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Growth rate extremes of a Sciaenid in an ocean-warming hotspot

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Abstract

Argyrosomus inodorus is a cool water Sciaenid, important to the recreational and commercial coastal fishery in Namibia, the northern Benguela. Given recent findings on the northern Benguela as an ocean-warming hotspot and *A. inodorus* being more sensitive to warm temperatures than its congeneric *A. coronus*, it is important to study long-term growth responses of this Sciaenid. We developed a 34-year otolith biochronology for *A. inodorus*. The linear mixed-effects models fitted to *A. inodorus'* otolith biochronology indicated that the best linear unbiased predictor of growth was significantly positively correlated with mean sea surface temperatures (SSTs) in September of the year of formation and significantly negatively correlated with mean summer SSTs (November y-1), in the central Namibian area (20-24°S, 12-14°E). Thus, faster annual growth was observed during warmer winter/spring temperatures (up to 16 °C) and slower growth was noted during warmer summer temperatures (> 16 °C). These results indicate that the species has a narrow range of thermal plasticity, and highlight the recent reductions in growth of this species in response to rapid thermal change observed in the ocean warming hotspot. Our findings suggest that *A. inodorus* would not be able to adapt readily with future climate warming predicted to happen and already happening along the northernmost part of the Namibian coast.

Keywords

Argyrosomus, Benguela, biochronology, Otoliths, Ocean warming, Tolerance range

Highlights

- We described the relationship between SSTs and annual growth of *Argyrosomus inodorus* using otolith biochronologies
- *A. inodorus* grew faster in years with high winter SSTs (up to 16 °C) but slower in years with high summer SSTs (>16 °C)
- *A. inodorus* has a narrow temperature tolerance and is likely to react negatively to predicted ocean warming over time

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1. Introduction

Human-induced climate change has been placing immense pressure on exploited fish stocks (Fincham et al., 2013) with increasing ocean temperatures being one of the main concerns for marine species (e.g., Sims et al., 2004; Pankhurst and Munday, 2011; Potts et al., 2014a, b; Latif et al., 2016; Smoliński and Mirny, 2017; Denechaud et al., 2020). Average global ocean temperature is predicted to increase by about 3.0 °C by the year 2100 (Hoegh-Guldberg and Bruno, 2010), and will drive sea level rise (0.5–1.2 m by 2100), enhance ocean stratification, decrease the extent of sea-ice, and alter the patterns of ocean circulation, precipitation, and freshwater flux into the ocean (e.g., Doney et al., 2012; Bordbar et al., 2015; Smoliński and Mirny, 2017; Denechaud et al., 2020).

Evaluating and understanding how fish populations adapt and respond to climate change is critical for adaptive management plans. Broadly, fish populations are thought to respond to climate changes by altering their abundance (e.g., Lloyd et al., 2012), spatial distributions (e.g., Campana et al., 2020), demography (e.g., Otero and Hidalgo, 2023), physiology (Duncan et al., 2019), behaviour (Guzzo et al., 2017) and phenology (Fincham et al., 2013). Changes in the growth of fish species is a critical factor that will influence their demography (Ohlberger et al., 2022). Therefore, managing future fish populations will require an understanding of the factors that influence growth rates. However, the factors that determine somatic growth can often be difficult to detect due to multiplicity of possible natural stressors, anthropological activities, such as exploitation (e.g., Lorenzen and Enberg, 2002; Enberg et al., 2012) as well as the varying responses of organisms at individual, population, species, and group levels (Morrongiello and Thresher, 2015).

Despite the difficulties of detecting the drivers, the dendrochronology approach is useful to understand environmental drivers of spatio-temporal variations in the growth of fishes, particularly because it is possible to examine variation in population growth (Morrongiello and Thresher, 2015). Here, the increments in the hard parts of marine organisms can provide long-term chronologies of growth, which is analogous to tree rings (e.g., Dean, 1997; Black et al., 2005; Gillanders et al., 2012). In fishes, the dendrochronology technique measures the width between annulus rings of fish otoliths and uses this measurement as a proxy for somatic growth. This approach delivers long-term data on a fish' response to environmental or biotic factors because annual otolith growth can reflect the condition of a fish' physical environment during its growth period and thus otolith chronologies can be used to examine the relationship between temperature or other environmental or biotic drivers and fish growth (e.g., Matta et al., 2010; Neuheimer et al., 2011; Morrongiello et al., 2012; Gillanders et al., 2012; Black et al., 2013; Tanner et al., 2019; Wilhelm et al., 2020; Brinkman et al., 2025a).

Namibia's marine waters are among one of the richest in the world, in part, driven by the nutrient-rich Benguela Current, which is an eastern boundary upwelling system (EBUS) along the south eastern Atlantic Ocean bordering Angola, Namibia, and South Africa. The upwelling across this region is primarily wind-driven and characterised by several distinct upwelling cells. The Benguela upwelling system is divided into two distinct regions by the Lüderitz Upwelling Cell; namely the northern Benguela upwelling system (nBUS) and southern Benguela upwelling system (sBUS) (Shannon 1985; Duncombe Rae, 2005; Hutchings et al., 2009; Brandt et al., 2024). Marine ecosystems across EBUSs are believed to be vulnerable to climate change (Lima et al., 2019; Brandt et al., 2024). This has been demonstrated over the past decades in the northern Benguela, where the rapid ocean warming (0.8 °C per decade) and increased thermal variability, driven by the periodic intrusion of the warm Angola Current waters at the Angola-Benguela Frontal Zone (ABFZ) ocean current convergence, has been recognised as a global marine hotspot (Hobday and Pecl, 2014; Yemane et al., 2014; Potts et al., 2014a; Brandt et al., 2024). The warming sea surface is believed to be caused by an increasing strengthening of the Angola Current and weakening of the Benguela Current and in doing so, affect the seasonality and displacing the ABFZ southwards (Potts et al., 2014a; Koseki et al., 2018, 2019). This warming trend and subsequent shift in the position of the ABFZ has an influence on the distribution (Potts et al., 2014a), reproduction (e.g., Sims et al., 2004; Pankhurst and Munday, 2011; Potts et al., 2014b) and productivity of several species. While the northern boundary of the northern Benguela, the ABFZ, is warming rapidly, the Lüderitz Upwelling Cell, the southern boundary of the northern Benguela, is strengthening and cooling (Lamont et al., 2019). It is therefore likely that the convergence zone between the northern Benguela and the Lüderitz Upwelling Cell may be a thermal refuge for some species.

The linefishery (fishery where fishes are captured using hook and line) in Namibia, comprised of commercial, recreational and subsistence subsectors, is of great economic importance, but also essential for livelihoods (Kirchner et al., 2000; Stage and Kirchner, 2005; Khan, 2023; Gusha et al., 2024; Engelhard et al., 2024). The dominant recreational and commercial linefish species in the northern Benguela is the silver kob *Argyrosomus inodorus* (Sciaenidae), and to a lesser extent, its congener, the west coast dusky kob *A. coronus* (Griffiths and Heemstra, 1995; Kirchner, 1998; Potts et al., 2010). *Argyrosomus* spp. in Namibian waters have been exploited for many decades, with the first land-based records recorded in 1964 (Kirchner, 1998; Kirchner et al., 2001a), and records from the "Sea Around Us" database (https://www.seaaroundus.org/data/) show catches were made as far back as 1950 (Heymans and Sumaila, 2007).

