FEATURE ARTICLE

Long-term increase in growth of an estuarine predator, mulloway *Argyrosomus japonicus,* predicted to continue under future warming scenarios

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ABSTRACT: Understanding the effects of climate change on fish biology and ecology is crucial for effective management of fisheries resources. Estuaries are warming at a faster rate than nearby oceans in south-eastern Australia, yet there is little understanding of how this may impact the growth of estuarine fish. We examined long-term changes and drivers of growth in an ecologically and economically important estuarine fish in this region, the mulloway *Argyrosomus japonicus*, using a growth chronology spanning 39 yr (1980–2018). The chronology was developed using 3112 otoliths collected over 12° of latitude. Mixed effects models identified a long-term increase in the growth rate of *A. japonicus* spanning nearly 3 decades in south-eastern Australia and a positive growth response to temperature. Temperature during the months of November–February best explained this growth response, likely representing a specific growing season for the species. However, there also remained some variation in growth not explained by increasing temperature over the period. We also found evidence of faster growth in individuals sampled at both younger and older ages, potentially caused by selectivity mechanisms. Regional climate forecasts predict that, based upon the observed response to temperature, the mean annual growth rate of *A. japonicus* in south-eastern Australia may increase by up to 8.9% by 2099. These results add to the growing body of literature demonstrating positive growth responses by marine species in warming environments and highlight the value of understanding the drivers of long-term growth variation in exploited fish stocks in order to predict future productivity under a range of environmental and fisheries management scenarios.
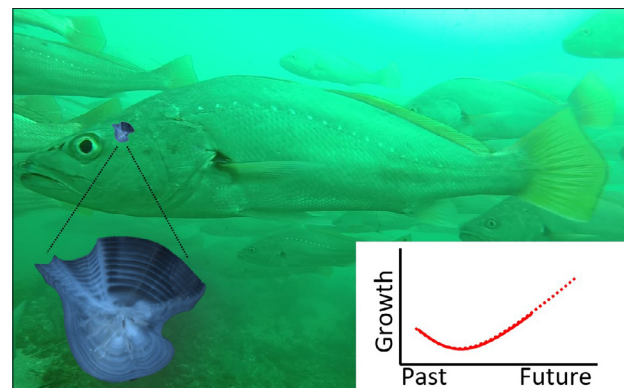
Growth histories hidden in the ear-bones of an estuarine predator (*Argyrosomus japonicus*) uncover decades of increasing growth rates, suggesting positive growth trajectories under future warming scenarios

Photo: D. van der Meulen. Graphic: P. Nicolle

1. INTRODUCTION

The ocean off south-eastern Australia is a global warming hotspot (Hobday & Pecl 2014), warming 3–4 times faster than the global average (Malan et al. 2021). Climate predictions for Australia's east coast also suggest a continued increase in mean air temperatures and more common heat waves as well as extended periods of drought (Evans et al. 2014). These

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changes are particularly evident in estuaries; key coastal ecosystems that are highly influenced by both neighbouring terrestrial and oceanic conditions (Gillanders et al. 2011, Statham 2012, Kimmerer & Weaver 2013). Estuaries in south-eastern Australia are warming at twice the rate of the neighbouring Pacific Ocean (Scanes et al. 2020). Understanding how environmental change affects estuarine species, both directly and indirectly, may help to better define individual species vulnerability to future change and inform conservation and fisheries management.

The rate at which organisms convert food to energy (metabolic rate) is directly influenced by environmental conditions such as temperature (Gillooly et al. 2001). Metabolic rates largely determine individual rates of growth, development, reproduction and many aspects of species ecology, including ecosystem levels of biomass production (The Metabolic Theory of Ecology; Brown et al. 2004, Clarke 2006). The Metabolic Theory of Ecology proposes that metabolic rate is a fundamental biological rate, controlling the majority of observed ecological patterns. Relationships between environmental variables and metabolic rates are often tested within a controlled laboratory setting, which generates a metabolic performance curve (Claireaux & Lagardère 1999, Sinclair et al. 2016, Lawson et al. 2018). Considering fishes' ectothermic physiology, such studies commonly focus on metabolic response to temperature changes, which can reveal a thermal optimum — the temperature above which an organism's metabolic function and linked physiological performance such as growth begin to decline (Pirozzi & Booth 2009, Vinagre et al. 2015). However, such laboratory studies are incapable of testing the metabolic responses of organisms in a natural setting or over large spatio-temporal scales (10s to 100s of km and years). Metabolically optimal and critical thermal temperatures in the wild often differ from those determined within laboratory settings due to the range of additional factors influencing physiological performance (Martin & Huey 2008, Sunday et al. 2012, Norin et al. 2014, Payne et al. 2016).

Biochronological studies generate long-term data from biological growth increments such as tree rings, revealing a temporally resolved individual growth history (Douglass 1941, Fritts 1971, Ricker et al. 2020) By combining long-term growth data with environmental data, historical archives of hard anatomical structures from long-lived individuals can provide insights into ecological responses over extended periods that are not possible to resolve in a contemporary experimental setting. One benefit of such long-term ecological data is the ability to test for stochastic and slowly manifesting changes such as climate change, and hence more accurately isolate drivers of growth throughout an individual's life history (Morrongiello & Thresher 2015). However, the nature of such investigations means that exact processes affecting growth may not be resolved. For example, faster growth may be linked to increasing environmental temperature, but whether this was driven directly through altered metabolic rate or indirectly through altered ecological interactions (e.g. increased prey availability), or some combination thereof, cannot be determined.

Otoliths are metabolically inert calcified structures found within the ear of all bony fish that can be used to develop growth chronologies. Increments are formed on an annual basis and can be counted to estimate age, a process extensively used in fisheries science (Campana 2001, 2005). The distance between otolith increments (widths) can be used to estimate growth because otolith growth usually correlates strongly with somatic (body) growth (Casselman 1990). Combining time series of annual increment widths across multiple fish provides a data set of temporally discrete annual growth estimates for a population. Examined through mixed effects modelling frameworks, the biological and environmental variables which affect growth can be examined (Morrongiello & Thresher 2015). This approach has been used to investigate long-term growth trends and environmental drivers for numerous fish species (Morrongiello & Thresher 2015, Barrow et al. 2018, Tanner et al. 2019, Morrongiello et al. 2021), but few studies have investigated large-bodied species inhabiting estuaries. Mixed effects modelling is required to investigate drivers of growth in fishes, given the numerous intrinsic and extrinsic factors involved. Annual growth rate is primarily dictated by age and decreases throughout life, with faster growth usually occurring before maturity is reached (Charnov 2008). Growth may also vary between individuals (Morrongiello & Thresher 2015), sexes (Silberschneider et al. 2009) and cohorts (Whitten et al. 2013), while being influenced by environmental factors like temperature (Morrongiello et al. 2014), rainfall/flow (Doubleday et al. 2015) and associated changes in productivity and food availability (Tanner et al. 2019).

Argyrosomus japonicus (mulloway) are predatory fish within the estuarine and near-shore environments of Australia, Africa, India, Pakistan, China, Korea and Japan (Silberschneider et al. 2009). The species is large (up to 75 kg and 180 cm), long-lived (over 40 yr old) and likely to play an important role in estuarine

ecosystem function via predator-mediated top-down control (Hughes et al. 2013). *A. japonicus* have significant economic, cultural and ecological importance throughout their global distribution (Griffiths & Heemstra 1995, Taylor et al. 2006). In New South Wales (NSW), Australia, they are a single genetic stock (Barnes et al. 2016) and a key species of the $3.4 billion annual recreational fishery (McIlgorm & Pepperell 2013), with approximately 90 t being retained each year by the recreational fishery (Murphy et al. 2020) and similar annual landings by the commercial harvest over the past decade (Earl et al. 2020).

