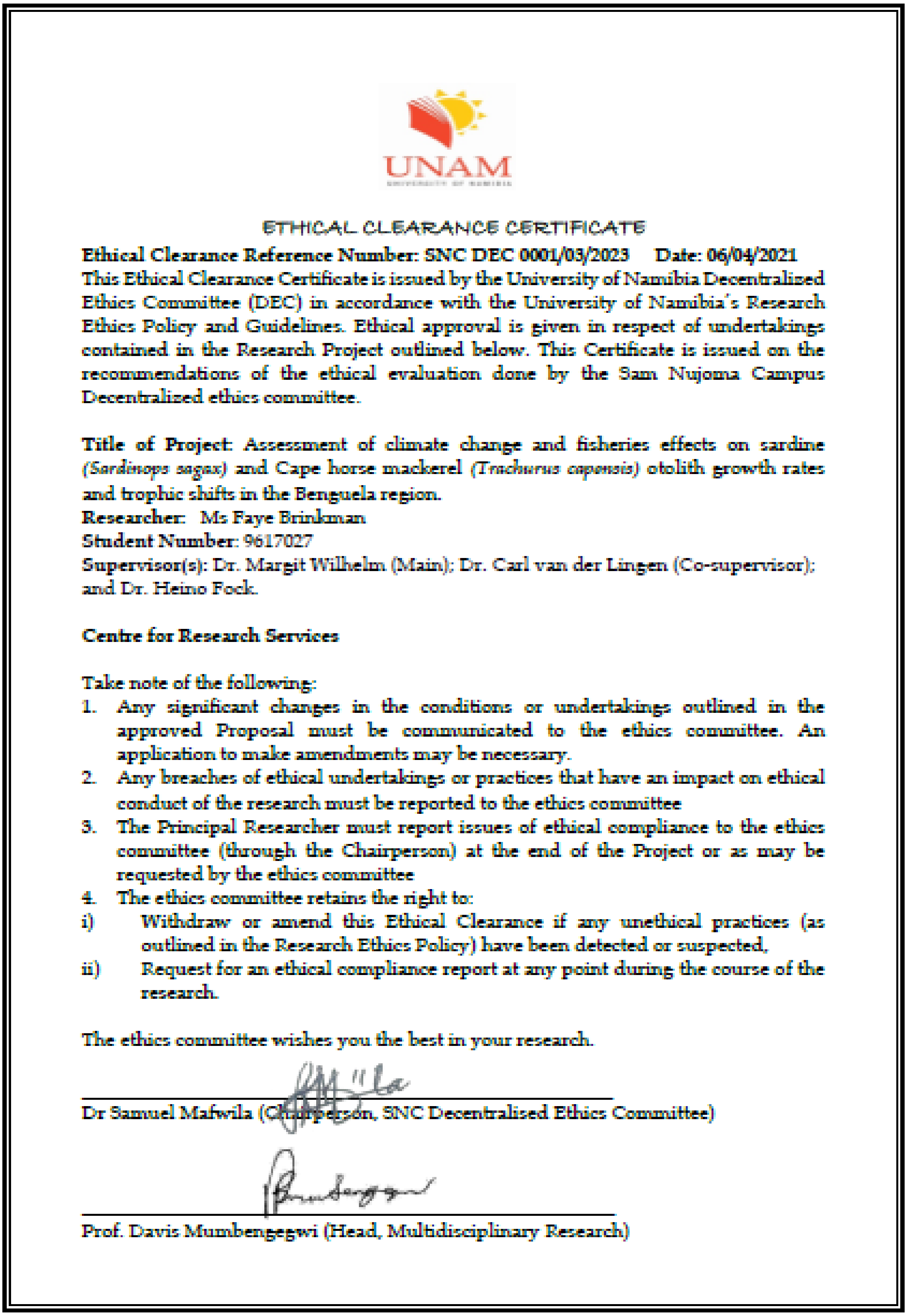
Best Regards,

Signature: Date: 20 April 2023

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

CENTRE FOR RESEARCH SERVICES
Office of the Director
2023 -04- 20
University of Namibia
UNAM

(A2) Research ethical clearance from the Postgraduate studies committee.



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ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SNC DEC 0001/03/2023 Date: 06/04/2021

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: Assessment of climate change and fisheries effects on sardine *(Sardinops sagax)* and Cape horse mackerel *(Trachurus capensis)* otolith growth rates and trophic shifts in the Benguela region.

Researcher: Ms Faye Brinkman

Student Number: 9617027

Supervisor(s): Dr. Margit Wilhelm (Main); Dr. Carl van der Lingen (Co-supervisor); and Dr. Heino Fock.

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,

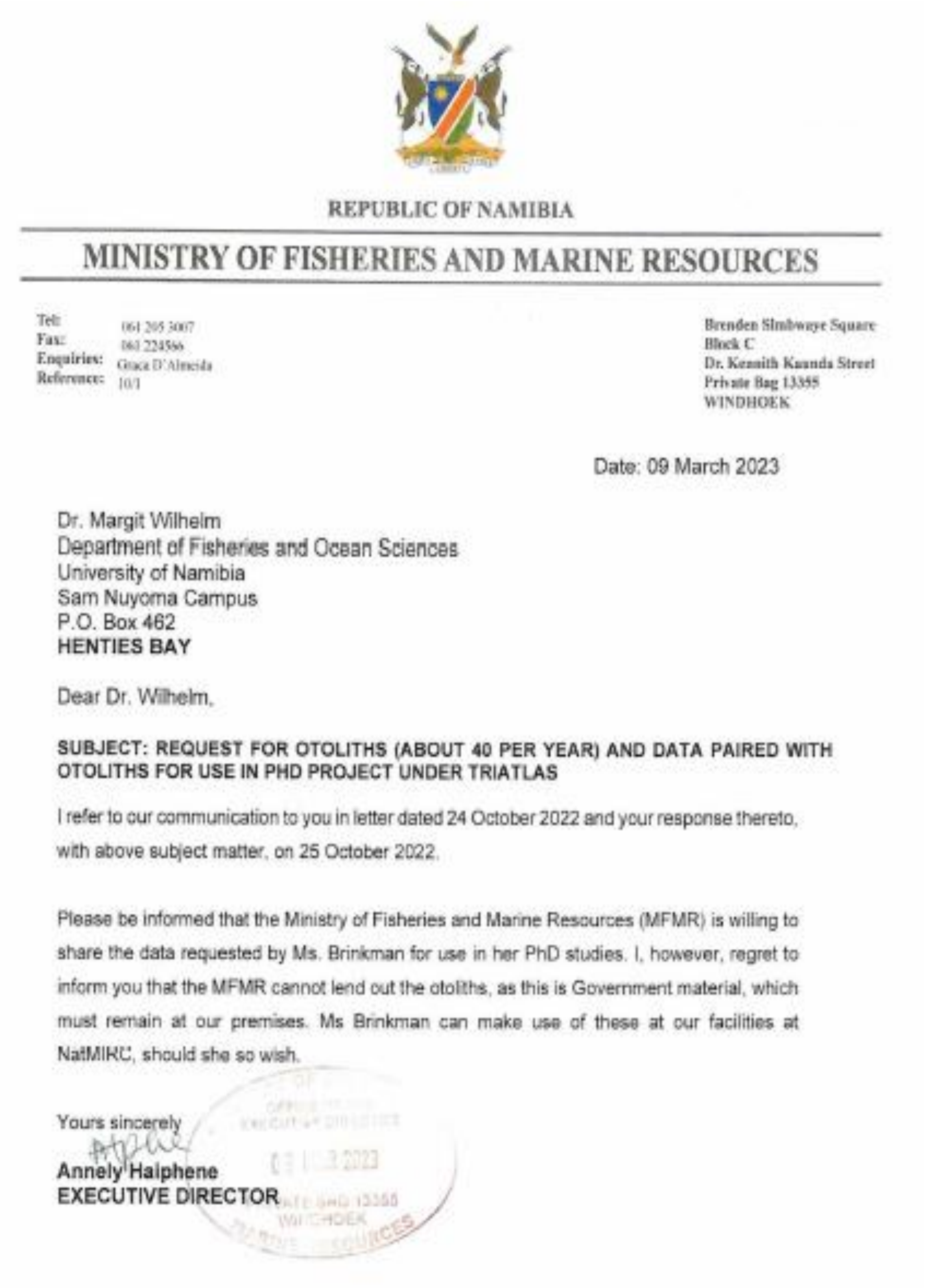
ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

Dr Samuel Mafwila (Chairperson, SNC Decentralised Ethics Committee)

Prof. Davis Mumbengegwi (Head, Multidisciplinary Research)

(A3) Permission letter from the Ministry of Fisheries and Marine Resource (government of Namibia)



REPUBLIC OF NAMIBIA

MINISTRY OF FISHERIES AND MARINE RESOURCES

Tel: 061 205 3007
Fax: 061 224566
Enquiries: Graca D'Almeida
Reference: 10/1

Brenden Simbwaye Square
Block C
Dr. Kenneth Kaunda Street
Private Bag 13355
WINDHOEK

Date: 09 March 2023

Dr. Margit Wilhelm
Department of Fisheries and Ocean Sciences
University of Namibia
Sam Nuyoma Campus
P.O. Box 462
HENTIES BAY

Dear Dr. Wilhelm,

SUBJECT: REQUEST FOR OTOLITHS (ABOUT 40 PER YEAR) AND DATA PAIRED WITH OTOLITHS FOR USE IN PHD PROJECT UNDER TRIATLAS

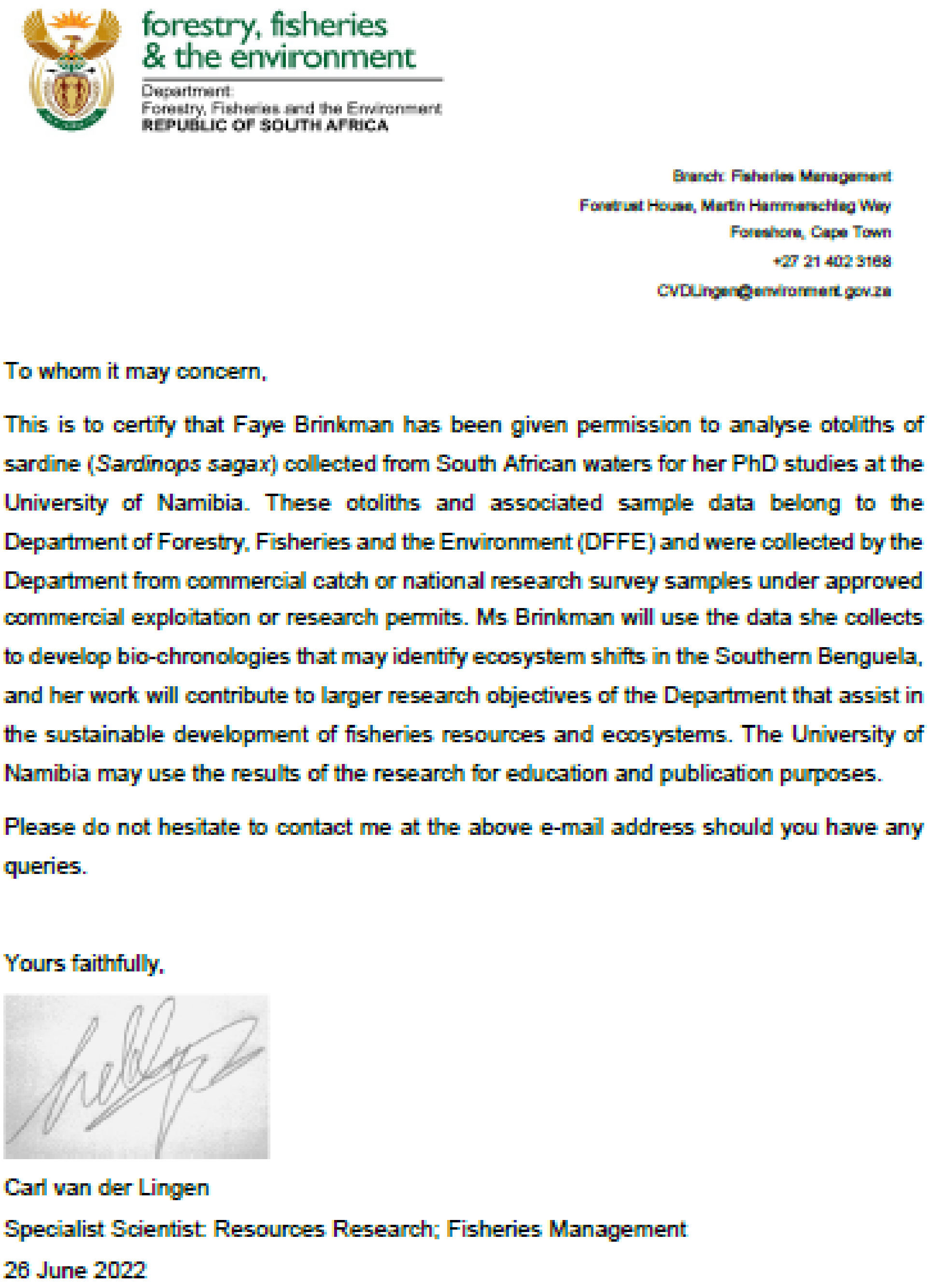
I refer to our communication to you in letter dated 24 October 2022 and your response thereto, with above subject matter, on 25 October 2022.

Please be informed that the Ministry of Fisheries and Marine Resources (MFMR) is willing to share the data requested by Ms. Brinkman for use in her PhD studies. I, however, regret to inform you that the MFMR cannot lend out the otoliths, as this is Government material, which must remain at our premises. Ms Brinkman can make use of these at our facilities at NatMIRC, should she so wish.

Yours sincerely

Annely Halphene
EXECUTIVE DIRECTOR

(A4) Permission letter from Department of Forestry, Fisheries and Environment (government of South Africa)



forestry, fisheries
& the environment
Department:
Forestry, Fisheries and the Environment
REPUBLIC OF SOUTH AFRICA

Branch: Fisheries Management
Foretrust House, Martin Hammerschlag Way
Foreshore, Cape Town
+27 21 402 3168
CVDLingen@environment.gov.za

To whom it may concern,

This is to certify that Faye Brinkman has been given permission to analyse otoliths of sardine (*Sardinops sagax*) collected from South African waters for her PhD studies at the University of Namibia. These otoliths and associated sample data belong to the Department of Forestry, Fisheries and the Environment (DFFE) and were collected by the Department from commercial catch or national research survey samples under approved commercial exploitation or research permits. Ms Brinkman will use the data she collects to develop bio-chronologies that may identify ecosystem shifts in the Southern Benguela, and her work will contribute to larger research objectives of the Department that assist in the sustainable development of fisheries resources and ecosystems. The University of Namibia may use the results of the research for education and publication purposes.