A. inodorus has a size and age at maturity of 35–36 cm and 1.5–1.6 years, for females and males respectively (Kirchner et al., 2001b), with females thus appearing to grow slightly faster than males (Kirchner and Voges, 1999). *A. inodorus* is a cool-water species with a Namibian distribution ranging from 18^{o}S to 26^{o} S occurring in the surf zone at depths less than 20 m due to the anoxic conditions in Namibia at depths greater than 20 m. In contrast, the warmer water species, *A. coronus*, is found from 0.8°S to 23^{o}S in central Namibia (Potts et al., 2010, 2014a; Beckensteiner et al., 2016; Henriques et al., 2018). However, there is evidence to suggest that the southward part of the distribution has only been occupied recently, possibly due to a climate driven distributional shift (Griffiths and Heemstra, 1995; van der Bank and Kirchner, 1997; Kirchner, 1998, 2001; Kirchner and Beyer, 1999; Kirchner and Holtzhausen, 2001a). *A. inodorus* undergo annual spawning migrations from the SCNP (17°14'S to 21°11'S) area southwards to Sandwich Harbor (23°46'S) and Meob Bay (24°31'S) (Fig. 1) during austral summer (October–April). This migration is thought to be triggered by a change in temperature (Kirchner and Holtzhausen, 2001b). In winter, the adult stock is believed to move northwards again to feeding grounds in the Skeleton Coast National Park (SCNP). The increasing overlap between the adult stock of *A. inodorus* and the poleward shifting *A. coronus* due to the steadily warming waters and southward shift of the ABFZ has resulted in species mixing and appears to have resulted in hybridization between the species (F1 and backcrosses) (Potts et al., 2014a;

Henriques et al., 2018). In a recent metabolic physiology study, Pringle et al. (2023) suggested that the two species and their hybrids have different responses to warm temperatures, with *A. inodorus* found to be less tolerant to the warming conditions when compared to *A. coronus* and their hybrids (Pringle et al., 2023).

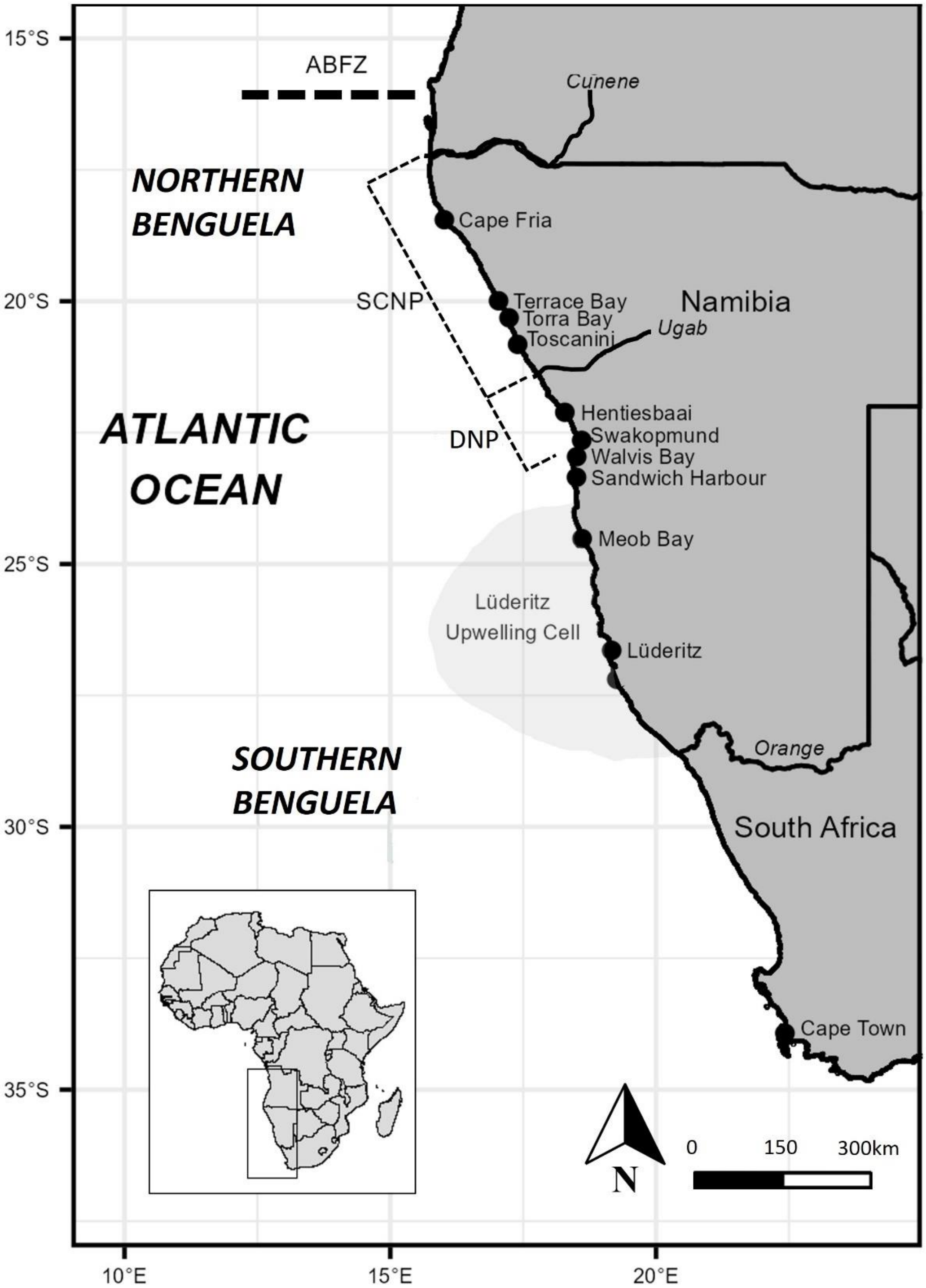

Figure 1. Map of the Namibian coast with Meob Bay, the Dorob National Park (DNP), and Skeleton Coast National Park (SCNP) indicated.

Given the rapid climate warming, and the seemingly reduced tolerance to warmer conditions, the aim of this study was to better understand the relationship between temperature and the growth of silver kob, *A. inodorus*, in order to understand their likely growth response to environmental change in the rapidly warming northern Benguela region. To do this, we viewed otolith biochronologies and then compared growth rate patterns with environmental conditions, including sea surface temperatures (SSTs), upwelling indices and a catch-per-unit effort time series.

2. Materials and methods

The care and use of animals complied with Namibian animal welfare laws, guidelines and policies as approved by National Commission for Research Science and Technology (NCRST), Namibia authorisation number: 20190204; University of Namibia Decentralised Ethics Committee (Reference number: SNC0002 of University of Namibia, 2021) and the Rhodes University Animal Research Ethics Committee (RU-AREC), reference number: 2019-0174-271.