Interannual variability in growth has been reported for *A. japonicus* (Izzo et al. 2016). Recruitment has also been linked to rainfall, with freshwater increases hypothesised to drive increases in ecosystem productivity and food availability (Stewart et al. 2020). Growth of the species has been linked to temperature in a laboratory setting (Pirozzi & Booth 2009), but the single previous field investigation was confined to one estuary and did not find any significant relationships between growth and environment (Izzo et al. 2016). Investigating the growth history of *A. japonicus* across a larger spatial and temporal distribution may capture a greater range of environmental conditions faced by individuals, improving power for detecting environment–growth relationships.

The aims of this study were therefore to (1) develop a multidecadal, annually resolved growth index for *A. japonicus* in south-eastern Australia using a biochronological analysis of otoliths; (2) examine potential biological and environmental drivers of growth variation in *A. japonicus* using a mixed effect modelling framework; and (3) apply climate model forecasts to predict how *A. japonicus* growth may be impacted by future temperature change in south-eastern Australia.

2. MATERIALS AND METHODS

2.1. Study area and sample collection

Argyrosomus japonicus individuals were collected from the south-east coast of Australia, between Fraser Island in Queensland and Eden in NSW (25.24–37.07°S; Fig. 1). This section of coastline spans more than 1500 km and contains hundreds of individual estuaries (Roy et al. 2001).

A. japonicus were collected via 2 NSW Department of Primary Industries (NSW DPI) sampling programs: the NSW Research Angler Program (using recreational hook and line methods) and the Commercial

Fisheries Port Monitoring Program (using commercial hook and line and mesh-netting methods). Between 1988 and 2018, all sampled *A. japonicus* were measured to the nearest 0.1 cm total length (TL) and the sagittal otoliths removed. For each individual, capture location and date information were also recorded. A total of 73 estuaries are represented in our data set. Otoliths and associated sampling data were accessed through the NSW DPI Otolith Archive.

2.2. Biochronology development and analysis

Prior to this study, otoliths from each fish were removed and processed as described in Silberschneider et al. (2009). Briefly, each otolith was set in epoxy resin (EpoFix), a transverse section was taken through the core with a diamond saw (Allied Tech-
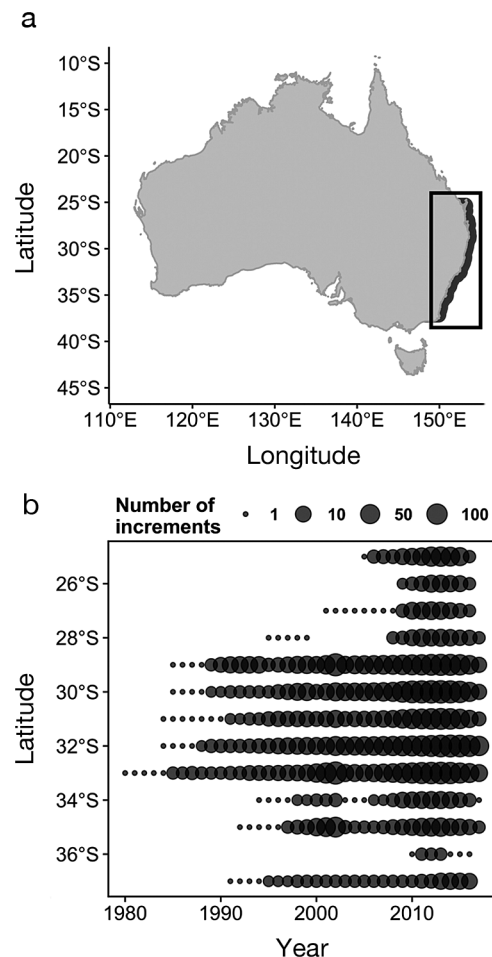

Fig. 1. (a) Sample collection area (black ribbon) in southeastern Australia from Fraser Island in Queensland (25.24°S) to Eden in New South Wales (37.07°S). (b) Number of otolith increments across 1° latitudinal bands and calendar years. Note the quasi-log scale of point size

cut 4) and then polished (Struers LaboPol 4) to reveal annual growth increments (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m688p001_supp.pdf). The section was then attached to a glass microscope slide and imaged using a dissecting microscope and mounted camera (QImaging MP5.0-RTV-CLR-10) under reflected light and constant magnification (6.70×). Starting from the core and then proceeding to the proximal edge, all otolith increment widths were measured for each otolith section (Fig. S1). Increment width was defined as the distance (µm) between the mid-points of 2 successive increments. The measuring process was performed using the ObjectJ package of Fiji 2 (Schindelin et al. 2012). Consistent with previous studies, first-year increment widths (core to first increment) and final year incomplete increment widths (Fig. S1) were omitted from the data set, as they are unlikely to represent a full growth year due to the temporal variability in birth and capture months (Morrongiello & Thresher 2015).

A marginal increment analysis (MIA) was performed to determine the timing of increment formation, and thereby define the growing season, for correlation with environmental data. MIA involves comparing the distance from the most recently completed (proximal) increment to the otolith edge and expressing this value as a proportion of the previous completed increment width throughout the year. A small MIA value suggests the proximal increment has formed recently. MIA results indicated that opaque increments in *A. japonicus* were fully formed by November each year (Fig. S2). A growth year was therefore assigned to be the 12 months starting on 1 November and ending on 31 October the following year. Environmental data could then be related to this growth year for analyses. *A. japonicus* are known to have very small movement ranges, and most indi-

viduals stay within single estuary systems (Hughes et al. 2022). Using this knowledge, we assumed the region of capture is consistent with where a fish spent the majority of its life, allowing us to align historical environmental data to each increment in the biochronology.

To confirm the relationship between otolith growth and somatic growth, an allometric validation was performed. The relationship between otolith accretion and somatic growth was quantified for the samples used in the present study by regressing total otolith radius (proximal; µm) against fish TL (cm). This analysis demonstrated a significant positive linear relationship (r = 0.91, p < 0.0001; Fig. S3), suggesting a 1 µm increase in otolith width is equivalent to a 0.23 mm increase in total fish length.