Please do not hesitate to contact me at the above e-mail address should you have any queries.

Yours faithfully,

Carl van der Lingen
Specialist Scientist: Resources Research; Fisheries Management
28 June 2022

APPENDIX B

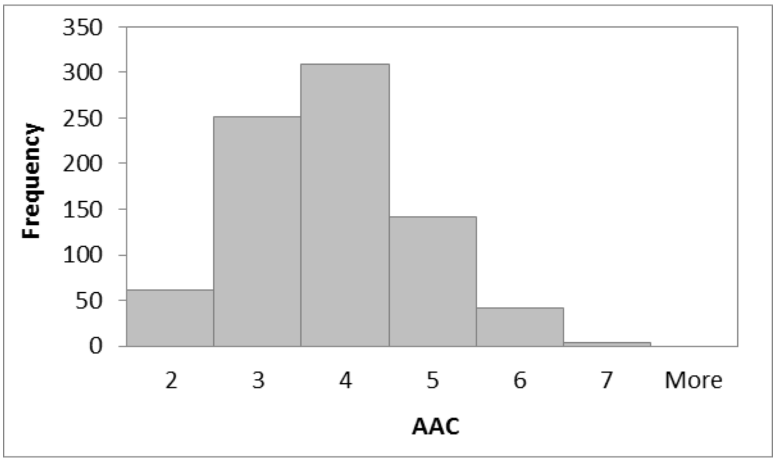


Figure B1. Age-at-capture distribution of the 808 otoliths used in the biochronology analysis.

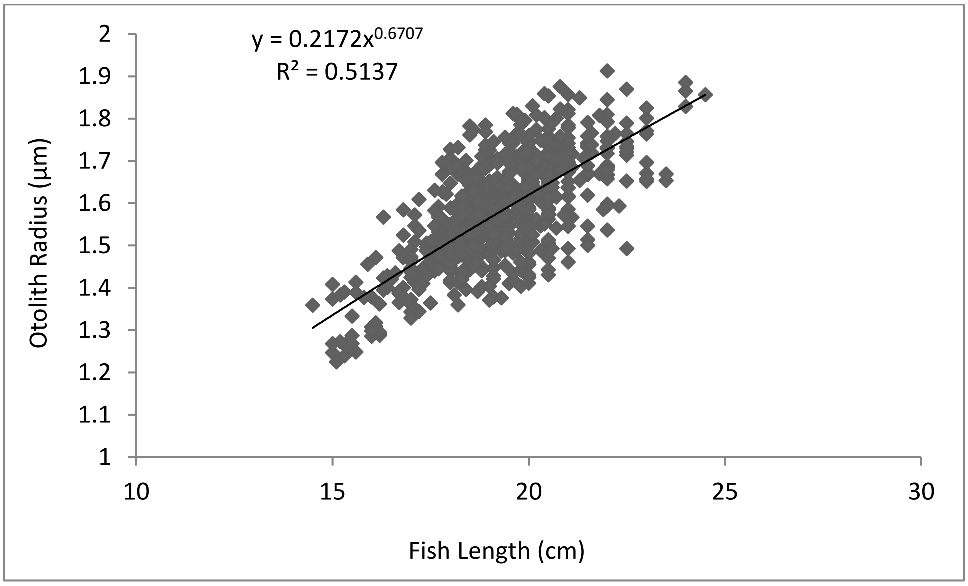


Figure B2. Log otolith radius (µm) and total fish length (cm) relationship for sardine otoliths collected from annual surveys in November as well as commercial port samples for the area West of Agulhas in South Africa.

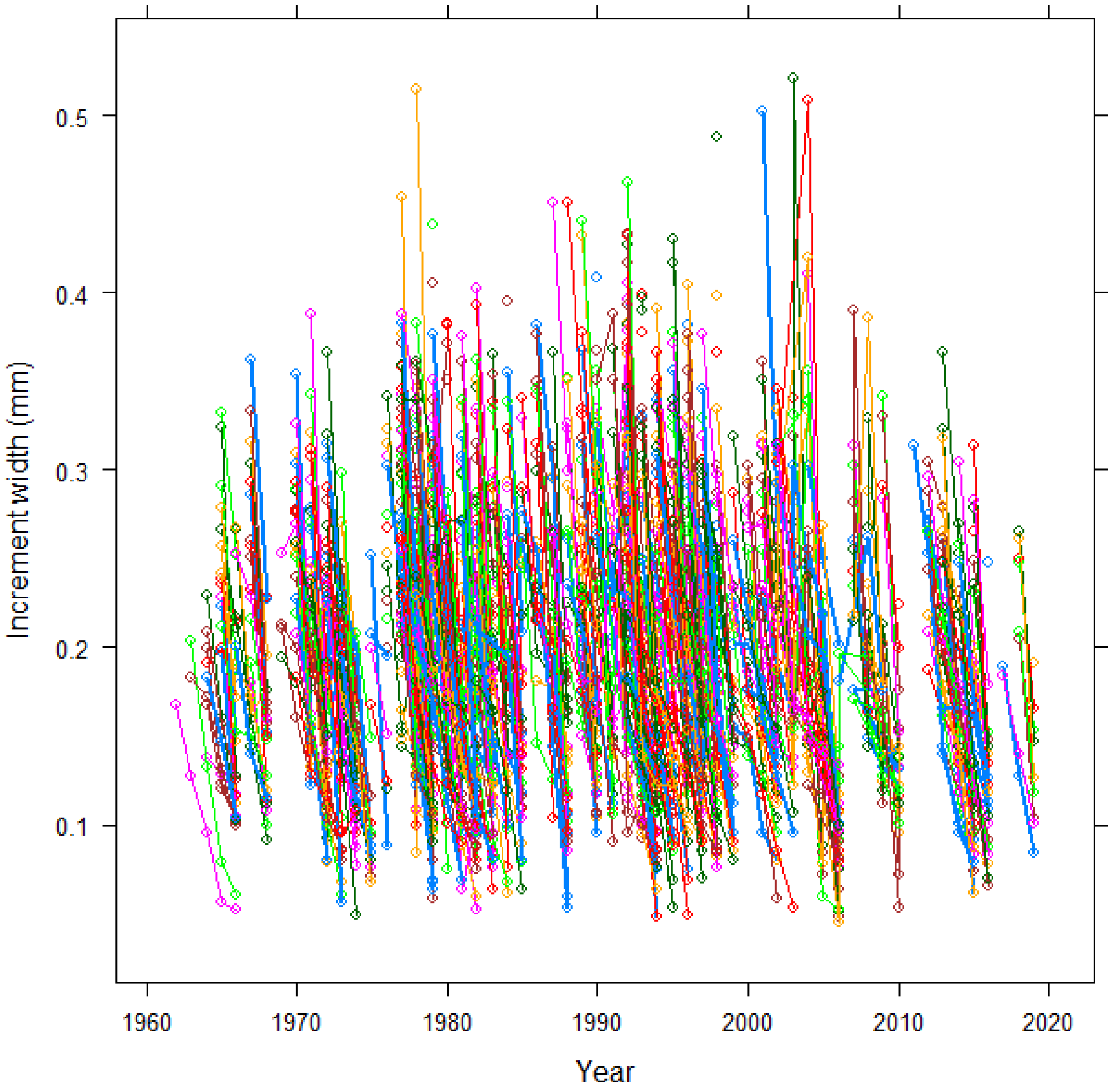


Figure B3. Absolute increment width against year of formation for all 808 otoliths of sardine caught off caught off the west coast of South Africa.

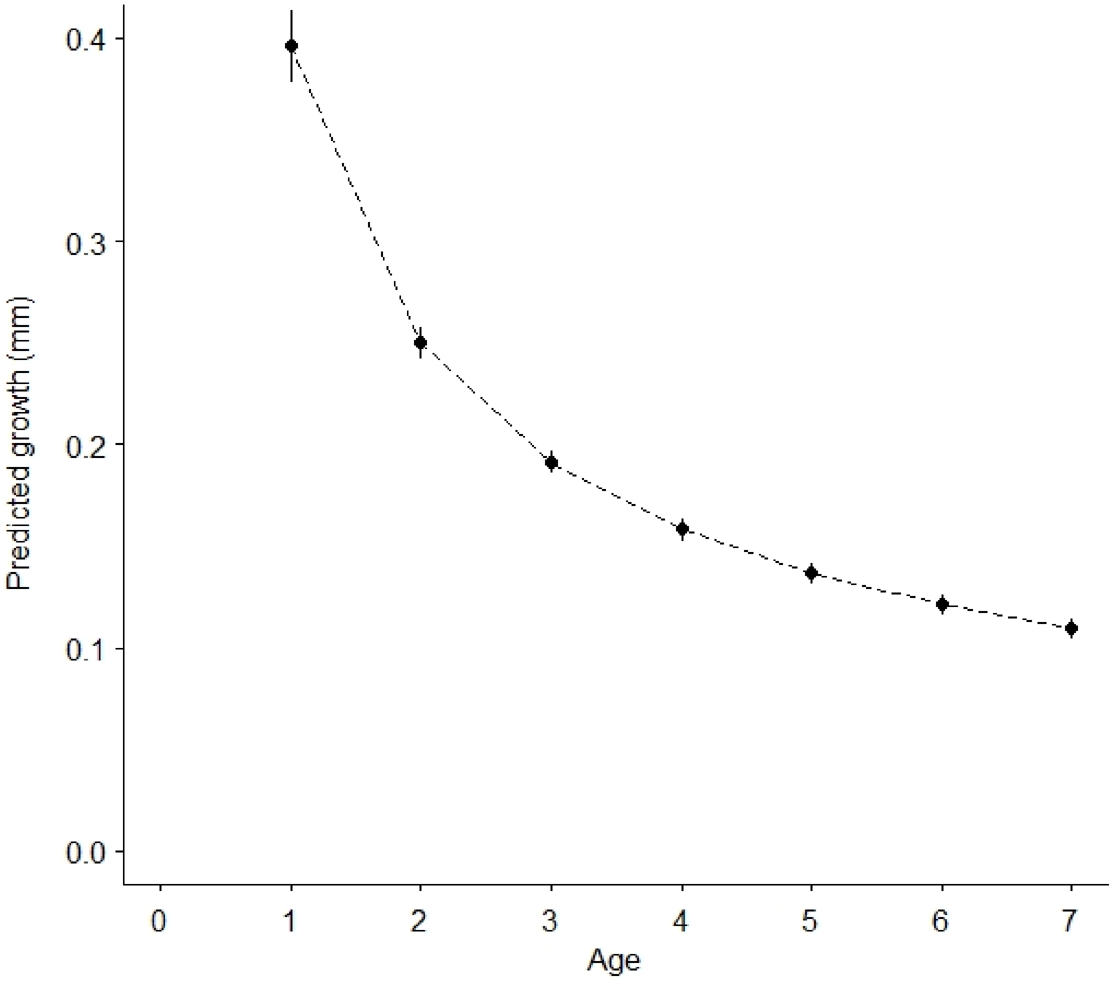


Figure B4. Predicted growth (mm) against age estimated in the full mixed effects model (mean age-related growth decline), back-transformed to the original scale.

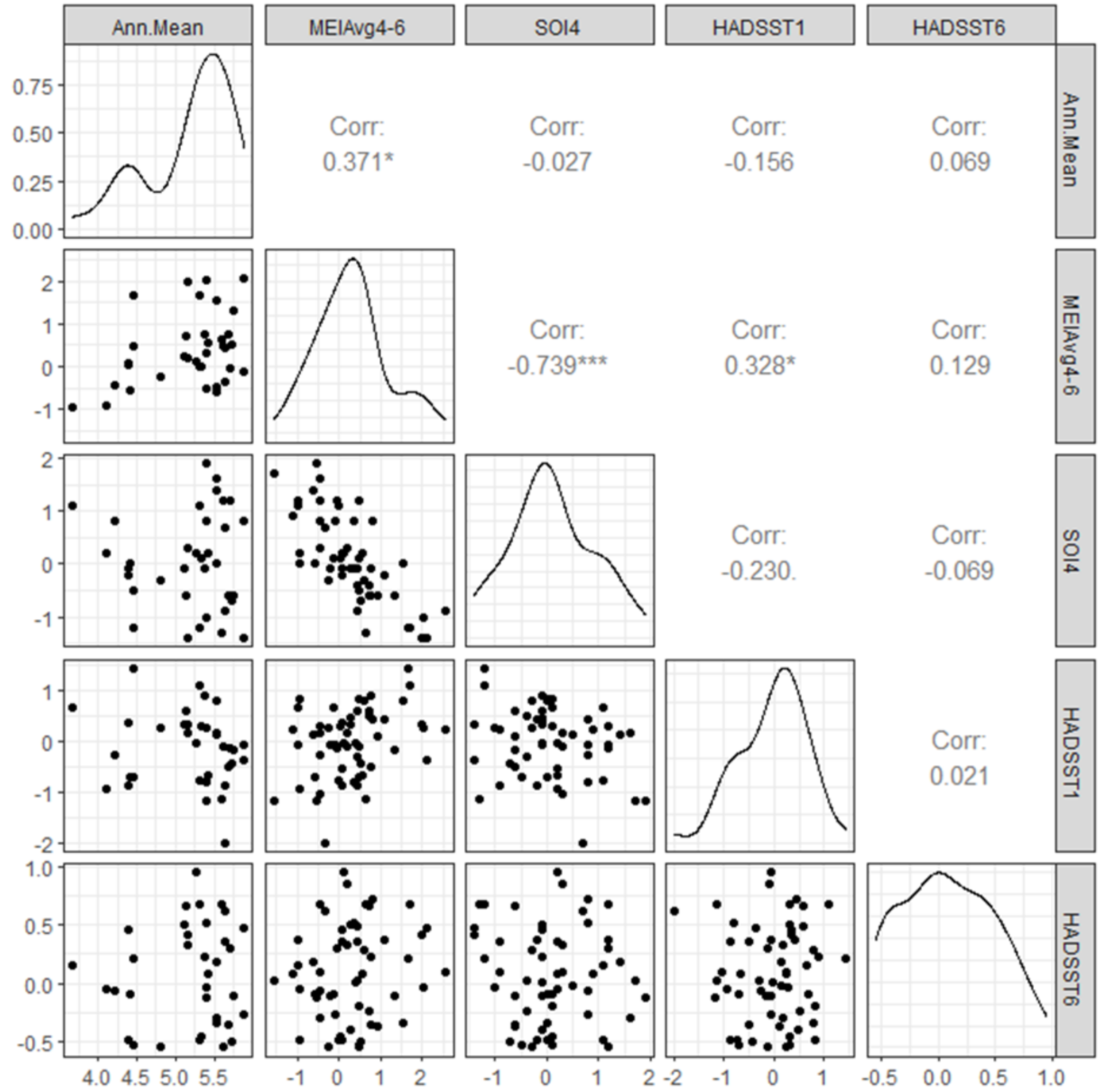


Figure B5. Scatter plots between environmental variables (HADSST, SOI and MEIv2) and copepod abundance. Scatter plots demonstrates the correlation between MEIv2/SOI and Copepod/MEIv2 for both model periods 1962-2019 and 1984-2019. HADSST1 = Monthly HADSST anomaly (SST-long-term-mean) for January (ºC); HADSST6 = Monthly HADSST for June (ºC); Ann.Mean = Annual mean of copepod abundance (Log10 (No. m-2 + 1); SOI4 = Monthly Southern Oscillation Index for April (normalized and standardized sea level pressure in millibar and SST in ºC); and MEIAvg4-6 = Monthly Multivariate ENSO index averaged April-June (normalized and standardized).