2.1. Study area and sample sizes

This study was conducted in the northern Benguela region, from the SCNP (17°14’S to 21°11’S) in northern Namibia to the Dorob National Park in central Namibia (21°11’S, 13°38’E to 23°19’S, 14°29’E) and then in Meob Bay (24°31’S) (Fig. 1). A total of 236 individuals of *A. inodorus* were randomly and opportunistically collected from fish catches of recreational and commercial fishers between September 2018 and August 2019. In addition, 89 archived otoliths were prepared for an otolith biochronology (Table 1). No fish were collected from the southern region (Meob Bay, see Fig. 1) during the contemporary period because of sampling permit restrictions. Thus, the contemporary samples only represented the central and northern regions as defined by Kirchner and Voges (1999) and were categorised as such (Table 1).

For each fish, the species (as per external features), the total fish length (TL, to the nearest cm), the sex (when possible), and the approximate catch location was recorded. Otoliths were removed and stored dry in labelled envelopes after they were cleaned of any residual material. Most of the otoliths were collected during the austral summer months, from November to April (Table 1), the period of the highest catches in the fishery (Kirchner, 1998) (Table 1). *A. inodorus* ranged in size from 33.5 to 99.9 cm TL and from 34.2 to 91.0 cm TL (historical and contemporary, respectively) with only 60 of the 236 contemporary samples being juveniles (Table 1).

Table 1. Number of *Argyrosomus inodorus* (determined after genetic and otolith shape analysis) used for final analysis per month during the historical (1994-1996) and contemporary (September 2018 – August 2019) periods in the different sampling regions, northern and central, 17-23°S (N&C), and southern, 24-25°S (S) Namibia. For the contemporary period, also indicated is the sample size of mature (adults), and fish are immature fish (juveniles)

Year	**Month**	**1994-1996**		**2018-2019**	
		N&C	**S**	**N&C**	
				Adults	**Juveniles**
2018	Sep	0	0	1	0
2018	Oct	12	0	9	1
2018	Nov	19	1	25	2
2018	Dec	12	0	6	0
2019	Jan	2	1	21	0
2019	Feb	8	8	25	12
2019	Mar	3	3	32	19
2019	Apr	3	9	38	10
2019	May	4	2	10	8
2019	Jun	0	0	6	0
2019	Jul	0	2	3	7
2019	Aug	0	0	1	1
	Total	**63**	**26**	**176**	**60**

*Note: The historical samples were otoliths collected by MFMR during the 1994–1996 linefish data collection period. The mature fish were those either classified as gonad stages 2 + or above the length at 50 % maturity of 35 cm total length (Kirchner et al., 2001b).

2.2. Species identification

Species were identified either by molecular genotyping, using mitochondrial DNA and five nuclear microsatellite loci (n = 202) (Jagger, 2024), or by otolith shape analysis using a test sample of 217 fishes of known genotype (Wilhelm et al., 2025) when DNA material was not available (n = 34). Only those individuals that were assigned as “pure” *A. inodorus* genotypes were used for the present study.

2.3. Otolith preparation and increment measurements

The otoliths were embedded in clear casting polyester resin and longitudinally sectioned at approximately 0.5 mm thick through the primordium (otolith core) with a low-speed double-bladed, diamond-edged saw. Otoliths were sectioned longitudinally (see Fig. 2), instead of laterally, using the method for *Argyrosomus* in southern Africa established by Kirchner and Voges (1999), based on Griffiths (1996a); (1996b). The thin sections were mounted onto glass slides with DPX mountant for microscopy and then photographed using reflected light against a black background (Kirchner and Voges, 1999). Two camera-attached stereo microscopes, a Zeiss Stemi DV4 microscope with an AxioCam ERc 5s at up to 160 x magnification or an Olympus SZ61 microscope with an Olympus SC30 camera were used to photograph the otoliths at up to 200 x magnification. Two different microscopes and cameras were used due to their availability at different times during Covid-19 lockdown restrictions.

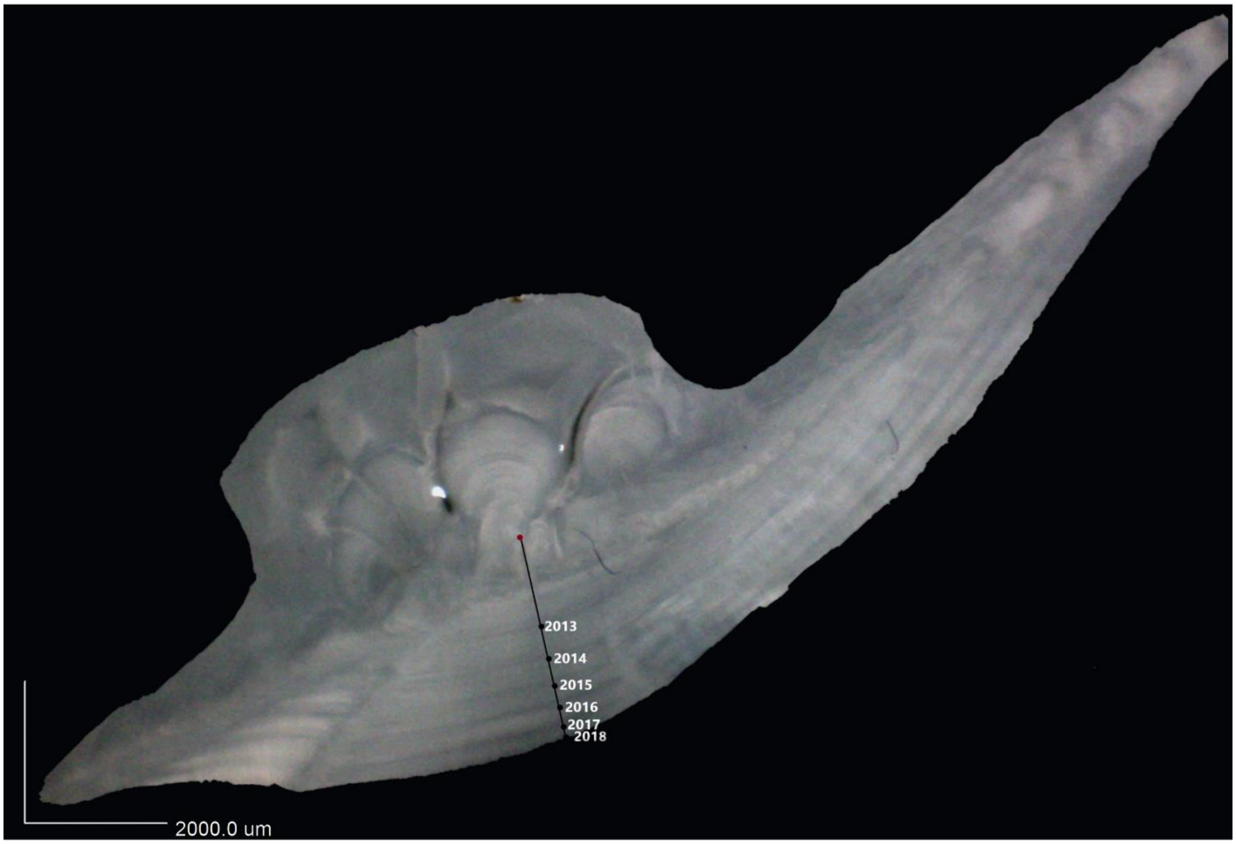

Figure 2. Thin section of an otolith of a 5-year-old *Argyrosomus inodorus* caught in central Namibia in 2019. Annual growth increments and their calendar years assigned are indicated.