2.3. Statistical modelling

To investigate sources of growth variation within the otolith increment biochronology, linear mixed effect models were used following the procedure detailed in Morrongiello & Thresher (2015). This process allowed for the partitioning of multiple sources of variance, isolating the individual effects of biological, temporal and environmental factors. The models tested the degree to which otolith increment widths (µm; log-transformed) were explained by a range of intrinsic (Table 1) and extrinsic factors (Table 2). All continuous factors were centred and scaled to facilitate model convergence, and the non-independence of increments common to individual fish was addressed using the random model structure defined below. Forward stepwise model selection was conducted with Akaike's information criterion (AIC), balancing both the overall explanatory power and

Table 1. Intrinsic (biological and temporal) variables tested using mixed modelling (following Morrongiello & Thresher 2015)

Variable	Description	Variable type
FishID	Individual fish identifier. Accounts for non-independence of increments sourced from the same fish	Random: biological
Age	Biological age of fish when each increment was formed. Each increment has its own age	Fixed: biological
Age-at-Capture (AAC)	The age of each fish at capture. Accounts for potential growth selectivity	Fixed: biological
Cohort	Back-calculated spawning year (Year of Capture − AAC). Each fish has one Cohort value. Accounts for potential differences in growth rate among different cohorts	Random: temporal
Year	Calendar year of increment formation. Each increment has its own Year value	Random: temporal

Table 2. Environmental (extrinsic) modelling variables. All variables spanned 1980–2018, and all were fixed effects. Data sources: [1] BARRA reanalysis (Su et al. 2019); [2] ECMWF ERA5 reanalysis (4th Gen) (Hersbach et al. 2020); [3] Bureau of Meteorology Climate data archives (http://www.bom.gov.au/climate/enso/soi); [4] National Oceanic and Atmospheric Administration (NOAA) climate data archives (https://psl.noaa.gov/data/climateindices/list/)

Variable	Description	Data sources
Temperature	Spatially resolved mean monthly surface air temperature (°C)	[1], [2]
Max. temperature	Spatially resolved mean maximum monthly surface air temperature (°C)	[1], [2]
Rainfall	Spatially resolved total monthly average rainfall (mm)	[1], [2]
Climate indices	Mean monthly Southern Oscillation Index (SOI)	[3]
	Mean monthly Interdecadal Pacific Oscillation (IPO)	[4]
	Mean monthly Southern Annular Mode (SAM)	[4]
	Mean monthly Indian Ocean Dipole (IOD)	[4]

simplicity of the models. Models were built using the 'glmmTMB' package (Brooks et al. 2017) in R v.4.0.3 (R Core Team 2020).

Following Morrongiello & Thresher (2015), our modelling procedure first considered the degree to which intrinsic (biological and temporal) factors could explain growth. All models included the full intrinsic fixed effect parameterisation of Age and Age-at-Capture (AAC) (Zuur et al. 2009) as well a random intercept of FishID, after which forward stepwise model selection was used. Firstly, non-linear AAC fixed effect terms were tested for model improvement. Then, random intrinsic variables were tested with both fixed and random Age slopes. Once the best performing intrinsic model was determined, environmental variables were tested as fixed effects. The best performing environmental variable proceeded to the next modelling step, where other environmental variables were included in the same model. Model selection was based on AIC values; however, if AIC values were considered equivalent (difference < 2; Burnham & Anderson 2002), the simplicity of the model was considered so as to omit terms that provide little explanatory power from the final model. Where fixed effect terms were compared, maximum likelihood estimation was fit to each model; alternatively, when random terms were compared, restricted maximum likelihood was fit. Effect size estimates and p-values are presented for all fixed terms in the final model.

2.4. Intrinsic variables

The intrinsic variables tested in this study were the biological age of the fish when the increment was formed (i.e. Age), AAC, an individual fish identifier (i.e. FishID), the calendar year in which the fish formed the increment (Year), and the year the fish was born (Cohort) (Table 1).

Age and AAC were tested as fixed factors and log transformed to meet model assumptions. AAC was included to test for possible sampling or survival bias resulting from fishing selectivity (Ricker 1969) or natural selection (Sogard 1997, Munday et al. 2013), whereby the growth of an individual determines its likelihood of selection in the data set. FishID was tested as a random intercept variable to account for the non-independence of increment widths derived from the same fish, allowing the model intercept to vary with each individual fish. Year was tested to induce correlation between fish that formed increments in the same calendar year, revealing otherwise unexplained annual variability in the growth chronology. Similarly, Cohort was tested to account for possible unexplained spawning strength and age class density effects on growth. Age was included as a varying slope for the FishID, Year and Cohort random effects, developing an age-dependent relationship for each random effect. Intra-class correlation (ICC) is a statistic that describes how strongly the variance within units of the same group resemble each other, represented as a number between 0 and 1, with low numbers indicating poor agreement. ICC was used to explore the relative contribution of random temporal factors in the model.

2.5. Extrinsic variables

Three classes of environmental (extrinsic) data were included in the modelling process: estuary surface (air) temperature, rainfall and climate indices (Table 2). As there was high correlation be-

tween variables of the same class (i.e. between temperature variables; Fig. S4), each model included no more than one variable from each environmental class. The best performing single environmental variable within each class was used to test for additive environmental effects, where more than one environmental data class was tested in the same model.

Model-derived estimates of temperature and rainfall were obtained from the Australian Bureau of Meteorology (BOM) BARRA reanalysis (post-1990, ~12 km resolution; Su et al. 2019) and the ECMWF ERA5 reanalysis (4th Gen) model (Pre-1990, ~30 km resolution; Hersbach et al. 2020). Both these models are constrained by and show high agreement with observed values for both temperature and rainfall. The BARRA reanalysis is itself nested within the ERA-Interim reanalysis model (superseded by ERA5) to force the model boundaries; hence the models we used are highly compatible. Monthly temperature and rainfall data were extracted from the reanalysis models based upon the capture location of each fish and then averaged over the annual growing season defined by the MIA (November–October) or as specified in the sliding window analysis described later. The 12–30 km spatial scale matches the known movement and estuary-resident patterns of *A. japonicus* (Taylor et al. 2006, 2014, Hughes et al. 2022).

2.6. Temperature

As estuary-specific water temperature was not available for all locations in this study (modelled or observed), consistent with similar studies in the region (Morrongiello et al. 2014, Izzo et al. 2016), we tested the correlation between observed monthly average air temperature (Bureau of Meteorology 2020) and observed monthly average surface water temperature (WaterNSW 2021) in 3 estuaries with sufficient data. Over a 7 yr period (2013–2020), average monthly estuary water temperature and average monthly surface air temperature were highly correlated (Clarence River, 29.5°S: r = 0.94, p < 0.001; Hunter River, 33°S: r = 0.92, p < 0.001; Shoalhaven River, 35°S: r = 0.89, p < 0.001). Modelling then proceeded with the use of estuary surface air temperatures as a proxy for estuary water temperature. Both average monthly and mean maximum monthly temperature were tested in the mixed model process. The correlation between estuary temperature and nearby coastal sea surface temperature (SST) was also tested for 3 locations and found to be significant

(Eden, 37°S: r = 0.81, p < 0.001; Sydney, 33°S: r = 0.52, p = 0.006; Yamba, 29.4°S: r = 0.67, p < 0.001). However, the previously tested estuary air temperature was more highly correlated with estuary water temperatures; hence, we retained the use of air temperature as a proxy.

2.7. Rainfall

As estuary-specific freshwater flow was not available (modelled or observed) for all locations in this study, rainfall data (total monthly average; mm) was used to represent the physical and biological effects of changing freshwater input, such as changes to primary productivity, salinity and turbidity, as per the method used in Stewart et al. (2020). The 12–30 km spatial scale of the reanalysis models were considered coarse enough to represent the influence of rainfall effects on *A. japonicus* individuals in both estuarine and nearshore marine habitats but fine enough to separate neighbouring estuarine systems. The data was log transformed to meet the assumptions of normality and homoscedasticity in the model.