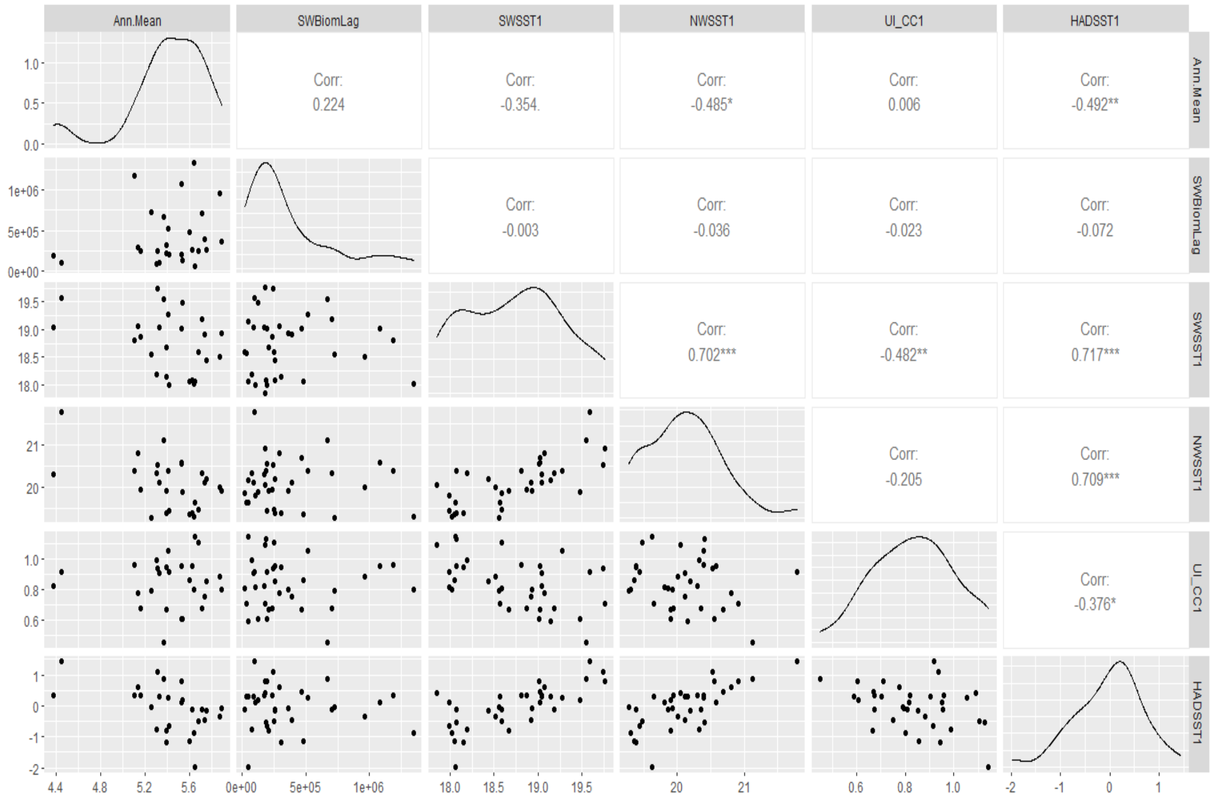


Figure B6. Scatterplots between environmental variables (SST and Upwelling) and copepod abundance. Scatter plots demonstrates the correlation between HADSST/ SST by Reynolds et al. (2002) and summer SSTs by Reynolds et al. (2002) for NW and SW area, HADSST/Copepod and Upwelling index and summer SST in SW area. Thus, either HADSST OR SST (Reynolds et al. 2002) can be used in the model. Where: HADSST1 = Monthly HADSST for January (ºC); HADSST6 = Monthly HADSST for June (ºC); Ann.Mean = Annual mean of copepod abundance (Log10 (No. m-2 + 1); UI_CC1 = Upwelling index at Cape Columbine for January (m^{2}s^{-1}); SOI4 = Monthly Southern Oscillation Index for April (normalized and standardized sea level pressure in millibar and SST in ºC); and MEIAvg4-6 = Monthly Multivariate ENSO index averaged April-June (normalized and standardized).

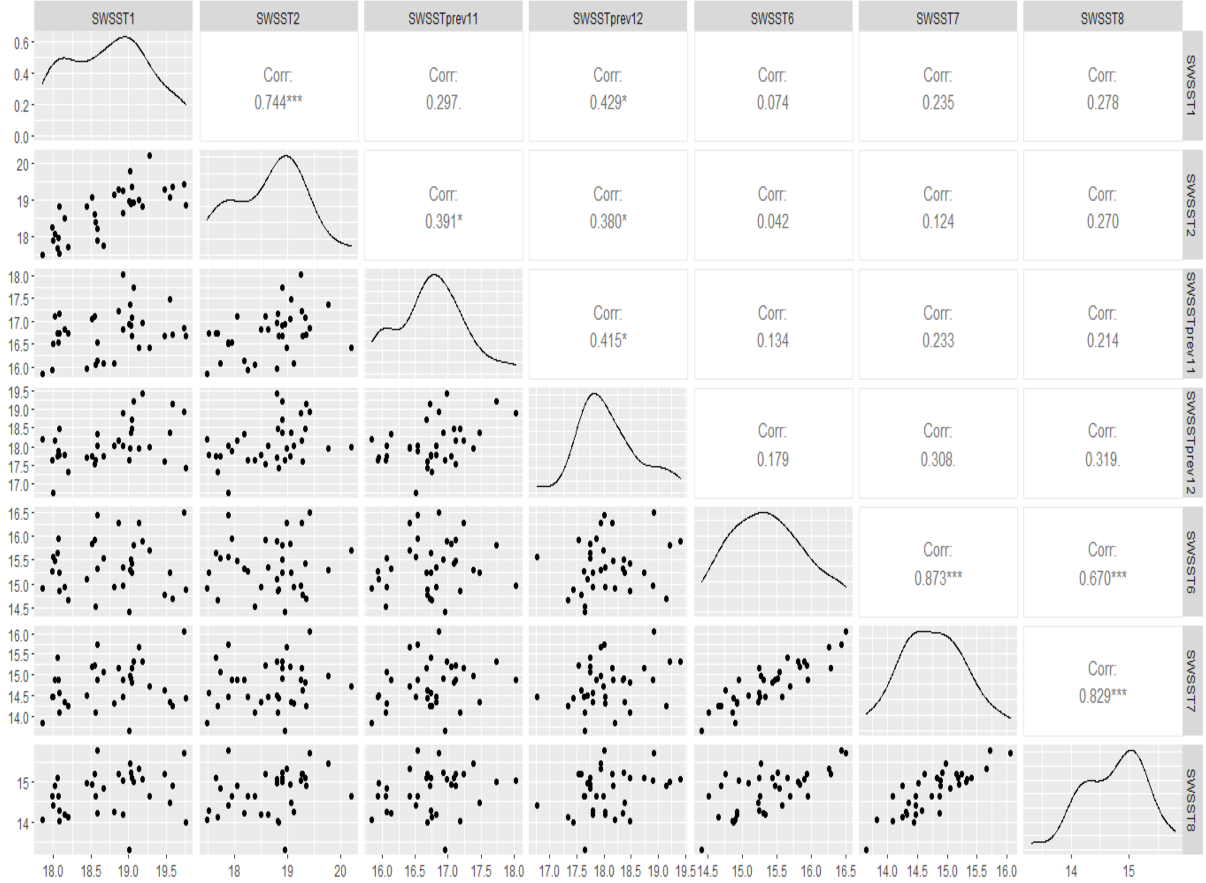


Figure B7. Scatterplots of summer and winter SST by Reynolds et al. (2002) in SW area. Scatter plots demonstrates the correlation between summer SSTs and winter SST for model period 1984-2019. Thus, the most significant summer and winter SST variables can be used. Where: SWSST1 = Monthly SST for January SW area (ºC); SWSST2 = Monthly SST for February SW area (ºC); SWSSTprev11 = Monthly SST lagged with 1 year for November SW area (ºC); SWSSTpev12 = Monthly SST lagged by 1 year for December in SW area (ºC); SWSST6 = Monthly SST June SW area (ºC); SWSST7 = Monthly SST July SW area (ºC) and SWSST8 = Monthly SST August SW area (ºC).

Table B1: Results of intrinsic effects (Fixed and random) optimal base model fitted to data from 1962-2019 (Number of observations: 2352, groups: FishID, 808; Year, 58). Random age slopes for FishID, Cohort and Year are denoted by “|”. Best model (in bold) was selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; Res.LL = restricted log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

Fixed	Random effects	K	AICc	ΔAICc	Res.LL	Cond.R^2
Age, AAC	**Age|FishID, Age|Year**	**10**	**-23.7**	**0**	**21.90**	**0.791**
Age	Age|FishID, Age|Year	9	-19.05	4.20	18.56	0.795
Age, AAC	Age|FishID, Age|Year, 1|Cohort	11	-6.51	17.19	14.31	0.794
Age, AAC	Age|FishID, Age|Year, Age|Cohort	13	-5.65	18.05	15.90	0.794
Age, AAC	Age|FishID, 1|Year	11	-4.22	19.48	13.17	0.791
Age, AAC	Age|FishID, 1|Year, 1|Cohort	9	-0.63	23.07	9.35	0.792
Age, AAC	Age|FishID, 1|Year	8	4.89	28.59	5.59	0.791
Age, AAC	Age|FishID, Age|Cohort	10	54.86	78.56	-17.38	0.774
Age, AAC	Age|FishID, 1|Cohort	8	67.45	91.15	-25.7	0.776
Age, AAC	Age|FishID	7	104.19	127.89	-45.07	0.737
Age, AAC	1|FishID,	5	134.86	158.86	-62.42	0.774
AAC	Age|FishID, Age|Year	9	148.22	171.92	-65.07	0.832
Age, AAC		4	267.39	291.10	-129.69	0.636

Table B2: Results of extrinsic fixed-effects (SST, MEI or SOI and copepod abundance) fitted to data from 1962-2019 (Number of observations: 1261, groups: FishID, 429; Year, 27). The best model (in bold) was selected based on the lowest AICc and a ΔAICc < 2 compared to the model with the lowest AICc and higher K = number of estimated parameters; ΔAICc = difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; Copepod = Annual mean of total copepod abundance; HADSST6 = Monthly HADSST for June ; HADSST1 = Monthly HADSST for January; SOI4 = Monthly Southern Oscillation Index for April; and MEIAvg4-6 = Monthly Multivariate ENSO index averaged April-June.

Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + Copepod, SOI4, HADSTT6	13	2.90	0	11.67	0.79
BM + Copepod, HADSTT6	**12**	**3.28**	**0.38**	**10.46**	**0.79**
BM + Copepod, MEIAvg4-6, HADSST6	13	5.27	2.37	10.49	0.79
BM + Copepod, SOI4, HADSST6, HADSST1	14	4.77	1.87	11.76	0.79
BM + HADSST6	11	14.63	11.73	3.77	0.79
BM + Copepod, SOI4	12	3.37	0.47	10.42	0.79
BM + SOI4, HADSST1	12	18.57	15.67	2.82	0.79
BM + Copepod	11	6.42	3.52	7.88	0.79
BM + Copepod, SOI4, HADSST1	13	5.14	2.24	10.55	0.79
BM + SOI4, HADSST6	12	16.13	13.22	4.04	0.79
BM + MEIAvg4-6, HADSST6	12	16.00	13.10	4.10	0.79
BM + HADSST1	11	19.61	16.71	1.28	0.79
BM	10	18.04	15.13	1.06	0.79
BM + SOI4	11	17.82	14.92	2.18	0.79
BM + MEIAvg4-6, HADSST1	12	17.96	15.06	3.13	0.79
BM + Copepod, HADSST1	12	8.44	5.53	7.89	0.79
BM + Copepod, MEIAvg4-6 BM	12	7.81	4.91	8.20	0.79
BM + Copepod, MEIAvg4-6, HADSST1	13	9.53	6.63	8.36	0.79
BM + MEIAvg4-6	11	18.15	15.25	2.02	0.79

Table B3: Results of extrinsic fixed-effects (environmental, copepod abundance and sardine biomass) fitted to data from 1984-2019 (Number of observations: 1261, groups: FishID, 429; Year, 27). The best model (in bold) was selected based on the lowest AICc and ΔAICc > 2. K = number of estimated parameters; ΔAICc = difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; Copepod = Annual mean of total copepod abundance; SWSST1 = Monthly SST Reynolds et al. (2002) for January of South West area; SWSST6 = Monthly SST (Reynolds et al.2002) for June of South West area; NWSST1= Monthly SST Reynolds et al. (2002) for January of North West area; UI_CC7 = Monthly Upwelling index at Cape Columbine for July; UI_CCPrev11 = Monthly Upwelling index at Cape Columbine lagged with 1 year for November; SOI4 = Monthly Southern Oscillation Index for April and SarBiom = Annual biomass estimates lagged by 1 year for the area West of Agulhas.