Sectioned otoliths comprised of broad opaque zones and narrow translucent zones and showed clear, visible growth rings (Fig. 2). Otolith increments were measured manually using the Image processing package ImageJ version 1.53a (http://imagej.nih.gov/ij/) (Abràmoff et al., 2004) with the ObjectJ version 1.05e (https://sils.fnwi.uva.nl/bcb/objectj/index.html) plug-in. A similar method to Wilhelm et al. (2020) for increment measurements was used, and each increment was defined as the distance from the end of the translucent zone (beginning of the opaque zone) to the end of the next translucent zone so that each annual increment contained an opaque and a translucent zone. Each complete growth increment was measured from the nucleus to the dorsal edge perpendicular to the annual growth zone along the medial section of the otolith (Fig. 2). Each individual fish was assigned a final age-at-capture (AAC) (number of complete growth increments) and Cohort (Year of birth of the fish = Year of Capture – AAC) after the increments were marked and measured. Otolith increment width measurements in mm

(Inc) were assigned an age and calendar year at the time of increment formation (Year) (Morrongiello and Thresher, 2015).

2.4. Environmental data

Mean monthly SSTs were extracted from the NOAA National Centre for Environmental System (NCEP) database http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.sst/ (Reynolds et al., 2002). Monthly averages from January 1982 to December 2018 were calculated for two areas: Northern (17–20°S, 10–12°E) and Central (20–24°S, 12–14°E) Namibia. Additionally, we used surface wind field data from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 product from 1979 to 2021 to estimate the wind-driven upwelling indices, including upwelling associated with alongshore wind stress near the coast and the divergence of Ekman transport offshore. The former is limited to a narrow coastal strip of a few tens of kilometres, whereas the latter covers a few hundred kilometres offshore and is shown to be proportional to the local wind stress curl (Bordbar et al., 2021, 2023). Both upwelling indices were derived from the cross-shore integral of upwelling from the coast to the offshore distance where the long-term mean of the wind stress curl becomes zero.

The monthly time series of several climate variability indices, including the Antarctic Oscillation Index (AAO), the Southern Oscillation Index (SOI), and the multivariate El Niño index (MEI), were also used in this study. These indices were obtained from https://climexp.knmi.nl/start.cgi for January 1982 to December 2018. The Southern Oscillation is an important climatic index which measures air pressure (sea level pressure) difference across the Pacific Ocean from the south-east in Tahiti to the west in Darwin, Australia (Power and Kociuba, 2011).

A mean annual catch-per-unit-effort (CPUE) time series for *A. inodorus* was used as indicator of overall stock size in central Namibia, collected by the Ministry of Fisheries and Marine

Resources, Namibia, roving creel surveys, based on Kirchner and Beyer (1999), available from October 1995 to September 2017 (M.R. Wilhelm, unpublished data).

2.4. Data analysis

In order to verify the "annual" increment (what time period constitutes a year of growth), edge analysis was performed. The proportion of otoliths with a translucent zone on the edge was plotted against month, separated by juvenile (immature) and adult (mature) fish identified as mature either by their gonadal stage (stage 2 +) or by their size when gonadal stage was not available, above the length at 50 % maturity (35 cm total) length being considered mature (Kirchner et al., 2001b), see Table 1. Proportions of translucent zones against month were visually inspected for an annual peak for age verification.

Prior to modelling, otolith increment width in mm (Inc), Age (at increment formation) and Age-at-capture (AAC) were log-transformed to satisfy normality assumptions and all continuous variables were mean centred Morrongiello and Thresher, 2015). Increment width (Inc), the response variable, was related to potential intrinsic (ontogenetic or individual-specific) and extrinsic (environmental or intra- or interspecific interactions) sources of variation for *A. inodorus* annual growth rates in a linear mixed effects model (Morrongiello and Thresher, 2015). Intrinsic factors included Age, AAC, Sex (either male or female or unsexed), allowing for the interaction between Age and Sex, and FishID (each specific fish had a unique identification). The Age, AAC, Sex and Area (North-Central or South) variables were treated as fixed effects. The extrinsic effects were Cohort, Area and Year (of increment formation). The effects of Year, Cohort and FishID were treated as random effects (allowing for intercepts and slope $\log(Age)|$ or just intercept $1|$). The full model is shown in Eq. 1.

$$log\ (Inc) \sim \log(Age) * Sex + \log(AAC) + Area + \log(Age)\ |\text{FishID} + \log(Age)|\text{Year} + \log(Age)\ |\text{Cohort} \qquad (1).$$

A method modified from Morrongiello and Thresher (2015) was used to test for the best possible combination of the explanatory variables, testing all possible combinations of fixed effects and random effects, and intercept or slope for random effects (Morrongiello and Thresher, 2015). This modelling approach considers the hierarchical structure of the biochronological data (repeated measurements of otolith annual increments from one individual, year, or cohort) and allows for robust assessment of different sources of variation (Morrongiello and Thresher, 2015). The lowest Akaike's Information Criterion corrected for small sample sizes (AICc) was used to select the most parsimonious model (all combinations of Eq. 1) – fitted with maximum likelihood (Akaike, 1973; Burnham and Anderson, 2002; Johnson and Omland, 2004; Zuur et al., 2009). A change in AICc of > 2 was considered significant. The optimal selected model was refitted with restricted maximum likelihood (REML) to produce unbiased parameter estimates (Zuur et al., 2009), using the random effects of year to produce the best linear unbiased predictor of annual otolith growth (BLUP) 1981–1995, 2000–2018), n = 1532 growth increments, groups FishID = 326, Years = 34.

To examine the protentional effects of extrinsic environmental parameters on fish growth, a series of models were tested including SST, coastal upwelling, and the kob CPUE index. Due to the restriction of the length of the CPUE time series, this was done in two steps, first only including environmental indices (SST, upwelling, AAO, SOI), n = 1529 growth increments, groups: FishID = 326, Years = 32, 1983–1995, 2000–2018; and second including the CPUE index (available 1996–2017) in addition to the environmental indices, n = 846 growth increments, groups: FishID = 247, matching environmental data with 17 years (2000–2017).

Initial exploratory correlation analyses showed that austral summer (October to March) and winter (July to September) monthly SSTs were strongly correlated within seasons, but not between seasons, i.e. a cold summer did not necessarily mean a following cold winter (Figure S1). SSTs from the central area were also strongly correlated with SSTs from the northern area in the same month (Figure S2). MEI was strongly correlated with SOI, but not AAO, and SOI and AAO were not correlated (Figure S3), while the SSTs as well as the Walvis Bay upwelling index were positively correlated with both the AAO and the SOI in both summer (Figure S4) and winter (Figure S5). The August Walvis Bay coastal upwelling index was negatively correlated with the central September SST (Figure S6), and the January Walvis Bay upwelling index was correlated with the central November and December SST (two months, and one month prior, respectively) (Figure S7). The Walvis Bay upwelling index was correlated with the Cape Columbine and Kunene upwelling index in both winter (Figure S8) and summer months (Figure S9). Thus, for testing potential effects of the environment on *A. inodorus* growth, only SST from central Namibia was used, and collinear indices were only used separately. When including environmental parameters, the random effect of year was removed to reduce the complexity of the models for the sample size (singular fit). It was also assumed that the effect of the year was included with the annual environmental or biological parameters. CPUE was log-transformed before being used as a co-variate.