2.8. Climate indices

The strength of 4 monthly resolved climate indices were tested in the model (Southern Oscillation Index [SOI], Interdecadal Pacific Oscillation [IPO], Indian Ocean Dipole [IOD] and the Southern Annular Model [SAM]; Table 2). These indices represent gradients of temperature or mean sea level pressure across the Pacific, Indian and Southern Oceans, and capture the effects of large-scale weather trends (Murphy & Timbal 2008). This study was situated within the Western Pacific (Eastern Australia), making the SOI and IPO indices most spatially relevant. However, due to the large spatial extent of the study, SAM was tested for possible influence in the southern section of the population (Gillett et al. 2006). IOD was included as it has considerable influence on eastern Australian climate, especially during the winter months (Ashok et al. 2003).

2.9. Sliding window analysis

Following the identification of environmental variables that maximised model performance, a sliding window analysis was performed. This analysis tested

which time window within sub-annually resolved environmental data best explained an environmental relationship with growth, thereby identifying key months during which the environment is contributing most to growth variation (Denechaud et al. 2020, Reis-Santos et al. 2021). This was done by testing all combinations of monthly averaged environmental variables in the model, varying the temporal scale of the window (1–12 mo) as well as the start and end months, constrained by the growth season determined by the MIA. To ensure the best sliding windows were not selected by chance alone (i.e. false positive), a randomisation test was run, comparing the likelihood of the best performing model against the distribution of AIC values from 1000 iterations of the model with randomised environmental data and varying sliding windows (van de Pol et al. 2016, Reis-Santos et al. 2021).

2.10. Climate change forecasting

The best overall performing environmental growth model was used to predict how the growth of *A. japonicus* in NSW may change over the next 80 yr. Growth forecasting was performed using projections from the NSW and ACT Regional Climate Modelling (NARCLiM) project (Evans et al. 2014). The NAR-CLiM v1.5 project consists of 3 global climate models (CSIRO BOM ACCESS 1.0, CSIRO BOM ACCESS 1.3 and CCCma-CanESM2), 2 downscaling models (R1, R2) and 2 emission scenarios (RCP 4.5, RCP 8.5), forecasting daily resolution data from 2020–2099 at a 10 km resolution. The RCP 4.5 emission scenario is described by the IPCC as an intermediate emission scenario, with RCP 8.5 representing continued high emissions, remaining 'highly plausible' in 2100, and which best tracks the current global emission scenario (Schwalm et al. 2020). We used all 6 model outputs (3 climate models × 2 downscaling models) for each emission scenario to calculate ensemble mean monthly temperatures between 2020 and 2099 for 3 locations in our study. The 3 locations were Yamba (29.4°S), The Hawkesbury River (Sydney) (33.5°S) and Eden (37.3°S), chosen to represent the northern, central and southernmost part of the distribution of *A. japonicus* in eastern Australian. The variation in predicted temperatures between climate models (within ensemble error) was small relative to the error in our linear mixed model. Changes in future rainfall and climate indices were not included, as the best performing environmental mixed model did not include these variables.

3. RESULTS

Between 1980 and 2018, otoliths from a total of 3112 individual *Argyrosomus japonicus* were collected. TL at capture ranged from 39–168 cm, and AAC ranged from 2–34 yr. This resulted in a final data set of 9219 individual increment widths formed between 1980 and 2018 for use in the analyses.

3.1. Intrinsic growth effects

After following the described stepwise selection process, the best performing intrinsic model included Age, AAC and all random effects, with a random slope for log(Age) (M3b; Table 3). Age explained the most variability in growth chronology, with growth decaying exponentially as age increased (Table 4, Fig. 2a). AAC improved model explanation as a non-linear effect, with growth rate initially decreasing and then increasing as AAC increased, indicating fastest growth in both young (AAC < 5) and old (AAC > 15) fish (Fig. 2b; hereafter 'AAC curve or effect'). Both Age and AAC were significant factors (p < 0.001) and, together with a random effect for FishID, explained >85 % of the variability in growth (conditional R^2 = 0.856). Both Cohort and Year terms explained temporal variability (Fig. 2c,d); however, the ICC was 0.08 for Cohort and 0.12 for Year, indicating relatively low temporal growth agreement in the data set. Despite considerable variation in growth among years, a long-term increase in growth rate was observed from the late 1980s–early 1990s through 2018 (Fig. 2d). This trend remained after the inclusion of extrinsic factors in the model (see Section 3.2).

3.2. Extrinsic growth effects

Initial extrinsic modelling revealed annually averaged temperature to be the most important environmental variable, with a positive linear relationship over a temperature range of 16–25°C (M4a–M4c; Table 3). A quadratic effect of average annual temperature was also tested to detect a potential thermal optima, but the model did not converge and was not considered further.

SAM and mean annual rainfall (mm) were then tested as additive effects in the temperature model, but each addition provided no improvement from the base temperature model (M5a–M5b; Table 3). Adding SAM to the temperature model produced an

Table 3. Linear mixed effect model performance ranked by Akaike's information criterion (AIC) score. Low AIC scores indicate better model performance, centred on the best intrinsic model (M3b). ΔAIC represents the difference in AIC value from the best intrinsic model. All Age, Age-at-Capture (AAC) and rainfall terms are log transformed in the models, and all continuous factors were centred to assist model convergence. SAM: Southern Annular Model

Model name	ΔAIC	Model structure/terms	Description
Intrinsic models			
M1a	542.85	Increment ~ Age + AAC + AAC^2 + (1|FishID)	FishID random effect
M1b	336.79	Increment ~ Age + AAC + AAC^2 + (Age|FishID)	FishID with random age slope
M2a	223.33	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (1|Year)	M1b + Year random effect
M2b	50.02	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year)	M1b + Year with random age slope
M3a	27.29	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (1|Cohort)	M2b + Cohort random effect
M3b	0.00	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort)	M2b + Cohort with random age slope (best intrinsic model)
Extrinsic models			
M4a: rain	1.94	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort) + av_rainfall	M3b + annual mean rainfall
M4b: temp	−63.20	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort) + av_temp_year	M3b + annual mean temperature
M4c: SAM	0.00	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort) + SAM	M3b + annual mean SAM index
M5a: temp and rain	−61.20	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort) + av_temp_year + av_rainfall	M4b + additive effect of annual mean rainfall
M5b: temp and SAM	−63.20	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age |Year) + (Age|Cohort) + av_temp_year + SAM	M4b + additive effect of annual mean SAM index
M5c: temp sliding window	−74.34	Increment ~ Age + AAC + AAC^2 + (Age|FishID) + (Age|Year) + (Age|Cohort) + av_temp_sliding window	M3b + mean temperature during Nov–Feb from the sliding window analysis

equivalent model in terms of AIC; however, the simpler temperature-only model was retained.

Sliding window analysis revealed that the average temperature starting in November and ending in February outperformed all other temporal periods, suggesting that changes to temperature in this summer period had the greatest influence on growth

Table 4. Parameter estimates from best performing environmental extrinsic model M5c, including SE, test statistic z-value and p-values (Pr(>|z|)) for each logged model term: Age, Age-at-Capture (AAC) and Temperature (Nov–Feb). Av_temp represents average temperature (Nov–Feb)

	Estimate	SE	z	Pr(>|z|)
Intercept	6.2460	0.012	517.6	<0.001
Log(Age)	−0.7720	0.024	−32.2	<0.001
Log(AAC)	−0.2097	0.05	−4.2	<0.001
Log(AAC)^2	0.0549	0.012	4.4	<0.001
Av_temp	0.0211	0.002	8.8	<0.001

(Fig. 3). The randomisation test supported the use of summer temperature compared to a randomised set of temperature data (significantly different from chance alone, p = 0.001; Fig. S5).