a) Environmental factors fitted to data from 1984-2019					
Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SWSST6, SarBiom, NWSST1	**11**	**-110.68**	**0**	**66.43**	**0.81**
BM + SWSST6, SarBiom	10	-108.26	2.41	64.21	0.81
BM + SWSST6, SarBiom, SWSST1	11	-106.65	4.03	64.42	0.81
BM + SWSST6, SarBiom, UI_CCprev11	11	-106.45	4.22	64.32	0.81
BM + Copepod, SWSST6, SarBiom, UI_CCprev11	11	-106.45	4.22	64.32	0.81
BM + SOI4, SWSST6, SarBiom	11	-106.26	4.41	64.22	0.81
BM + SOI4, SWSST6, SarBiom, SWSST1	12	-104.64	6.03	64.43	0.81
BM + SWSST6, NWSST1	10	-103.53	7.15	61.84	0.81
BM + SWSST6, SWSST1	10	-99.98	10.7	60.07	0.81
BM + SarBiom, NWSST1	10	-99.73	10.94	59.94	0.80
BM + SOI4, SWSST6, SWSST1	11	-98.68	12.00	60.43	0.81
BM + SarBiom, UI_CC7	10	-98.24	12.43	59.20	0.81
BM + SOI4, SWBiomLag, UI_CC7	11	-96.71	13.96	59.45	0.81
BM + SarBiom, UI_CC7, UI_CCprev11	11	-96.59	14.08	59.39	0.81
BM + SWBiomLag	9	-95.97	14.71	57.05	0.80
BM + SOI4, SarBiom, UI_CC7, UI_CCprev11	12	-95.23	15.44	59.73	0.81
BM + SOI4, SarBiom	10	-94.62	16.06	57.39	0.80
BM + SarBiom, UI_CCprev11	10	-94.50	16.17	57.33	0.80
BM + SarBiom, SWSST1	10	-94.07	16.61	57.11	0.80
BM + UI_CC7	9	-91.43	19.25	54.78	0.80
BM	8	-91.08	19.59	53.59	0.80
BM + SOI4	9	-90.84	19.84	54.48	0.80
BM + UI_CC7, UI_CCprev11	10	-89.40	21.28	54.78	0.80
BM + UI_CCprev11	9	-89.08	21.60	53.60	0.80
BM + Copepod, SOI4, SWSST6, SarBiom, UI_CCprev11	13	-45.99	64.68	36.14	0.80

Table B4: Summary of the historic significant regime shifts (robust/possible) recorded in the Southern Benguela region. The regime shifts were detected by applying the STARS analysis, change point analysis and the Chow breakpoint test to upwelling and sea surface temperature at 30ºS and 32ºS. Only significant (robust/possible) shifts were reported. Data taken from Blamey et al. (2012).

Regime shift year identified	**Environmental Variable**	**Method**	**Reference**
Robust: 1950, 1956, 1998, 2001 Possible: 1969, 1984	SST at 32ºS	STARS analysis	Howard et al. 2007*
1911, 1957,	SST at 32ºS	Change Point analysis	Blamey et al. 2012*
1956, 1957, 2000	SST at 32ºS	Chow Breakpoint test	Blamey et al. 2012*
Possible: 1956, 1971, 1985, 1991, 2004/2005	SST at 30ºS	STARS analysis	Howard et al. 2007*
1912, 1957, 1992	SST at 30ºS	Change Point analysis	Blamey et al. 2012*
1956, 1957, 1971, 1991, 1992	SST at 30ºS	Chow Breakpoint test	Blamey et al. 2012*
Robust: 1971/72 Possible: 1964, 2000/2001, 2004/2005	Upwelling 32ºS	STARS analysis	Howard et al. 2007*
1933, 1973	Upwelling 32ºS	Change Point analysis	Blamey et al. 2012*
1964, 1971, 1973	Upwelling 32ºS	Chow Breakpoint test	Blamey et al. 2012*
Possible: 1951, 1956, 1991, 1998, 2004/2005	Upwelling at 30ºS	STARS analysis	Howard et al. 2007*
1922	Upwelling at 30ºS	Change Point analysis	Blamey et al. 2012*
1922	Upwelling at 30ºS	Chow Breakpoint test	Blamey et al. 2012*
1963, 1974, 1984, 1995, 1999, 2010, 2019	Benguela Niño events		Howard et al. 2007*

*References are located in the reference list.

APPENDIX C

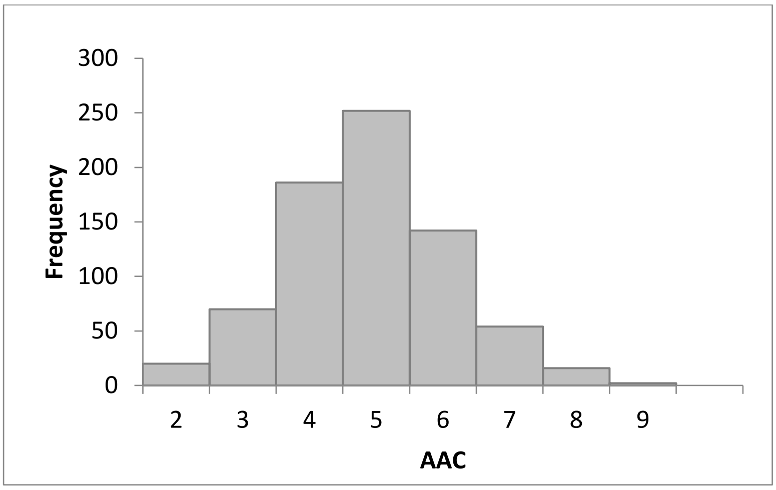


Figure C1. Age-at-capture distribution of the 700 otoliths used in the mixed effects analysis.

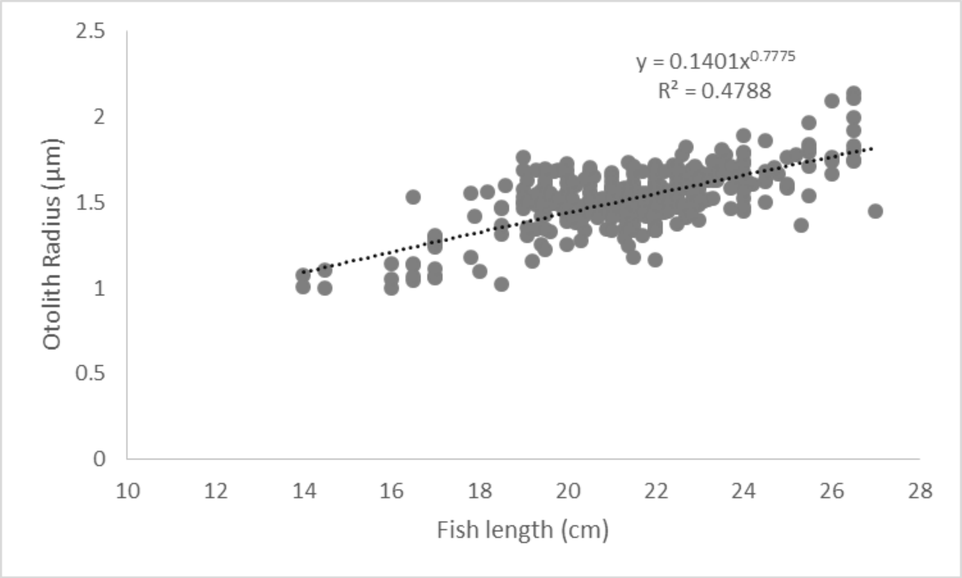


Figure C2. Otolith length and total length relationship for sardine otoliths collected from annual surveys as well as commercial port samples for Namibia in northern Benguela.

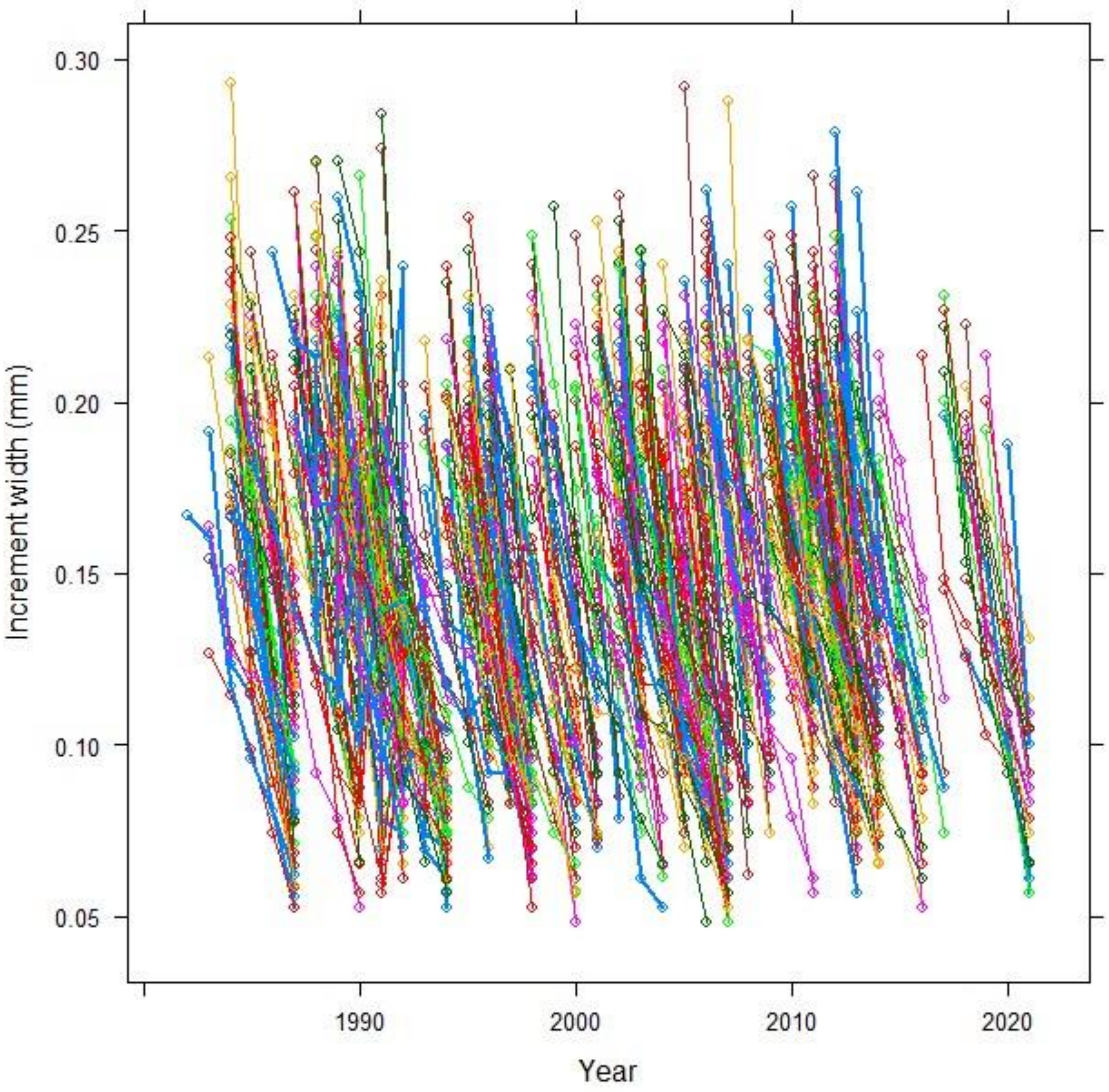


Figure C3. Annual increment width of sardine 700 otoliths from 1974-2021 caught off northern Benguela, Namibia.

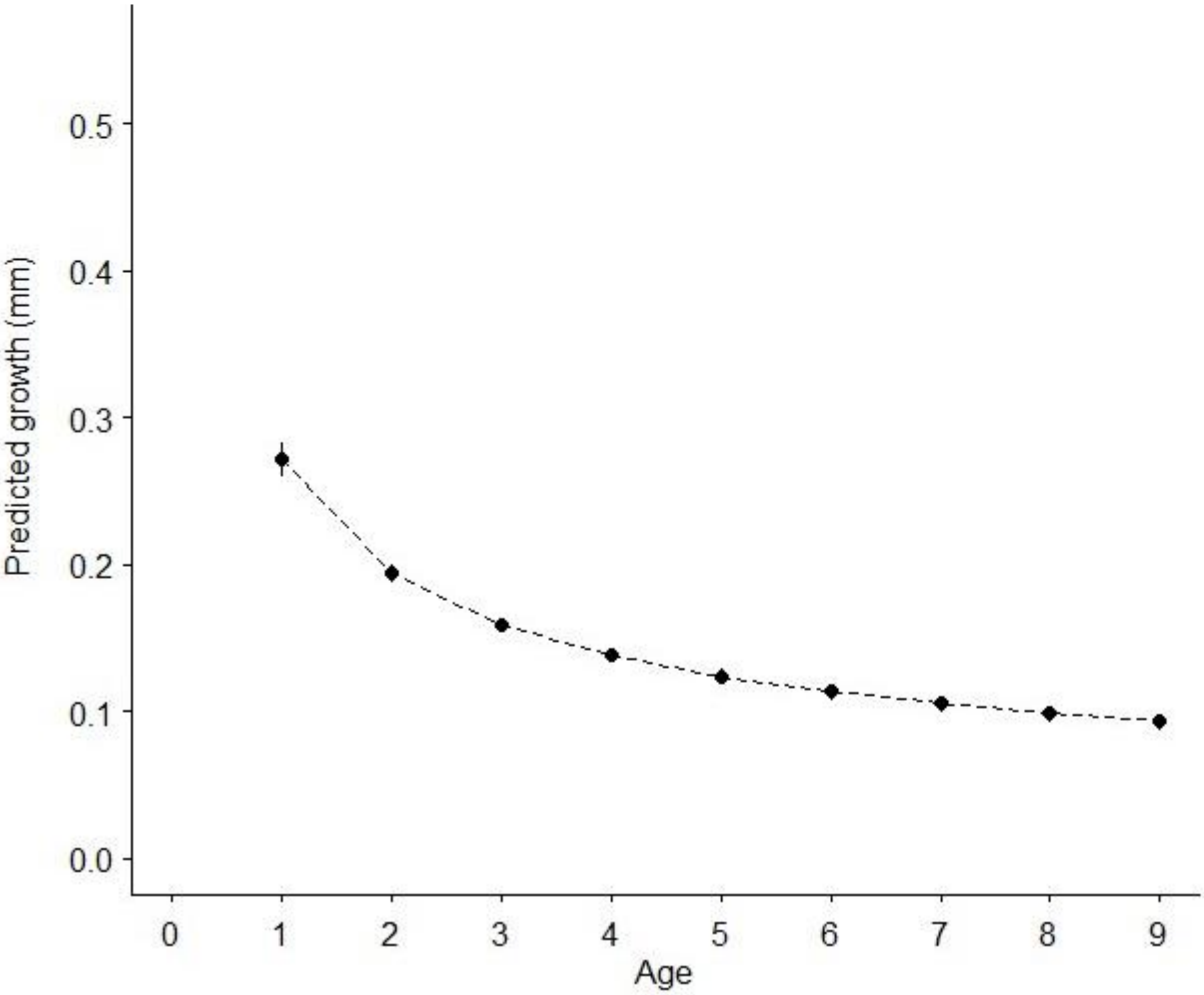


Figure C4. Predicted growth (mm) against age estimated in the full mixed effects model demonstrating mean age-related growth decline, back-transformed to the original scale.