All analyses were performed in R Version 4.3.0 (R Core Team, 2023) and RStudio version 2023.3.1.446 (Posit team, 2023), with libraries “lme4” (Bates et al., 2015), “AICcmodavg” (Mazerolle, 2023), “effects” (Fox and Weisberg, 2019), “GGally” (Schloerke et al., 2023), “latticeExtra” (Sarkar, 2008; Sarkar and Andrews, 2022), and “tidyverse” (Wickham et al., 2019; Wickham, 2023).

3. Results

Although few samples were available in August and September, it appeared that overall, an increase of proportion of translucent zones of mature fish was observed during austral spring and summer (October–March), with a peak in October, and the lowest proportion of translucent zones, i.e. highest proportion of opaque zones, formed in austral winter (Fig. 3).

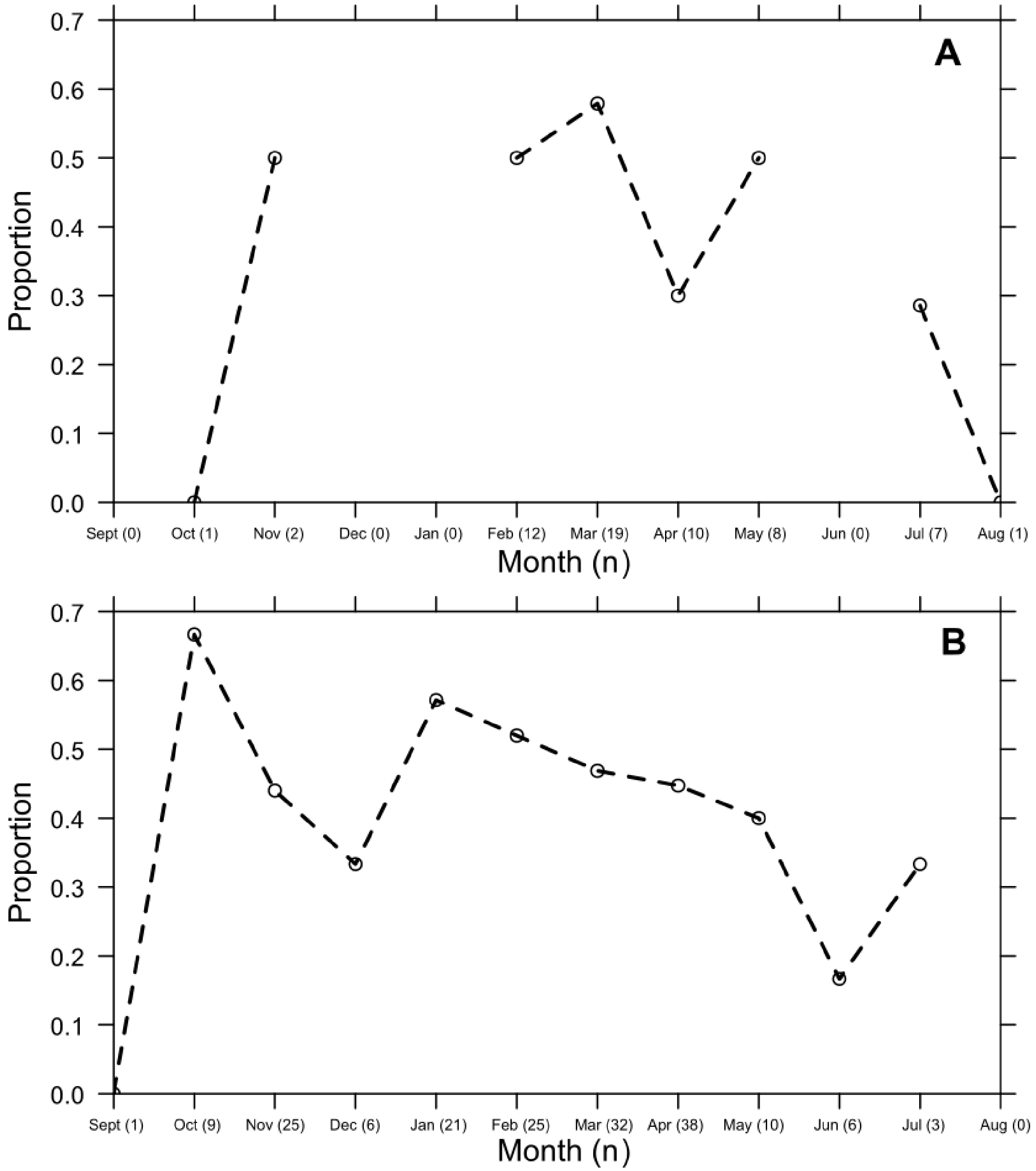

Figure 3. Proportion of translucent zone edges found on otoliths of A. immature and B. mature *Argyrosomus inodorus* and caught in the northern and central regions of Namibia from September 2018 to August 2019 against month. The numbers in parentheses indicate the number of otoliths sampled per month.

Based on a total of 1532 increments measured on 326 individual historical and contemporary *A. inodorus* otoliths (Figure S10), the most parsimonious base model was chosen (Table S1), including only significant variables (Table S2), for *A. inodorus*:

$$Log(Inc) \sim log(Age) + log(AAC) + log(Age)|FishID + 1|Year \qquad (2),$$

where Inc = increment width measurement in mm, Age = age at time of increment formation, AAC = age-at-capture, FishID = individual fish sample's unique identification, Year = calendar year of increment formation, 1| denotes random effect intercept for Year and Age| denotes slope and intercept for FishID (AICc = -126.94, Conditional R^2 = 0.682, Tables S1 and S2). Overall, the best supported model explained 68.2 % of variation in the annual growth of *A. inodorus*. Cohort and Area did not have a significant influence on the variation in growth (otolith increment width). Age had the greatest influence on growth among the tested variables (Table 2A, Fig. 4), but all fixed effects variables were highly significant (Table 2A).

Table 2. Optimal model parameter estimates and test statistics describing fixed and random sources of growth variation in *Argyrosomus inodorus* using restricted maximum likelihood (REML) caught along the Namibian coast during the historical (1994-1996) and contemporary (2018-2019) period without environmental parameters (A) and with environmental parameters (B).

A. Excluding environmental parameters (1981-1995, 2000-2018), n = 1532 growth increments, groups: FishID = 326, Years = 34

Fixed effects

Covariate	Estimate	SE	t-value	p-value
Intercept	-1.278	0.01594	-80.207	<0.0001
Log(Age)	-0.187	0.01607	-11.637	<0.0001
Log(AAC)	-0.340	0.03804	-8.939	<0.0001

Random effects

Covariate	Variance component	SD	Correlation
1|FishID (intercept)	0.0258	0.1607	
Log(Age)|FishID (slope)	0.0172	0.1313	-0.15
1|Year	0.0018	0.0422	
Residual	0.0344	0.1856	

B. Including environmental parameters (1983-1995, 2000-2018), n = 1529 growth increments, groups: FishID = 326

Fixed effects

Covariate	Estimate	SE	t-value	p-value
Intercept	-1.3318	0.2988	-4.456	<0.0001
Log(Age)	-0.1923	0.0125	-15.420	<0.0001
Log(AAC)	-0.3352	0.0340	-9.874	<0.0001
SSTC9	0.0565	0.0126	4.498	<0.0001
SSTClag11	-0.0477	0.0123	-3.881	<0.001