The best performing model including extrinsic factors was M5c (Table 3), which included a linear effect of temperature (average temperature between November and February). This model explained 89% of growth variability (conditional R^2 = 0.889), with all fixed model coefficients being statistically significant (p < 0.001; Table 4). The model indicated that a 1°C temperature increase resulted in a 2.02% increase in mean annual growth rate (Fig. 4).

3.3. Climate predictions

Growth predictions showed strong initial increases in growth in all 3 locations, with divergence between the 2 emissions scenarios around 2060 (Fig. 5). After
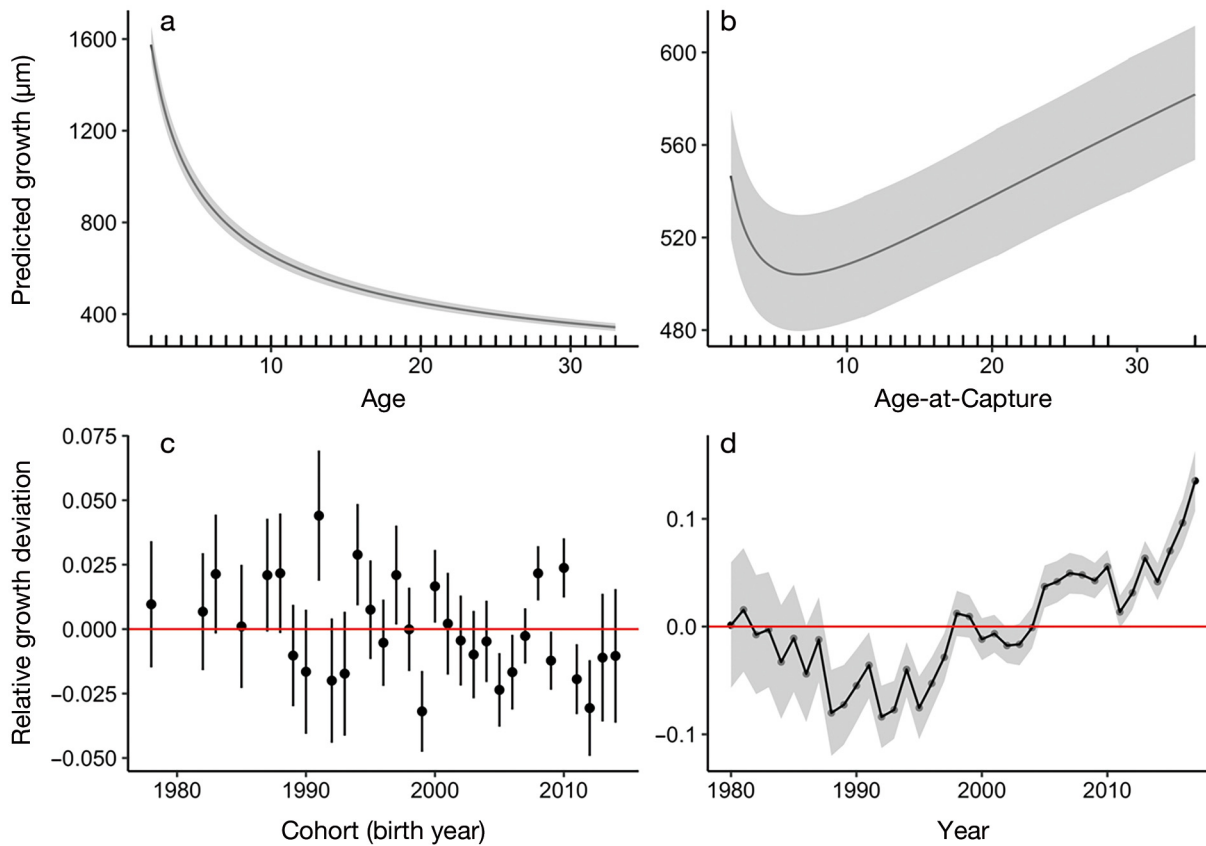
Fig. 2. Effect plots extracted from the best performing intrinsic model (M3b; Table 3). Both fixed and random variables are shown as the model mean otolith increment width, with all factors except the one of interest held constant. Error indicated for Cohort and Year (random factors) is standard deviation; error indicated for Age and Age-at-Capture (fixed factors) is standard error. (a) Growth age logarithmic decay relationship; (b) growth and Age-at-Capture (AAC) positive quadratic relationship; (c) relative lifetime growth deviation explained by Cohort (birth year); (d) relative annual growth deviation explained by the calendar year of growth

that time, RCP 8.5 (high emission scenario) showed a continued linear increase in growth, whilst RCP 4.5 (low emission scenario) showed a flattened and fluctuating growth trend reflective of forecasted temperature changes. Under the RCP 8.5 scenario, by 2099, predictions indicate that fish currently near Eden will experience growth rates like those currently observed 4° of latitude to the north, in Sydney. By 2050, predictions indicate that fish currently near Sydney will experience growth rates currently observed 4° of latitude to the north, in Yamba.
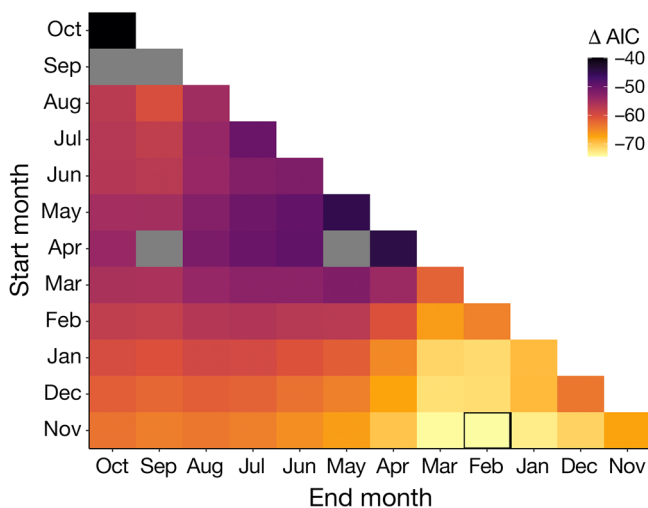

Fig. 3. Sliding window analysis of mean monthly temperature using the best performing environmental model before this analysis (M4b). All combinations of start (Nov–Oct) and finish month (Nov–Oct) for the window are shown. The ΔAIC comparison is based on the best performing intrinsic model (M3b; Table 3). The best performing temperature window was Start Month = November and End Month = February, with an AIC value 74.34 smaller relative to the M3b base model (highlighted by a black border). Grey squares represent model non-convergence
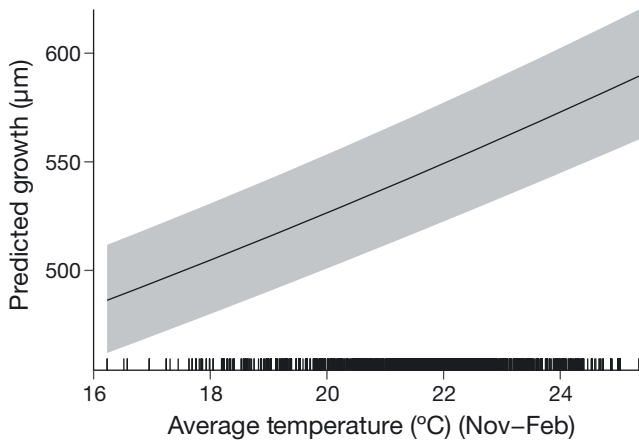
Fig. 4. Partial effect of average temperature (Nov–Feb) from best performing mixed effect model (M5c; Table 4). Grey shading: SE

Under the RCP 4.5 scenario, predictions indicate that by 2099, the growth rates of *A. japonicus* will still increase, but to a lesser extent than under the RCP 8.5 scenario. Greatest growth increases are predicted in Sydney, matching the mean growth rates currently observed in Yamba under both emission scenarios within the 80 yr forecast. Location-specific percentage changes in mean annual growth rates through the period of 2020–2099 are Eden: RCP 4.5 = 4.83%, RCP 8.5 = 8.02%; Sydney: RCP 4.5 = 5.58%, RCP 8.5 = 8.89%; Yamba: RCP 4.5 = 4.20%, RCP 8.5 = 8.11% (Fig. 5).