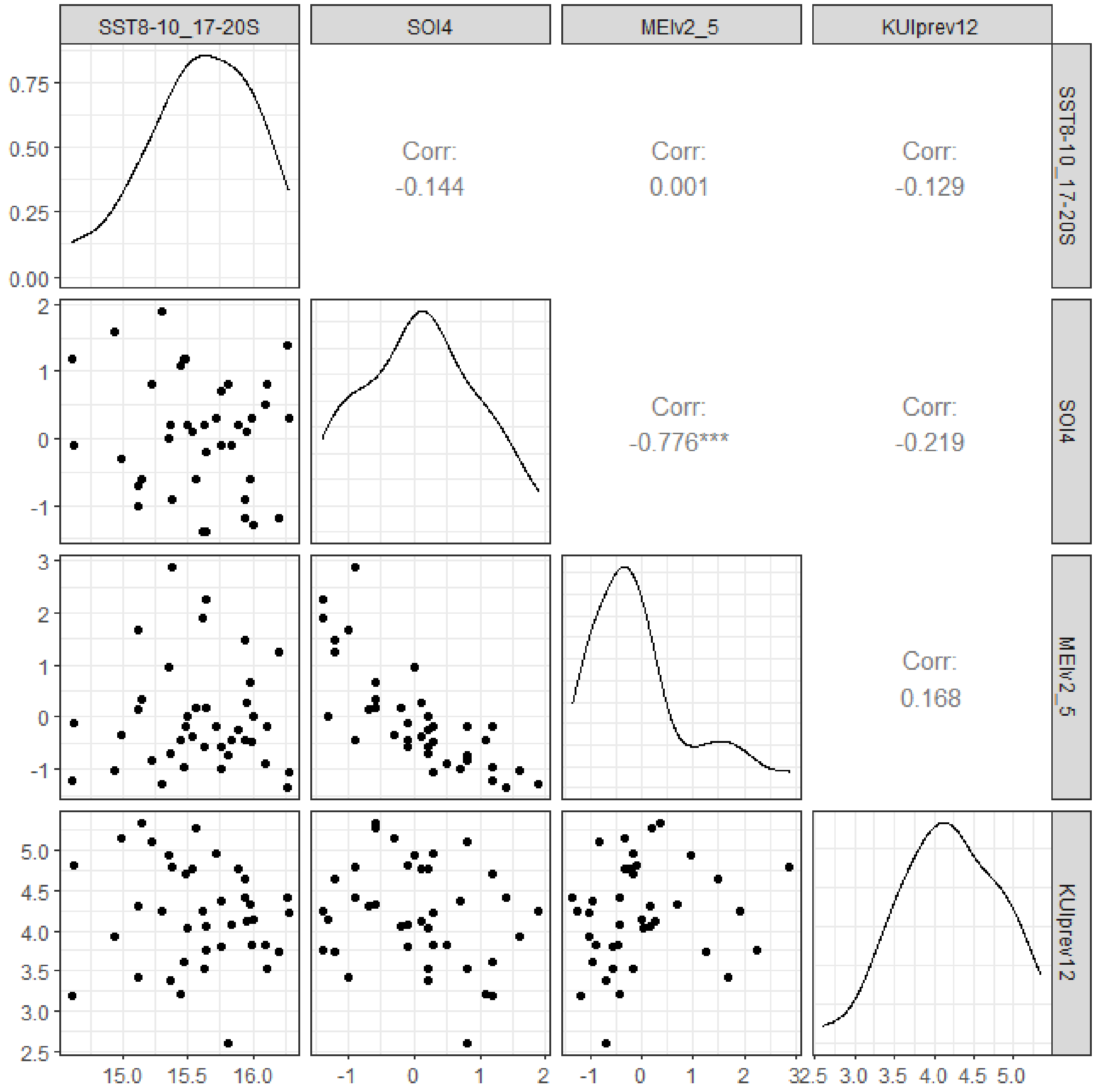


Figure C5. Scatter plots between environmental variables (SST, SOI and MEIv2). Scatter plots demonstrates the correlation between MEIv2/SOI for all model periods. Therefore, either MEIv2 or SOI can be used in the model.

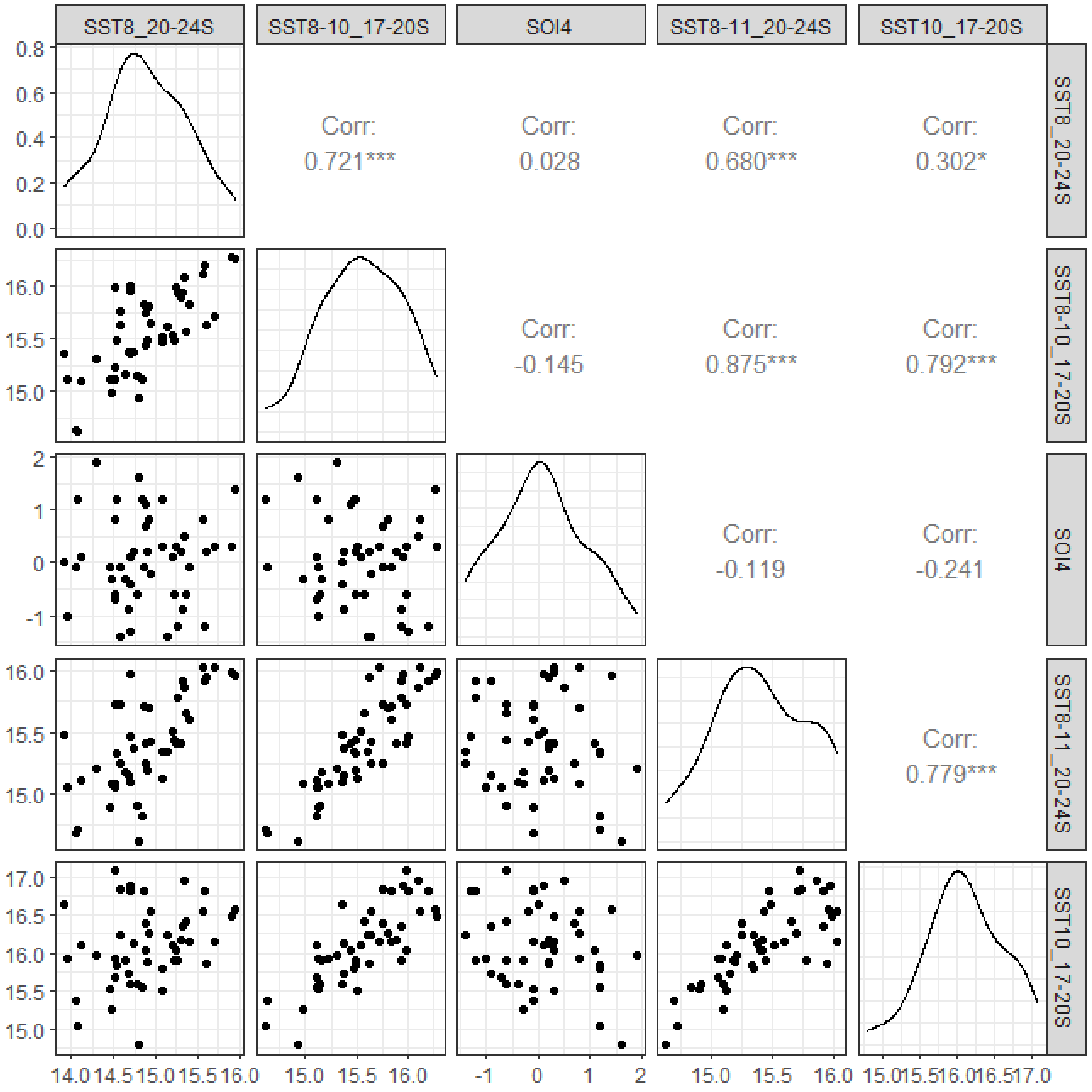


Figure C6. Scatterplots between environmental variables (ERSSTv5). Scatter plots demonstrates the correlation between SST8.10_17-20S (SST in northern Namibia) and SST8_20-24S (SST at 20-24ºS central Namibia) in spring. Thus, either SST in north or central in spring or summer can be used in the model.

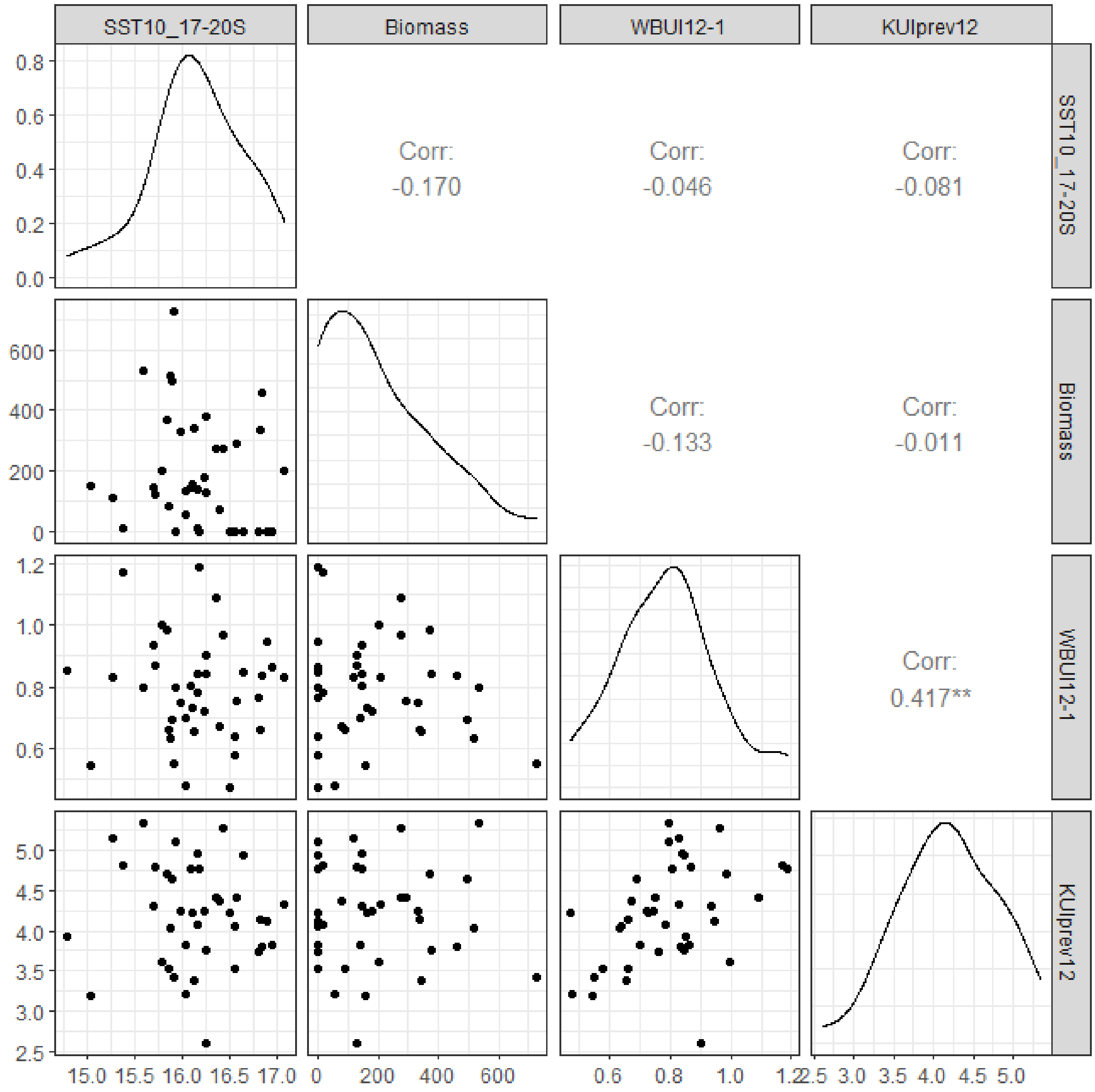


Figure C7. Scatterplots demonstrates the correlation between upwelling indices in the central and northern Namibia. Where WBUI12.1 = Walvis Bay Upwelling Index averaged Dec=Jan; KUIprev12 = Kunene Upwelling Index for December lagged by 1 year

Table C1: Results of intrinsic effects (Fixed and random) optimal base model fitted to data from 1974-2021 (Number of observations: 2862, Groups: FishID, 700; Year, 47; Cohort, 43). Random age slopes for FishID, Cohort and Year are denoted by "|". Best model (in bold) was selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; Res.LL = restricted log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