Random effects

Covariate	Variance component	SD	Correlation
1|FishID (intercept)	0.0261	0.1614	
Log(Age)|FishID (slope)	0.0180	0.1340	-0.16
Residual	0.0344	0.1854	

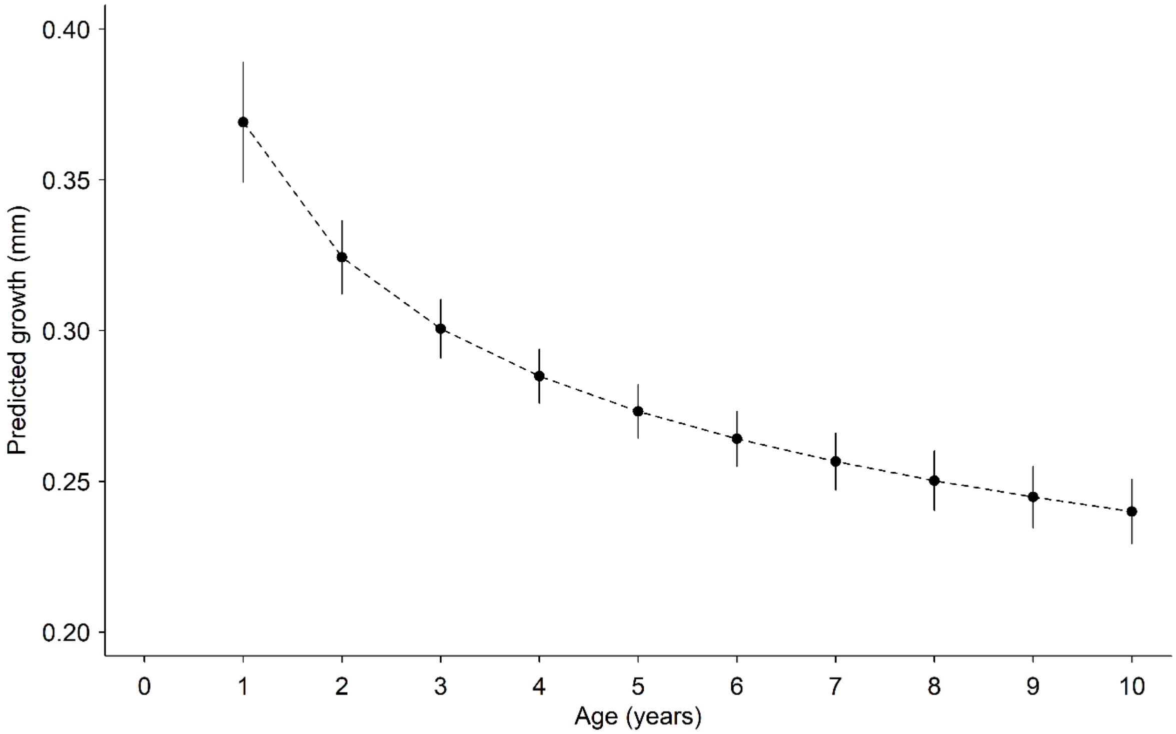

Figure 4. Predicted annual growth variation (mm) for *Argyrosomus inodorus* against age in years estimated in the full mixed effects model back transformed to the original scale.

The *A. inodorus* growth time series extracted from the best linear unbiased predictor (BLUP) (from the random effects intercept of Year) showed relatively low inter-annual variations of growth over the period 1981–1995 and 2000–2018 (34 years), but with below average growth for several years, in both historical and contemporary periods, most notably 2018; and above average growth in 1991, 1993 and 2008 (Fig. 5). Linear regression analysis showed a significant decline in otolith growth of 0.0007 mm per year (t = -2 .0375, df = 33, p = 0.0499).

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Jagger CE, Potts WM, Pringle BA, Bordbar MH, Henriques R, McKeown NH, Wilhelm MR. 2025. Growth rate extremes of a Sciaenid in an ocean-warming hotspot. *Fisheries Research.* DOI: 10.1016/j.fishres.2025.107366

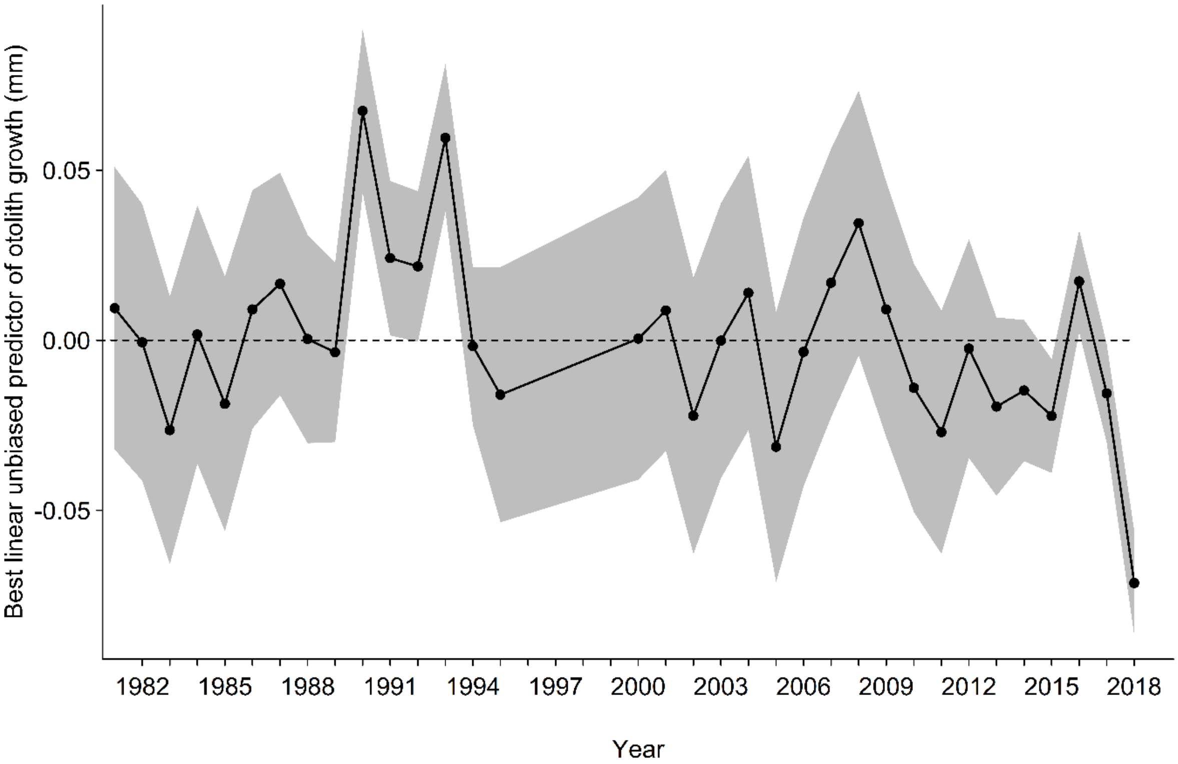

Figure 5. Best linear unbiased predictor of growth against year of *Argyrosomus inodorus* caught off Namibia estimated from the most parsimonious mixed effects model on otolith increments. The 95% confidence limits are indicated by the grey solid lines and the mean growth is indicated by the dashed grey line.