4. DISCUSSION

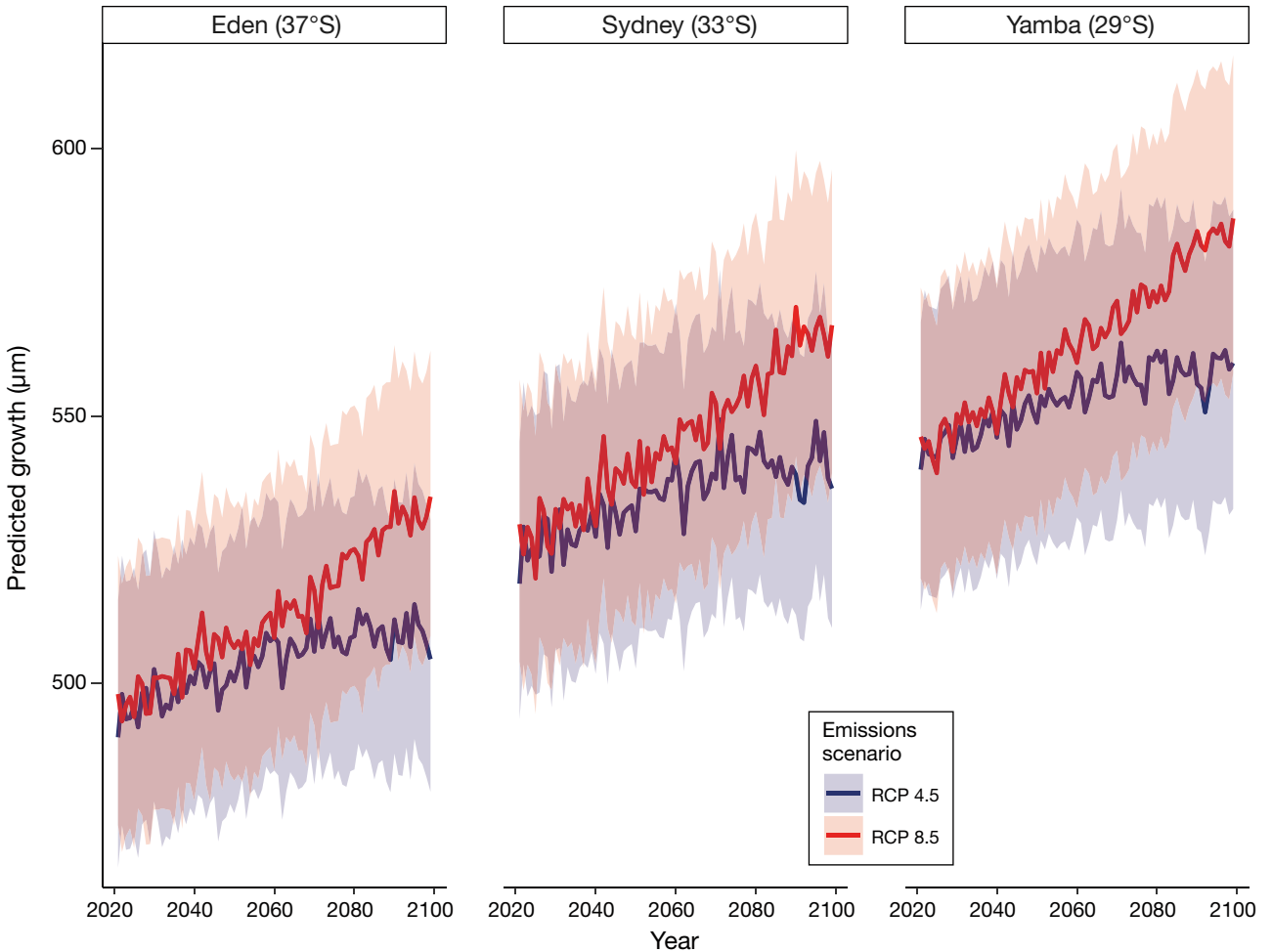This study identified a long-term increase in growth rate and a positive growth response to temperature

Fig. 5. Predicted annual otolith growth at 3 locations along the NSW coast (Yamba, Sydney and Eden) forecast under 2 emission scenarios (RCP 4.5, RCP 8.5), using NARCLiM climate model ensemble outputs between 2020 and 2099 (Evans et al. 2014). Error bands: SE associated with growth temperature relationships, as in Fig. 4. Year-to-year variance reflects the natural stochasticity captured by NARCLiM outputs

for *Argyrosomus japonicus* in south-eastern Australia. Temperatures during November–February had the greatest influence on growth, likely representing a specific growing season for the species. We also found that growth initially declined and then consistently increased with AAC, a pattern which was likely caused by selectivity mechanisms. We found no evidence of an influence of rainfall or climate indices on growth despite a previous study finding that rainfall increased recruitment of *A. japonicus* in the study region (Stewart et al. 2020). Based on published projections of temperature increase in the study region (Evans et al. 2014) and assuming the temperature–growth relationship developed in our modelling for the past 40 yr remains true, the growth rate of *A. japonicus* will continue to increase in south-eastern Australia, with the mean annual growth rate estimated to increase by up to 8.9% by 2099.

4.1. Intrinsic factors

As expected from the logarithmic nature of fish growth, the age at which an increment was formed (i.e. Age) explained the majority of variability in *A. japonicus* growth, with growth rate decreasing with increasing age (Silberschneider et al. 2009, Morrongiello & Thresher 2015). Other variables explained much smaller but still important fractions of variance in growth rate. The non-linear AAC effect suggests both sampling and environmental growth selectivity may have occurred. Otoliths for the current study were sourced from commercial and recreational fisheries, which potentially select for particular growth rates depending on fishing method and minimum legal-size requirements (Jørgensen et al. 2009, Vasilakopoulos et al. 2020). When young (AAC < 5 yr), the fastest growing fish may be selectively harvested by size-selective or behaviourally selective fishing gear (e.g. mesh nets) and therefore appear in the growth record before slower growing fish of the same age. Faster growing fish will also reach the minimum legal length (MLL; 70 cm TL in NSW) earlier than their slower growing conspecifics. These mechanisms are consistent with the Rosa Lee phenomenon (Ricker 1969), whereby slower growing young fish incur less fishing mortality, and potentially explain the initially elevated growth observed in our data set. Slower growing fish are then progressively included in the data set as they reach legal size, resulting in the growth minimum observed at 6 yr of age in the AAC curve. This point likely represents the age at which fishing selectivity is most uniform across faster and

slower growing phenotypes, with previous studies identifying that by age 6, the majority of *A. japonicus* have reached the MLL (Silberschneider et al. 2009).