Fixed effects	Random effects	K	AICc	ΔAICc	Res.LL	Cond.R^2
Age, AAC	**Age|FishID, Age|fYear, 1|fCohort**	**11**	**-2006.12**	0	1014.11	0.864
Age, AAC	Age|FishID, Age|fYear, Age|fCohort	13	-1986.08	20.04	1006.1	0.867
Age	Age|FishID, Age|fYear, 1|fCohort	10	-1970.36	35.76	995.22	0.872
AAC	Age|FishID, Age|fYear, 1|fCohort	10	-1875.93	130.19	948.00	0.911
Age, AAC	Age|FishID, Age|fYear,	10	-1924.46	81.66	972.27	0.866
Age, AAC	Age|FishID, 1|fYear	11	-1878.2	127.92	950.15	0.864
Age, AAC	Age|FishID, 1|fYear, 1|fCohort	9	-1841.89	165.00	929.98	0.855
Age, AAC	Age|FishID, 1|fYear	8	-1746.21	259.91	881.13	0.853
Age, AAC	Age|FishID, Age|fCohort	10	-1651.93	354.19	836.00	0.826
Age, AAC	Age|FishID, 1|fCohort	8	-1650.94	355.18	833.49	0.826
Age, AAC	Age|FishID	7	-1530.24	475.88	772.14	0.828
Age, AAC	1|FishID	5	-1487.62	518.50	748.82	0.813
Age, AAC		4	-813.01	1192.99	772.14	0.828

Table C2: Results of intrinsic effects (Fixed and random) optimal base model fitted to data from 1981-2021 (Number of observations: 2657, Groups: FishID, 656; Year, 40; Cohort, 38). Random age slopes for FishID, Cohort and Year are denoted by "|". Best model (in bold) was selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; Res.LL = restricted log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

Fixed effects	Random effects	K	AICc	ΔAICc	Res.LL	Cond.R^2
Age, AAC	**Age|FishID, Age|fYear, 1|fCohort**	**11**	**-1846.44**	**0**	**934.27**	**0.859**
Age	Age|FishID, Age|fYear, 1|fCohort	10	-1812.04	34.40	916.06	0.867
Age, AAC	Age|FishID, Age|fYear	10	-1769.48	76.96	894.78	0.861
AAC	Age|FishID, Age|fYear, 1|fCohort	10	-1731.79	114.65	875.93	0.906
Age, AAC	Age|FishID, 1|fYear, Age|fCohort	11	-1731.31	115.13	876.71	0.858
Age, AAC	Age|FishID, 1|fYear, 1|fCohort	9	-1701.72	144.72	859.90	0.849
Age, AAC	Age|FishID, 1|fCohort	8	-1607.75	238.69	811.90	0.848
Age, AAC	Age|FishID, Age|fYear, Age|fCohort	10	-1567.1	279.34	793.59	0.824
Age, AAC	Age|FishID, 1|fCohort	8	-1566.09	280.35	791.07	0.824
Age, AAC	Age|FishID,	8	-1455.32	391.12	734.68	0.828
Age, AAC	1|FishID	5	-1418.28	428.16	734.68	0.828
Age, AAC		4	-782.93	1063.51	395.47	0.635

Table C3: Results of extrinsic fixed-effects (SST, upwelling index and sardine biomass) fitted to data from 1974-2021 (Number of observations: 2862, groups: FishID, 700; fYear, 47; fCohort, 43). Best models (in bold) were selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; SST8-10_17-20S = Monthly SST (ERSSTv5) averaged Aug-Oct at 17-20º S; SST10_17-20S = Monthly SST (ERSSTv5) for October at 17-20º S; SST8_20-24S = Monthly SST (ERSSTv5) for August at 20-24º S and SOI4 = Monthly Southern Oscillation Index for April.

a) Environmental factors fitted to data from 1974-2021

Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SST8-10_17-20S	**12**	**-2010.29**	**0**	**1017.20**	**0.865**
BM + SST10_17-20S	12	-2009.9	0.39	1017.00	0.865
BM + SST8-11_20-24S	12	-2008.63	1.66	1016.37	0.864
BM + SST10_17-20S, SOI4	13	-2008.02	2.26	1017.08	0.865
BM + SST8-11_20-24S, SOI4	13	-2006.98	3.31	1016.55	0.864
BM	11	-2006.12	4.16	1014.11	0.864
BM + SST8_20-24S	12	-2005.03	5.25	1014.57	0.864
BM + SOI4	12	-2004.77	5.52	1014.44	0.864

Note: The model highlighted in bold was determined to be the most suitable fit.

Table C4: Results of extrinsic fixed-effects (SST and upwelling indices) fitted to data from 1981-2021 (Number of observations: 2657, Groups: FishID, 656; fYear, 40, Cohort, 38). Best model (in bold) were selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; SOI4 = Southern Oscillation Index Apr; SST8.10_17.20S = SST (ERSSTv5) averaged Aug-Oct 17-20º S; SST8.9_20.24S = SST (ERSSTv5) averaged Aug-Sep 20-24º S; KUIprev12 = Kunene Upwelling Dec lagged 1 year; KUIprev10 = Kunene Upwelling Oct lagged 1 year; WBUI12.1 = Walvis Bay Upwelling averaged Dec-Jan and MEIv2_5 = Multivariate ENSO version 2 for May.

a) Environmental factors fitted to data from 1981-2021

Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SOI4, SST8.10_17.20S, KUIprev12	14	-1853.23	0	940.69	0.86
BM + SST8.10_17.20S, KUIprev12	13	-1852.51	0.72	939.33	0.86
BM + SST8.10_17.20S, KUIprev10, KUIprev12	14	-1850.50	2.74	939.33	0.86
BM + SST8.10_17.20S	12	-1849.85	3.38	936.99	0.86
BM + SOI4, KUIprev12	13	-1849.64	3.60	937.89	0.86
BM + SOI4, SST8.10_17.20S	13	-1848.68	4.55	937.41	0.86
BM + KUIprev12	12	-1848.32	4.91	936.22	0.86
BM + SST8.10_17.20S, KUIprev10	13	-1847.86	5.37	937.00	0.86
BM + SOI4, KUIprev10, KUIprev12	14	-1847.62	5.61	937.89	0.86
BM + SOI4, SST8.10_17.20S, KUIprev10	14	-1846.66	6.57	937.41	0.86
BM + KUIprev10, KUIprev12	13	-1846.47	6.76	936.3	0.86
BM	11	-1846.44	6.79	934.27	0.86
BM + SOI4	12	-1845.66	7.57	934.89	0.86
BM + KUIprev10	12	-1844.63	8.60	934.38	0.86
BM + SOI4, KUIprev10	13	-1843.69	9.55	934.91	0.86
BM + SOI4, SST8.9_20.24S, KUIprev10, WBUI12.1	15	-1231.80	621.43	631.02	0.86
BM + MEIv2_5, SST8.9_20.24S, KUIprev10,	15	-1231.80	621.43	631.02	0.86
WBUI12.1	15	-1229.03	624.20	629.64	0.86
BM + SOI4, SST8.10_17.20S, KUIprev10, WBUI12.1	15	-1228.64	624.59	629.44	0.86
BM + SOI4, SST8.10_17.20S, KUIprev10, KUIprev12					

Note: The most suitable model, indicated by being in bold, was chosen as the best match due to a ΔAICc less than 2 compared to the model with the lowest AIC, and it also has one parameters (K) fewer than the model with the lowest AIC.

Table C5: Results of extrinsic fixed-effects (SST, upwelling indices and sardine biomass) fitted to data from 1990-2013 (Number of observations: 1972, groups: FishID, 552; Cohort, 29; Year, 23). Best model (in bold) were selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; SOI4 = Southern Oscillation Index Apr; SST8.10_17.20S = SST averaged Aug-Oct at 17-20º S; SST8.9_20.24S = SST averaged Aug-Sep 20-24º S; KUIprev12 = Kunene Upwelling Dec lagged by 1 year; KUIprev10 = Kunene Upwelling Oct lagged by 1 year; WBUI12.1 = Walvis Bay Upwelling averaged Dec-Jan; MEIv2_5 = Multivariate ENSO for May; Sarbiom = annual sardine biomass lagged by 1 year.

a) Environmental factors fitted to data from 1990-2013					
Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SST8.10_17.20S, KUIprev12, Sarbiom	14	-1290.78	0	659.49	0.86
BM + SST8.10_17.20S, Sarbiom	13	-1290.51	0.27	658.34	0.86
BM + SOI4, SST8.10, WBUI12.1, KUIprev10, Sarbiom	16	-1289.67	1.11	656.99	0.86
BM + SST8.10_17.20S	**12**	**-1289.11**	**1.67**	**656.63**	0.86
BM + SST8.10_17.20S, KUIprev12	13	-1289.11	1.67	657.64	0.86
BM + SST8.10_17.20S, WBUI12.1, Sarbiom	14	-1288.91	1.86	658.56	0.86
BM + SOI4, SST8.10_17.20S, KUIprev12	14	-1288.88	1.90	658.54	0.86
BM + SOI4, SST8.10_17.20S	13	-1287.99	2.79	657.08	0.86
BM + KUIprev12	12	-1281.78	9.00	652.96	0.86
BM + SOI4, KUIprev12	13	-1281.62	9.16	653.9	0.86
BM	11	-1280.72	10.05	651.43	0.86
BM + SOI4, KUIprev12, Sarbiom	14	-1280.36	10.42	654.28	0.86
BM + KUIprev12, KUIprev12	13	-1280.24	10.53	653.21	0.86
BM + SOI4	12	-1279.56	11.22	651.85	0.86
BM + SOI4, Sarbiom	12	-1278.93	11.85	651.54	0.86
BM + KUIprev12,	13	-1277.83	12.95	652.00	0.86
BM + SOI4, SST8.10_17.20S, KUIprev10, Sarbiom	14	-1247.67	43.10	637.94	0.86
BM + SOI4, SST8.10_17.20S, KUIprev12, Sarbiom	14	-1246.99	43.79	637.60	0.86
BM + SOI4, SST8.9_20.24S, KUIprev10, Sarbiom	14	-1246.99	43.79	637.60	0.86
BM + SOI4, SST8.10_17.20S, WBUI12.1, Sarbiom	14	-1246.15	43.63	637.18	0.86
BM + SOI4, SST8.9, WBUI12.1, KUIprev10, Sarbiom	15	-1241.08	49.70	635.66	0.86
BM + MEIv2_5, SST8.9, WBUI12.1, KUIprev10, Sarbiom	15	-1235.66	55.12	632.95	0.86

Note: The most suitable model, indicated by being in bold, was chosen as the best match due to a ΔAICc less than 2 compared to the model with the lowest AIC, and it also has fewer parameters (K) than the model with the lowest AIC.

APPENDIX D

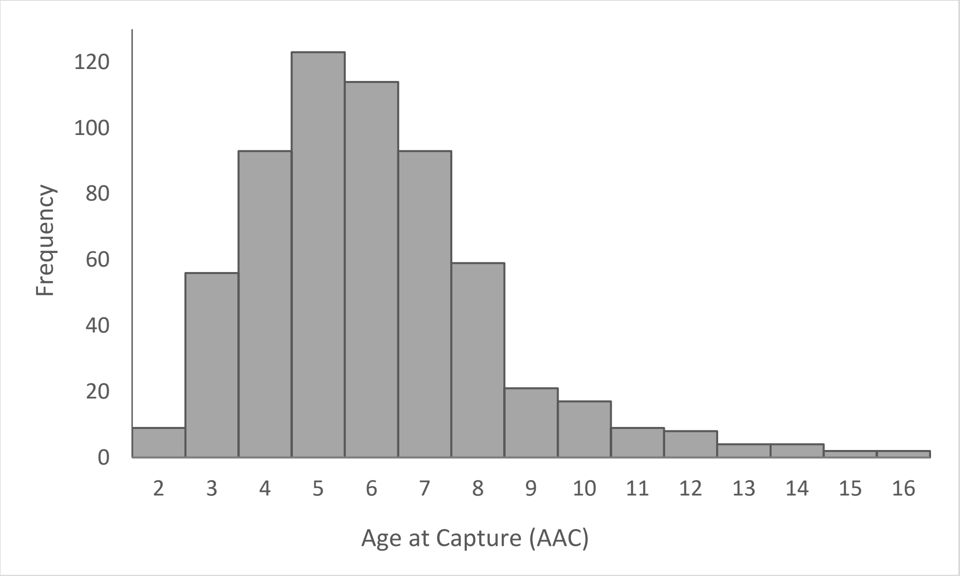


Figure D1. Age-at-capture distribution of the 614 otoliths used in the biochronology.

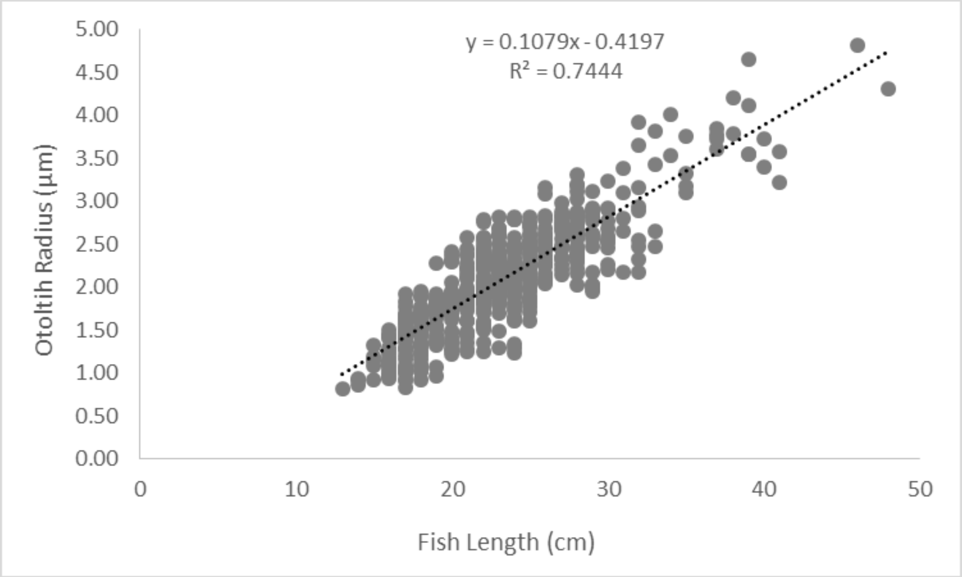


Figure D2. Relationship between otolith length and total length for Cape horse mackerel, based on otoliths collected from annual surveys and commercial port samples in Namibia.