Inclusion of environmental parameters fitted to data from 1983 to 1995, and 2000 to 2018 showed that including both central Namibian SST of September (current year) and November (previous year) significantly decreased the AICc (AICc = -144.4, Conditional R^2 = 0.683, Table S3), with all variables highly significant (Table 2B). Synchrony between the predicted growth from the base model, as well as September and previous November SSTs are shown in Fig. 6A and B, respectively, with the final growth model showing a positive response of *A. inodorus* growth with September SST and negative response of *A. inodorus* growth with the previous November SST (Table 2B, Fig. 7).

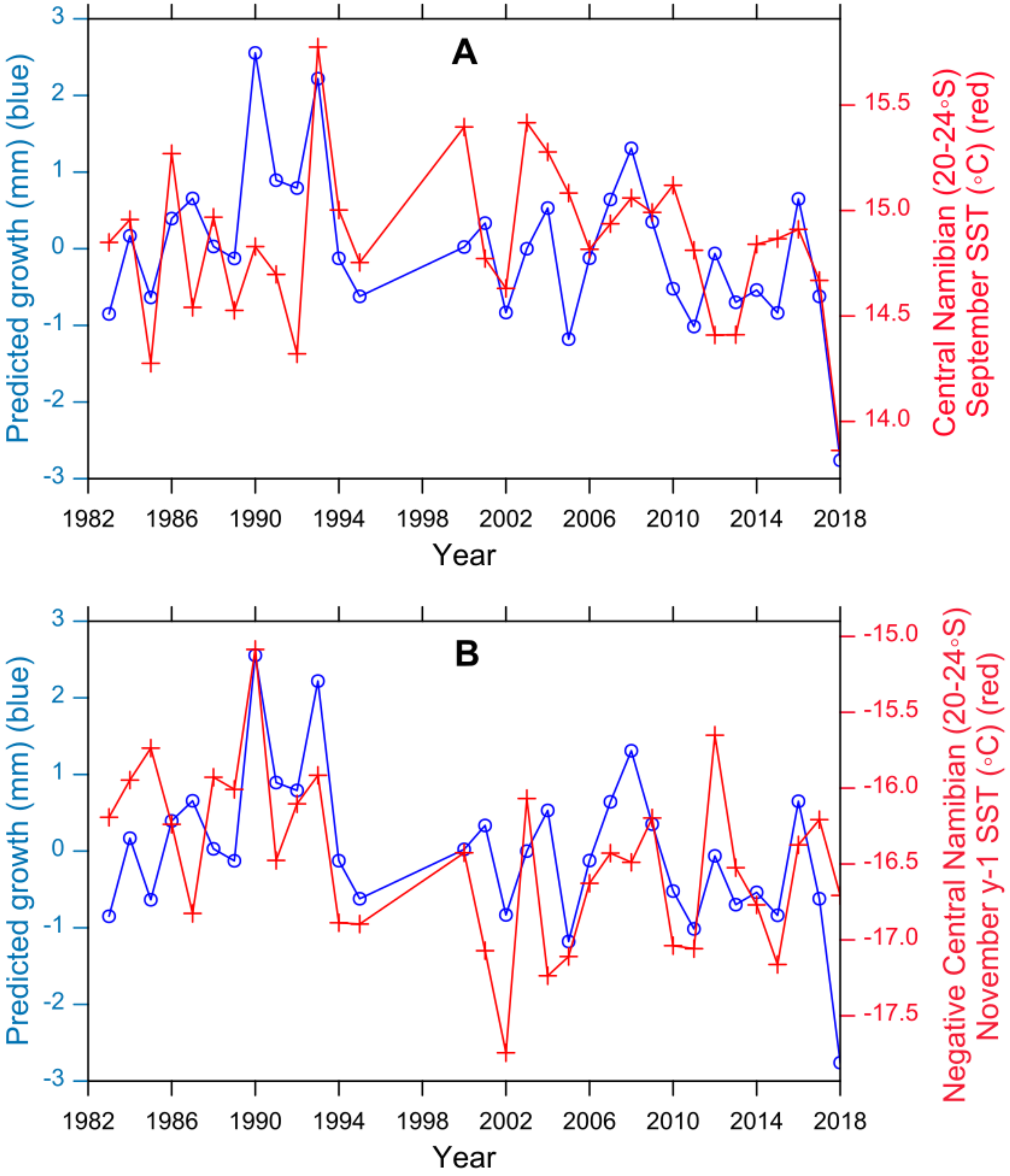

Figure 6. Best linear unbiased predictor (BLUP) of annual growth increments against year of growth for *Argyrosomus inodorus*, from Namibia, superimposed with (A) September (year of formation) SST and (B) lagged summer SST (November y-1) in the area 20–24˚S, 12–14˚E against year. In plot B, temperature is on a negative scale for visual effect.

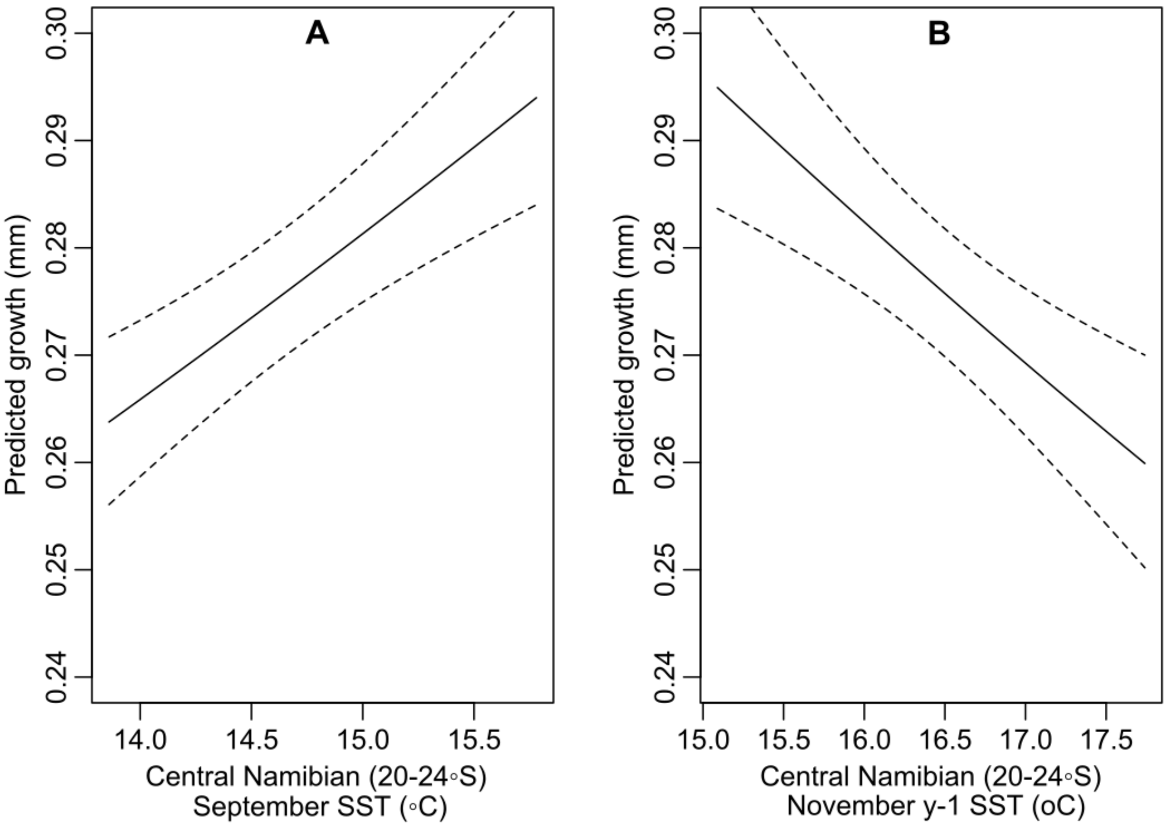

Figure 7. Model estimated relationship of *Argyrosomus inodorus* predicted growth with winter / cold (September) (A) and summer / warm (November y-1) (B) sea surface temperatures (SST) in central Namibia (20–24◦S, 12–14◦E).