A negative relationship between AAC and growth has been found for another estuarine species in southern Australia (black bream *Acanthopagrus butcheri*), with fishing selectivity also suggested as the driver (Doubleday et al. 2015). However, the current study detected an additional effect of AAC on growth in older individuals, whereby *A. japonicus* older than 10 yr displayed increasing growth rate with age. We suggest there is a long-term survival advantage for individuals who have faster growth rates, resulting in old age classes with high representations of fast-growing individuals. This hypothesised survival advantage of fast growers could result from superior competition for resources (Peters 1983), reduced predation pressure (the 'Big is Better' hypothesis; Miller et al. 1988) or simply a genetic link between growth and natural mortality (Jørgensen & Holt 2013). Unsurprisingly, our sample sizes for these old fish are smaller relative to the rest of the data set (increments formed when age ≥ 20, n = 107 annual growth increments). However, sample sizes were still large enough to achieve adequate statistical power based on recommended guidelines (Smoliński et al. 2020).

4.2. Extrinsic factors

4.2.1. Temperature

The positive effect of temperature on *A. japonicus* growth demonstrated here was expected, given the ectothermic physiology of fish and the inherent link between metabolism and growth (Brown et al. 2004). A controlled laboratory study suggested that optimal growth for *A. japonicus* is reached at a water temperature of 26°C (Pirozzi & Booth 2009); however, coastal SSTs in the northern extent of the study region occasionally exceeded 28°C during the study period (Condie & Dunn 2006), although these heightened temperatures may not currently be present long enough in the environment to be visible in an individual's annual growth record. Differences in thermal performance between laboratory and field studies have often been reported, with the latter more likely to indicate 'true' thermal optima that integrate the broad range of intrinsic and extrinsic ecological factors influencing performance ('ecologically optimal' temperature; Martin & Huey 2008, Norin et al. 2014, Payne et al. 2016). Large sample sizes (annual growth increments) in the northern extent of the

study (average Nov–Feb temperature >23°C, n = 1667; >24°C, n = 400) provide confidence that there is no indication *A. japonicus* are approaching their critical thermal maximum in south-eastern Australia at present. However, the species must eventually reach an 'ecological optimum' if temperatures continue to rise, leading to a decrease in growth rates and eventually increased mortality (Vinagre et al. 2015, Jutfelt et al. 2018). If these thresholds are exceeded, then our projections of increased growth rates with warmer temperatures will not be valid. Given the north–south orientation of the NSW coast, the northernmost section of the *A. japonicus* population will likely be the first region where the 'ecological optimum' is reached, providing an indicator of future deleterious change for more southerly (poleward) components of the stock. Marine heatwaves are increasingly common in this region (Kajtar et al. 2021), and it is possible that their effects could be obscured by focussing only on mean or maximum temperature. It would be interesting to incorporate heatwaves into future analyses of growth in this region, particularly for marine species.

Positive relationships between temperature and growth have also been noted for several other estuarine and marine fishes in south-eastern Australia, suggesting a common physiological response to rapidly rising temperatures in the region. These include the rock flathead *Platycephalus laevigatus* (Coulson et al. 2014, Barrow et al. 2018), black bream *A. butcheri* (Doubleday et al. 2015) and estuary perch *Percalates colonorum* (Morrongiello et al. 2014). However, the results presented here are not consistent with a biochronological study on *A. japonicus* in southern Australia, which did not find evidence of an effect of temperature on growth (Izzo et al. 2016). The latter finding is possibly due to its restricted spatial scale (a single estuary system) in comparison with that of the present study (1500 km, 12° of latitude) or differences in thermal performance among geographical regions or temperature ranges.

This study estimates that a 1°C increase in mean summer (November–February) temperature drives a 2.02% increase in mean annual otolith growth, which we have demonstrated is a reliable proxy for somatic (body) growth. This study does not separate the mechanisms by which temperature controls growth (physiological vs. ecosystem-level); however, it supports the physiological explanation provided by the Metabolic Theory of Ecology (Brown et al. 2004), whereby increased temperatures below a thermal optimum increase an individual's aerobic metabolic scope, allowing for greater somatic growth allocation. Although a significant relationship was found

between growth and temperature, this study finds little evidence that temperature explained high interannual growth variability (Fig. 2d), nor did temperature alone explain the growth trends over the last 3 decades (Fig. S6). It is therefore likely that there are additional factors to temperature which may help to explain the long-term increase in growth rates of *A. japonicus* observed in eastern Australia, as we discuss further in Section 5.

4.2.2. Rainfall

This study did not find evidence that rainfall affects the growth of *A. japonicus*. This finding is contrary to previous research showing that catchment inflows control the productivity of estuarine ecosystems (e.g. Gillanders & Kingsford 2002, Gillson 2011). The current study is, however, amongst a growing body of work identifying the variable sensitivity of estuarine species to environmental changes, including freshwater inflows (Doubleday et al. 2015, Izzo et al. 2016, Williams et al. 2017). *A. japonicus* have previously demonstrated sensitivity to rainfall and freshwater flows through recruitment success of juveniles, with increased abundance during periods following high rainfall (Stewart et al. 2020), which we hypothesised to potentially also be manifested in subsequent survival and growth. The current study did not consider the juvenile life history stage because of variation in birth date amongst individuals and the consequent variability in the duration of the recruitment year (Morrongiello & Thresher 2015). While we did not find evidence that rainfall influenced growth, the Cohort term in our intrinsic modelling captured lifetime growth variability common to individuals of the same spawning year, and it is possible that this included a residual growth effect associated with strong recruitment years driven by the rainfall-induced productivity (Stewart et al. 2020).

4.2.3. Climate

Biochronological studies have recently demonstrated significant relationships between fish growth and climate indices in other Western Pacific marine and estuarine predators such, as black bream *A. butcheri* (SOI; Doubleday et al. 2015), pink snapper *Chrysophrys auratus* (SOI; Martino et al. 2019), blue grenadier *Macruronus novaezelandiae* (IPO; Morrongiello et al. 2021) and pink ling *Genypterus blacodes* (IPO; Morrongiello et al. 2021). Martino et al.

(2019) found that the growth of pink snapper in Southern Australia was negatively influenced by extreme SOI events; however, climate indices did not make a significant contribution to explaining growth variability in *A. japonicus* in the current study, potentially indicating that either *A. japonicus* are less vulnerable to such broadscale climatic events or that extreme SOI events have a larger influence in the more southern waters of the Great Australian Bight. The climate indices may also have been too coarse spatially (single regional values) to explain the growth variability of *A. japonicus*, which are highly residential (Taylor et al. 2006, 2014, Hughes et al. 2022). Fine-scale (e.g. estuary-specific) environmental metrics are therefore likely more biologically relevant for this species.