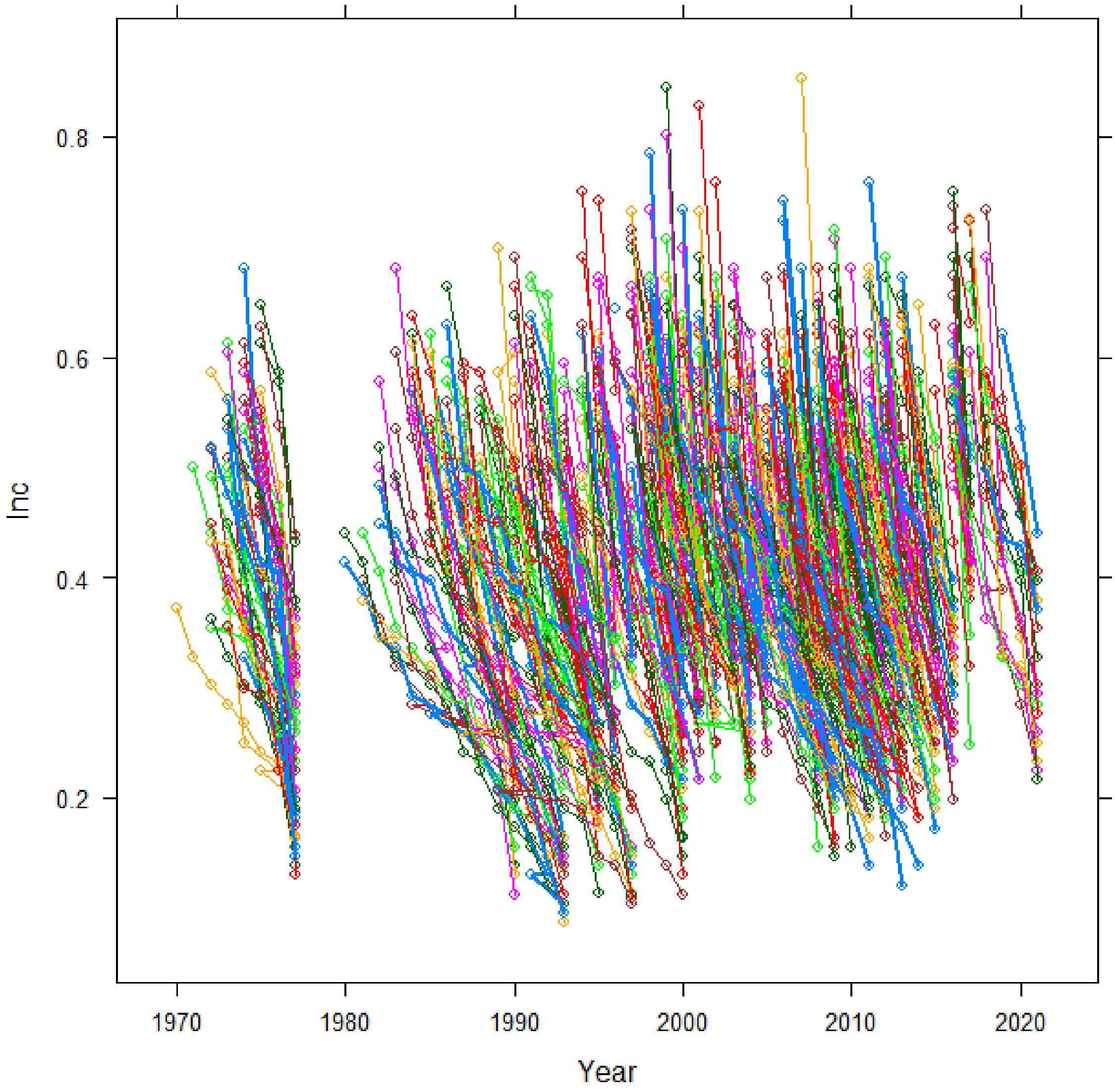


Figure D3. Annual increment width of 614 Cape horse mackerel otoliths collected from 1970 to 2021 off the northern Benguela, Namibia.

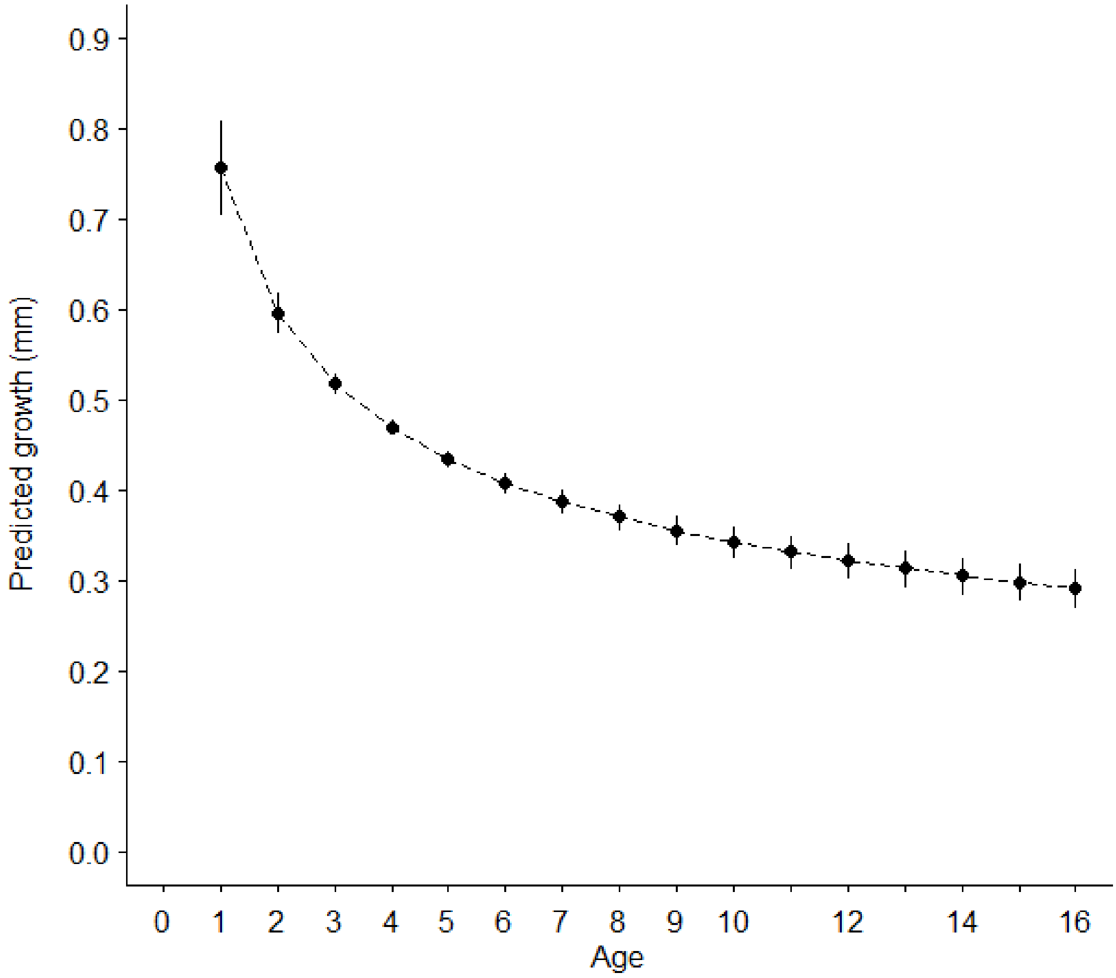


Figure D4. Predicted growth (mm) against age estimated in the full mixed effects model demonstrating mean age-related growth decline, back-transformed to the original scale.

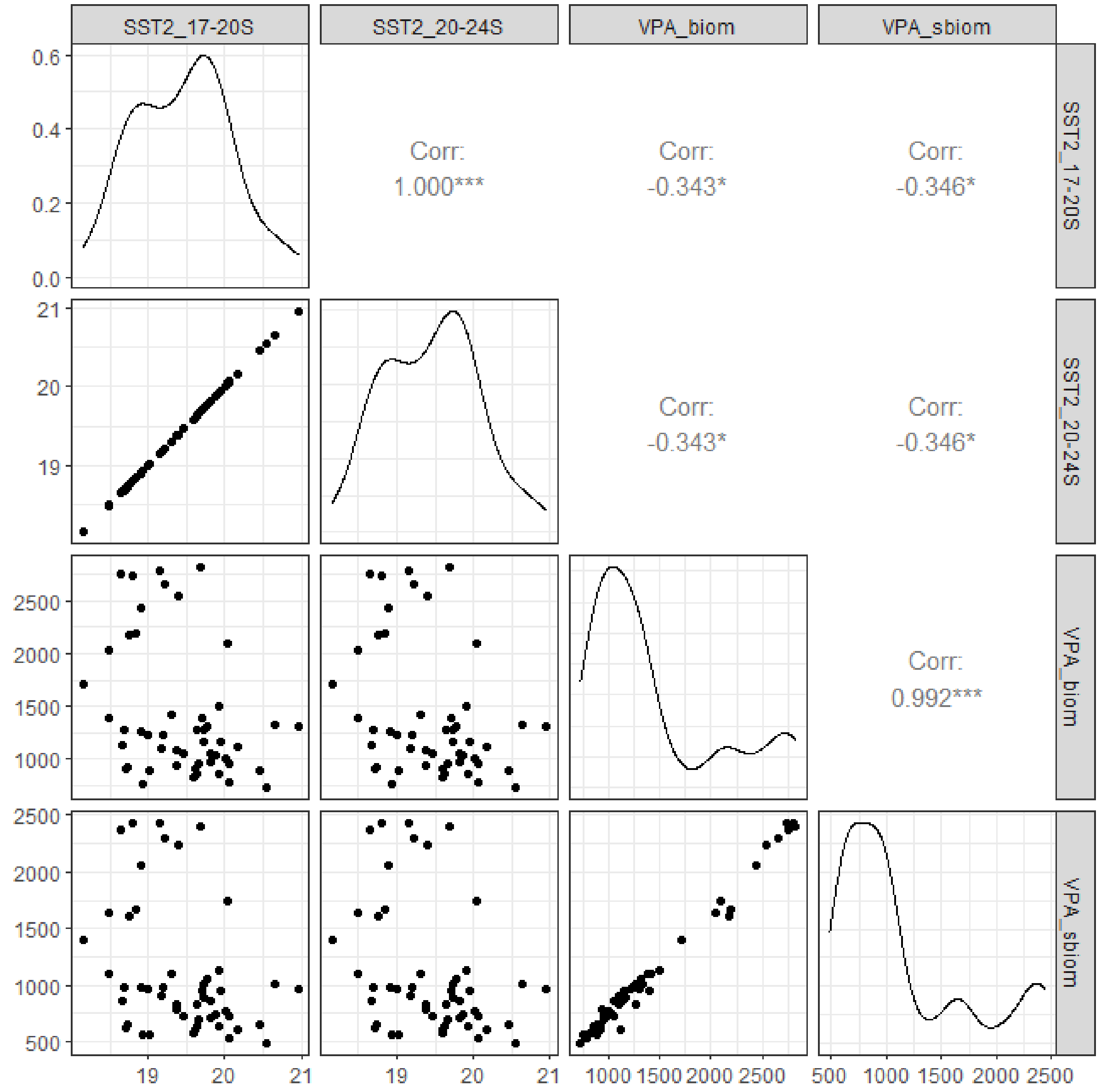


Figure D5. Scatter plots between environmental variables (SST and SOI). Scatter plots demonstrates the correlation between SST2_N (SST in February in northern Namibia) and SST2_C (SST in February in central Namibia) for all model periods. Therefore, either SST2_N or SST2_C can be used in the model.

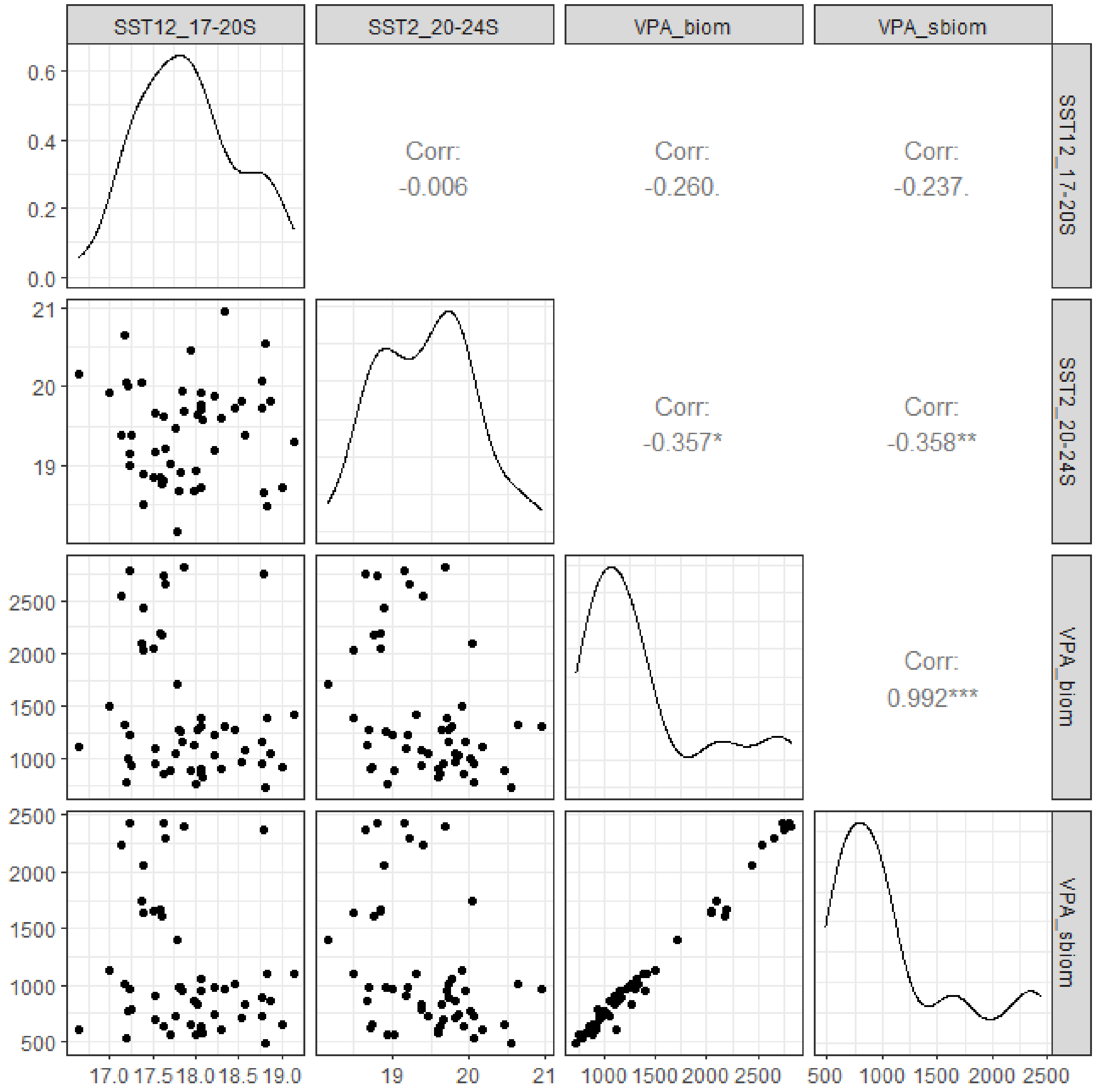


Figure D6. Scatterplots between Cape horse mackerel biomass (VPA_biom) and spawner biomass (VPA_sbiom) variable. Scatter plots demonstrates the significant correlation between Cape horse mackerel biomass (VPA_biom) and spawner biomass (VPA_sbiom) in the northern Benguela. Thus, either Cape horse mackerel biomass (VPA_biom) or spawner biomass (VPA_sbiom) can be used in the model.