Including CPUE, as well as the environmental parameters in the growth model fitted to data from 2000–2017 (n = 846 growth increments, groups: FishID = 247) also showed that central Namibian SST of September and November (previous year) explained most of the variation of *A. inodorus* growth, and CPUE did not significantly reduce the model AICc (Table S4).

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4. Discussion

The findings of this study showed that there has been a significant decline in the growth of *A. inodorus* between the 1980s and the end of the 2010s. During this time, the predicted growth for *A. inodorus* was significantly positively correlated with SSTs in September (coldest temperatures) and negatively correlated with SSTs in summer (November previous year). Based on these findings, it appears that the warming summer temperatures in recent years (2010s) may have negatively influenced the growth of the species. In addition, our results suggest that the growth of *A. inodorus* is related to the timing and movement of the Angola-Benguela frontal zone (ABFZ). These findings are in support of previous studies that showed temperature-dependent growth in marine fish (e.g., Pörtner et al., 2001; Matta et al., 2010; Smoliński and Mirny, 2017; Duncan, 2018), but not only increasing growth with increasing temperatures as for *A. japonicus* (Nicolle et al., 2022).

Marginal increment analysis suggested that growth increments of mature fish were formed in austral spring (October). This coincides with the onset of the six months protracted spawning season (October–March) for Namibia's *A. inodorus* (Kirchner and Holtzhausen, 2001b). The formation of a single opaque and translucent zone agrees with the findings from other *Argyrosomus* spp. growth studies in the Benguela, for example *A. japonicus* (Griffiths, 1996a); *A. inodorus* (Griffiths, 1996b; Kirchner and Voges, 1999) and *A. coronus* (Potts et al., 2010). This indicated that the growth period for this present study, measured from the end of the translucent zone to the end of the next translucent zone, was measured from October (previous year) to September (present year), explaining the correlations of growth in the present year with the previous year's summer (November) temperatures.

A. inodorus individual growth rates were significantly negatively related to the Age-at-capture (AAC) variable, indicating growth-rate-based selectivity of fishing occurring for this stock, namely that faster-growing fish are generally caught at younger ages than are slower-growing fish (Morrongiello and Thresher, 2015). This could mean a gradual fisheries-driven selection for slower-growing fish, and could partially explain the significant decline in growth of *A. inodorus* over the time period in the present study (1980–2019). However, since growth was not significantly related to CPUE as a measure of stock density, the trend is more likely explained by environmental changes over the time period.

Significant positive effect of cold temperatures (September) and negative effect of warm temperatures (November previous year) and no significant effect of upwelling on growth were identified in the present study. Given that the upwelling index and SST were correlated in lag and differently for summer and winter, it is worth noting that wind-driven upwelling is not the exclusive driver of SST. Other processes, such as lateral advection, radiation at the ocean surface, and ocean mixing, can also change the near-surface ocean temperature (Brandt et al., 2024), thus a strong indication that *A. inodorus* growth is directly linked with water temperature (rather than indirectly through upwelling). When considered together, it appears that the optimal growth temperatures for *A. inodorus* are narrow and likely range from only 15 to 16 °C, mostly observed throughout September. This finding supports a recent study by Pringle et al. (2023) showing that the aerobic scope of *A. inodorus* was highest at temperatures between 15 °C and 16 °C and sloped off after 18 °C, and suggesting that the aerobic scope of the species would decline rapidly above 24 °C with additional future ocean warming. Also, Dickens (2007) showed that the preferred temperature range of juvenile A. inodorus was 16.3–17.6 °C for the first cohort and 16.9–18.1 °C for the second. These findings explain the pattern seen in the present study, i.e. *A. inodorus* grew faster in warmer winters-springs (increasing growth up to 16 °C) but slower in warmer summers (decreasing growth > 16 °C).

While fast growth coincided with a cold austral summer and warm austral winter, the recent years (end of 2010s) indicated below average (significantly declined) growth for *A. inodorus*. This slower growth, especially in recent years, could be linked to the recent rapid warming observed in the northern boundary of the northern Benguela as well as to the weakening of upwelling intensity in the same area (Lima et al., 2019; Brandt et al., 2024). The rapid oceanographic changes predicted for the northern boundary of the northern Benguela will thus likely have negative implications for the *Argyrosomus* spp. and their fisheries. For example, the feeding grounds of *A. inodorus* in central and northern Namibia are predicted to become even warmer, which could further cause *A. inodorus* annual growth to decline with increased warming. This makes *A. inodorus* a potentially “sensitive” species (Izzo et al., 2016). It is therefore important to understand climate-induced temperature effects on growth performance (Pörtner et al., 2001) and it is critical that there is a continuous monitoring of the growth and composition of *Argyrosomus* spp. off Namibia, in order to incorporate climate-induced changes in fisheries management as well as to understand the consequences of rapid ocean warming on coastal fish and fisheries.

The findings in this study are not unique to the region. While deep water hake *Merluccius paradoxus* (Wilhelm et al., 2020) and sardine *Sardinops sagax* from the northern Benguela (Brinkman et al., 2025b) only showed positive responses of annual somatic fish growth to cold water temperatures and upwelling in winter and spring, sardine from the southern Benguela also showed positive responses of fish growth to warm winter temperatures and negative responses to warm summer temperatures (Brinkman et al., 2025a), similar to the growth responses of *A. inodorus* in the present study.

In conclusion, as a first for a coastal fish stock in the northern Benguela, this study showed the significant role of water temperatures on driving *A. inodorus*' annual growth through showing how their mean annual growth is negatively affected by both cold (< 16 °C) and warm (> 16 °C) water temperatures. The results suggest that *A. inodorus* growth rates will likely continue to decline with increased warming. A mechanistic understanding of this is therefore necessary to understand when SSTs and other environmental parameters will no longer be suitable for the growth and survival of *A. inodorus* in this ocean warming hotspot.

CRediT authorship contribution statement

Pringle, Brett A.: Writing – review & editing, Data curation. **Potts, Warren M.:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Jagger, Charmaine E.:** Writing – original draft, Funding acquisition, Formal analysis, Data curation. **Wilhelm, Margit R.:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **McKeown, Niall J.:** Writing – review & editing, Data curation. **Henriques, Romina:** Writing – review & editing, Data curation. **Bordbar, Mohammed Hadi:** Writing – review & editing, Data curation.

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Data availability

Data will be made available on request.

Appendix A Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107366

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