4.3. Ecological implications of increased growth

Increased growth is often considered biologically advantageous, as growth has been linked to resource acquisition, body maintenance and hence individual survival, reproductive output and offspring fitness and success (Peters 1983, Hendry et al. 2001, Sibly et al. 2015, Marshall & White 2019). This concept is consistent with our finding of increasing growth rate with age for *A. japonicus*, suggesting selection for faster growth rates throughout life. By virtue of their body size, larger fish are more fecund than smaller individuals, and in some cases, contribute disproportionately to the reproductive output of fish populations (e.g. Longhurst 2002, Berkeley et al. 2004, Barneche et al. 2018). Given sufficient time, the evolutionary selection of faster growing *A. japonicus* individuals via decreased mortality rates, greater reproductive output and stronger recruitment could potentially result in a population containing increasing proportions of fast-growing individuals if sufficient numbers survive to older ages and do in fact have disproportionate reproductive output, an idea which should be examined further for *A. japonicus*.

Variable growth responses to environmental change have been reported, both within and between marine species (Doubleday et al. 2015, Izzo et al. 2016). In this study, *A. japonicus* demonstrated a positive growth response to temperature increases throughout its distribution; however, it is clear that not all marine species respond positively, with the average response of over 600 marine fish species to warming temperatures being decreased growth (Cheung et al. 2013). Generally, growth responses are species-specific, related to individual tolerance to environmental change (Brown et al. 2004). Such variability amongst marine species in their growth responses to temperature may therefore have future impacts on ecosystems that are difficult to predict. While faster growth may be advantageous for *A. japonicus*, increased foraging associated with accelerated growth rates and potentially greater population size of this large predator in the future may have top-down impacts on ecosystem structure and function within estuaries (Audzijonyte et al. 2020, Chapman et al. 2020). However, the population size of this species is currently classified as depleted in NSW, with biomass estimated to be below 20% of unfished levels (Earl et al. 2020). An increase in predation pressure and population size may therefore represent a return to pre-existing ecosystem conditions.

4.4. Management implications of increased growth

Altered growth may be associated with biological changes that need to be considered in future fisheries and conservation management of *A. japonicus* in south-eastern Australia. In particular, the impact of changes to growth rates on the timing of maturity within fish is not well understood. Previous research on Atlantic salmon *Salmo salar* has suggested environmentally driven increased growth postpones maturation (increases age-at-maturity; Jonsson et al. 2003, Otero et al. 2012); however, most evidence regarding the evolutionary responses of marine fish to climate change pressures indicate decreasing age-at-maturity (Crozier & Hutchings 2014). Indeed, evidence of both increased and decreased age-at-maturity in response to reduced growth rate has been reported within a single estuarine fish species, black bream *A. butcheri*, over 22 yr in 4 separate estuarine environments in south-western Australia (Cottingham et al. 2018). This variability suggests that the link between growth rates and maturity is inconsistent even within marine species and hence should be specifically investigated in each species and region of interest. The projected increase in growth rates for *A. japonicus* identified here will result in fish more quickly reaching the current MLL (also the size-at-maturity for female *A. japonicus*; Silberschneider et al. 2009). Individuals will therefore be caught at a younger age despite their body length being equivalent. The size and age-at-maturity of the *A. japonicus* population in south-eastern Australia should therefore be monitored to avoid harvest of increasingly immature individuals from the population (e.g. Dickey-Collas et al. 2010, Hsieh et al. 2010).

5. LIMITATIONS AND FUTURE RESEARCH

Due to the north–south orientation of the study region, temperature and latitude are highly colinear (r = −0.77). These 2 factors could therefore not be tested within the same model. Fish growth is more likely to respond to changes in temperature that occur with latitude rather than latitude per se, hence the inclusion of temperature in our models. We acknowledge that without testing for the potential effect of space, the model lacks the ability to account for spatial differences in growth rates that are unrelated to temperature, e.g. potential differences arising from stock structure and resulting divergent biology. However, as there is no evidence of stock structure throughout southeastern Australia (Silberschneider et al. 2009, Barnes et al. 2016), we believe the space-independent temperature growth relationships as found in this study are valid. Due to the correlative nature of the current study, it is not possible to disentangle the exact mechanisms (direct or indirect) through which temperature has influenced growth, but future studies which attempt to decouple space and temperature within the study region to further investigate fine geographic patterns may also provide some insights into different mechanisms. This lack of an identified mechanism for the temperature effect implies the forecast growth changes based on temperature alone should be interpreted cautiously.

It is now well documented that the East Australian Current, the dominant oceanographic feature influencing marine processes in south-eastern Australia, is strengthening (Sun et al. 2012, Cetina-Heredia et al. 2014). The strengthening of this current is associated with local ocean warming 3–4 times the global average since the early 1990s (Malan et al. 2021). The ocean SST along coastal south-eastern Australia has also not warmed uniformly over the past 3 decades, with areas further south warming fastest (Malan et al. 2021). However, differences in estuarine warming trends seem to be driven by estuary type, not latitude (Scanes et al. 2020). Future studies may aim to develop estuarine-specific water metrics throughout south-eastern Australia, or to provide a more comprehensive understanding of the true drivers of estuarine temperature, allowing for the most accurate forecasts of estuarine temperature.

Results presented here suggest that once past the first year of life, *Argyrosomus japonicus* growth rates are predictable based on fish age, AAC and environmental temperature. However, there are several additional factors which may influence *A. japonicus*

growth that we did not specifically examine and should be considered in future research efforts. Commercial landings of mulloway in NSW steadily declined from almost 400 t in the mid-1970s to a historic low of 37 t in 2008–2009 (Earl et al. 2020). It is possible that historical fishing pressure, particularly through the 1980s and 1990s (Silberschneider et al. 2009), has reduced the abundance of *A. japonicus* in this region to the point that competition for resources is reduced, and that the increasing growth rates in recent decades are due to a release of density-limited growth (Lorenzen & Enberg 2002, Amundsen et al. 2007, Bacheler et al. 2012). There is some evidence that this may have occurred, as *A. japonicus* have previously been shown to exhibit density-dependent behaviour (Taylor et al. 2013). This could be tested with our data set in the future if a reliable index of mulloway density could be generated.

Finally, the difference in growth between male and female *A. japonicus* was not included as a variable in our modelling, as the sex of each fish was not recorded for most individuals in the data set. *A. japonicus* do, however, exhibit significant differences in growth between males and females (Silberschneider et al. 2009), and the inclusion of sex would likely improve model performance, as has occurred in similar otolith-based biochronological studies on other Australian estuarine species (e.g. Morrongiello et al. 2014, Izzo et al. 2016, Barrow et al. 2018). Insights into possible sex-specific growth rates may help to inform the knowledge gap in environmentally determined changes in maturation rate and hence are critical to informing the management and stock health of *A. japonicus* into the future.

6. CONCLUSIONS

We demonstrated that the growth rates of *Argyrosomus japonicus* have increased over the 39 yr period of our data set and will likely continue to do so throughout south-eastern Australia based on climate predictions for coming decades, highlighting the need to better understand the physiological implications of environmental changes for coastal aquatic organisms. Temperature during the summer growing season (November–February) was identified as the key environmental driver of *A. japonicus* growth, with modelling indicating that a 1°C increase in temperature results in a ~2% increase in mean annual growth rates. Based on climate forecasts for 2099, the mean annual growth rate of *A. japonicus* in south-eastern Australia may increase by up to 8.9%. Since

growth is a key driver of population dynamics and is closely linked with other critical biological processes like individual development and reproduction, our results highlight the value of understanding the drivers of long-term growth variation in exploited fish stocks to predict future productivity under a range of environmental and fisheries management scenarios.

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