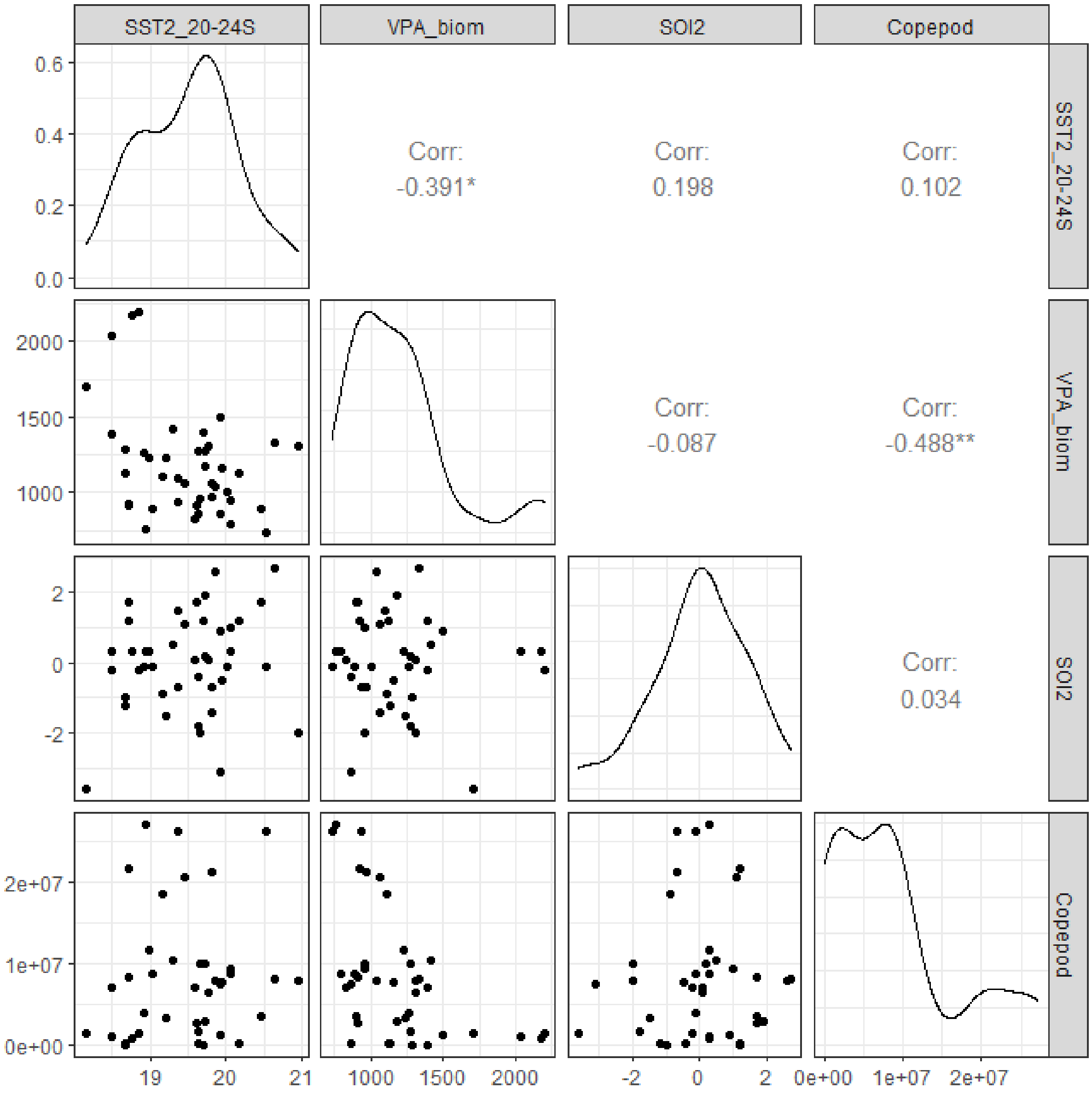


Figure D7. Scatterplots demonstrates the significant negative correlation between copepod abundance and Cape horse mackerel biomass (VPA_biom) in northern Benguela. It also demonstrates the negative correlation between Cape horse mackerel biomass (VPA_biom) and SST2_C (SST in February for central Namibia). This implies that either copepod abundance or Cape horse mackerel biomass (VPA_biom) can be used in the model. It also implies that either Cape horse mackerel biomass (VPA_biom) and SST2_C (SST in February for central Namibia).

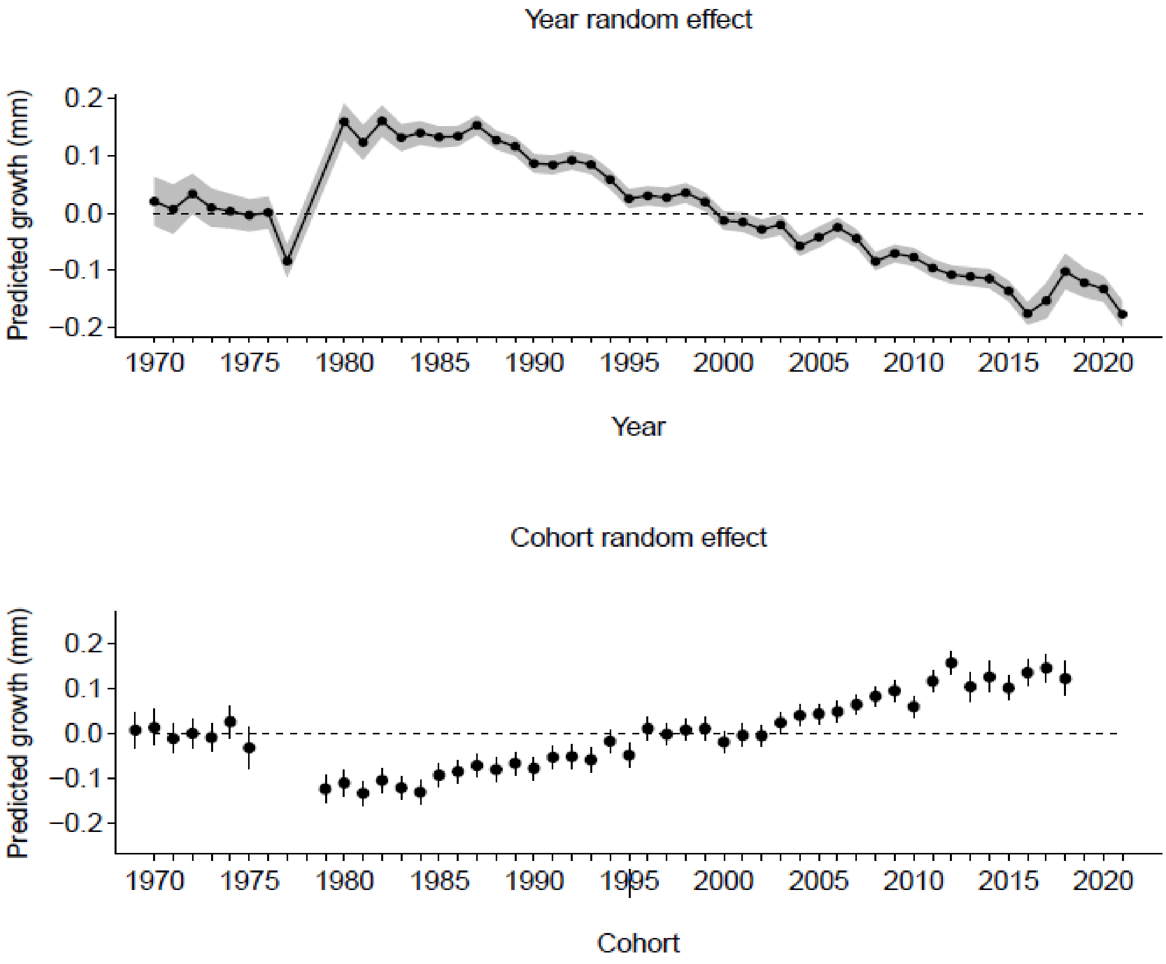


Figure D8. The year and cohort effects illustrating the model’s 'cancelling out' behavior. Consequently, the cohort effect was removed due to its impact on the year effect (Table D1).

Table D1. Results of intrinsic effects for selction of random effects optimal base model fitted to horse mackerel otolith data from 1970-2021 including Age (Number of observations = 3066, groups: FishID = 608; fYear = 50). Random age slopes for FishID, Cohort and Year are denoted by "|". K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; Res.LL = restricted log likelihood; Cond.R^2= conditional R^2, assessing variance explained by random effects.

Fixed effects	Random effects	K	AICc	ΔAICc	Res.LL	Cond.R^2
Age, AAC	Age|FishID, Age|Year, Age|Cohort	11	-3514.89	0	1772.53	0.974
Age, AAC	Age|FishID, Age|Year, 1|Cohort	13	-3240.75	274.15	1633.43	0.997
Age, AAC	Age|FishID, 1|Year, Age|Cohort	13	-3212.51	302.38	1619.32	0.998
Age, AAC	Age|FishID, 1|Year, 1|Cohort	11	-3196.41	318.49	1609.25	0.998
Age, AAC	**Age|FishID, Age|Year,**	**12**	**-3072.93**	**441.97**	**1548.52**	**0.905**
Age, AAC	Age|FishID, 1|Year	10	-2589.83	925.06	1304.95	0.875
Age, AAC	Age|FishID, Age|Cohort	12	-2364.62	1150.28	1194.36	0.830
Age, AAC	Age|FishID, 1|Cohort	10	-2359.91	1154.98	1189.99	0.830
Age, AAC	Age|FishID	9	-2351.1	1163.80	1184.58	0.830
Age, AAC	1|FishID	7	-2311.31	1203.58	1162.67	0.820

Note: The model chosen is indicated in bold, was chosen because it had the lowest AICc when excluding cohort since the most parsimoneous model showed opposite effects of year and cohort random effects, effectively "cancelling out" each other (Figure D8)

Table D2. Results of extrinsic fixed-effects (Age, Sex, SST, upwelling index, copepod abundance and Cape horse mackerel biomass) fitted to data from 1970-2021 (Number of observations: 3066, groups: FishID, 608; Year, 50). Best models (in bold) were selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; SST1_20-24S = Monthly SST for January at 20-24º S; SST2_20-24S = Monthly SST for February at 20-24º S; SST1_17-20S = Monthly SST for January at 17-20º S; SST2_17-20S = Monthly SST for February at 17-20º S; SST3_17-20S = Monthly SST for March at 17-20º S; Biomass = Annual Cape horse mackerel biomass from stock assessment model and SOI2 = Monthly Southern Oscillation Index for February.

a) Environmental factors fitted to data from 1970-2021

Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SST2_17-20S, Biomass	11	-3103.71	0	1562.90	0.902
BM + SST2_17-20S	10	-3103.48	0.24	1561.78	0.902
BM	**9**	**-3103.46**	0.26	**1560.76**	**0.902**
BM + SST2_17-20S, SOI2	10	-3102.93	0.79	1561.50	0.902
BM + SST2_17-20S, Biomass, SOI2	10	-3102.33	1.38	1561.20	0.902
BM + Biomass	11	-3102.05	1.66	1562.07	0.902
BM + SOI2	12	-3102.05	1.66	1563.08	0.902
BM + Biomass SOI2	11	-3101.6	2.12	1561.84	0.902
BM + SST3_17-20S, Biomass, SOI2	12	-3099.58	4.13	1561.84	0.902

Note: The most parsimonious model, indicated by being in bold, was chosen as the lowest AICc or a ΔAICc < 2 compared to the model with the lowest AIC, and two fewer parameters (K) than the model with the lowest AIC.

Table D3. Results of extrinsic fixed-effects (Age, SST, upwelling indices, copepod abundance and Cape horse mackerel biomass) fitted to data from 1980-2018 (Number of obervations = 2780, groups: FishID = 558; Year = 39). Best model (in bold) were selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects; BM = Best Optimal Base Model; SOI2 = Southern Oscillation Index Feb; SST2_20-24S = Monthly SST for February at 20-24° S; Biomass = Annual Cape horse mackerel biomass.; WBUI10-2 = Monthly upwelling index averaged for Oct-Feb at Walvis Bay; log(Copepod) = log of Copepod abundance.

a) Environmental factors fitted to data from 1980-2018

Fixed terms	K	AIC	ΔAICc	LL	Cond.R^2
BM + SST2_17-20S	10	-2859.28	0	1439.68	0.91
BM + WBUI10-2, log (Copepod)	10	-2859.19	0.09	1439.63	0.91
BM	**9**	**-2858.13**	**1.15**	**1438.10**	**0.91**
BM + SST2_20-24S, log(biomass), WBUI10-2	11	-2858.11	1.17	1440.10	0.91
BM + SST2_20-24S, WBUI7	11	-2857.62	1.66	1439.86	0.91
BM + SST2_20-24S, log(biomass),	11	-2857.58	1.70	1439.84	0.91
BM + WBUI7, WBUI10-2	11	-2857.38	1.90	1439.74	0.91
BM + WBUI7	10	-2856.48	2.80	1438.28	0.91
BM + SST2_20-24S, log(biomass), WBUI7	12	-2855.88	3.40	1439.99	0.91
BM + log(biomass), WBUI7	11	-2855.16	4.12	1438.63	0.91

Note: The most parsimonious model, indicated by being in bold, was chosen as the lowest AICc or a ΔAICc < 2 compared to the model with the lowest AIC, and two fewer parameters (K) than the model with the lowest AIC.