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Title: A boundary current drives synchronous growth of marine fishes across tropical and temperate latitudes

Running head: A boundary current drives growth of fishes

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Abstract

Entrainment of growth patterns of multiple species to single climatic drivers can lower ecosystem resilience and increase the risk of species extinction during stressful climatic events. However, predictions of the effects of climate change on the productivity and dynamics of marine fishes are hampered by a lack of historical data on growth patterns. We use otolith biochronologies to show that the strength of a boundary current, modulated by the El Niño-Southern Oscillation, accounted for almost half of the shared variance in annual growth patterns of five of six species of tropical and temperate marine fishes across 23° of latitude (3000 km) in Western Australia. Stronger flow during La Niña years drove increased growth of five species, whereas weaker flow during El Niño years reduced growth. Our work is the first to link the growth patterns of multiple fishes with a single oceanographic/climate phenomenon at large spatial scales and across multiple climate zones, habitat types, trophic levels and depth ranges. Extreme La Niña and El Niño events are predicted to occur more frequently in the future and these are likely to have implications for these vulnerable ecosystems, such as a limited capacity of the marine taxa to recover from stressful climatic events.

Introduction

Changes to the world's climate driven by the release of carbon dioxide and other greenhouse gases into the atmosphere due to human activities are having serious and increasing consequences for marine ecosystems. These range from changes in individual physiology and survival to effects on population dynamics, habitats and ocean productivity (Lehodey *et al.*, 2006, Munday *et al.*, 2008, Hoegh-Guldberg & Bruno, 2010, Cheung *et al.*, 2012). For marine fishes, research on climate change has largely focused on the implications of a warming ocean for thermal limits and distributions of species (Harley *et al.*, 2006, Pörtner & Peck, 2010). Many of these studies have identified "hotspots" of change in marine environments where pronounced temperature anomalies are now occurring and these serve as a focal point for the prediction of impacts likely to occur in other regions (Cheung *et al.*, 2012, Poloczanska *et al.*, 2013). However, alterations to the distributional limits of fishes are only part of the potential effects of climate change; this process is also likely to modify current flows (Bakun *et al.*, 2015), patterns of productivity (García-Reyes *et al.*, 2015) and population dynamics (Fordham *et al.*, 2013) of species in coastal and oceanic ecosystems. Because warming affects both regional (10-1000s km) and large scale (1000s km) climate phenomena, changes could occur simultaneously and dramatically at multiple spatial scales, rather than just in hotspots or progressively at the fringes of species distributions. Evidence for this possibility is shown by the links between population dynamics (growth patterns in particular) of many species to climatic features such as El Niño-Southern Oscillation (ENSO) events and the flows of regional boundary currents (Chavez *et al.*, 2003, Black *et al.*, 2008, Helser *et al.*, 2012, Black *et al.*, 2014, Ong *et al.*, 2016).

Studies have shown that such entrainment of growth patterns of species to single climate phenomena can increase the risk of species extinction through the reduction of "portfolio effects" both within species, e.g. butterfly communities (McLaughlin *et al.*, 2002) and also among species, e.g. salmon (Schindler *et al.*, 2010, Kilduff *et al.*, 2015). These effects are defined as a diversity of responses to climate drivers, allowing some individuals or species to survive through extreme events so that populations can recover to stabilise ecosystem processes. The degree to which species are entrained to individual climate signals thus provides a measure of likely ecosystem vulnerability to climate change.

The construction and analysis of biochronologies from otoliths or other calcified structures provides a powerful technique to assess the extent to which growth patterns of marine fishes are linked at large spatial scales and to determine the likely impact of climate change on the

drivers of these patterns (Morrongiello *et al.*, 2012). Growth integrates the effects of both physical and biological processes that can alter with climate change, allowing insight into their effects on key parameters (such as size-at-age) that determine the productivity and yields of species targeted by fisheries. Recently, this approach has been used to show how increasing sea surface temperature (SST) can affect the growth of temperate marine fishes (Gillanders *et al.*, 2012, Coulson *et al.*, 2014, Rountrey *et al.*, 2014) and how the drivers of growth patterns can even be linked across divergent taxa (trees, corals, fish and bivalves) in the same environment (Black, 2009, Ong *et al.*, 2016).

Here, we use an otolith biochronology approach to identify key climate drivers of growth of marine fishes from a variety of habitats and trophic guilds (Supplementary Table S1) across 23° of latitude encompassing tropical, subtropical transition, and warm and cool temperate zones (Fig. 1). We then examine the vulnerability to and likely scale of impact of the predicted effects of climate change on the growth patterns of these species. The marine environments of the continental shelf of Australia provide a suitable model to examine broad scale impacts of climate change on the growth of fishes, because the flow of both the Holloway Current and the Leeuwin Current are strongly correlated to and influenced by ENSO (D'Adamo *et al.*, 2009, Feng *et al.*, 2009). The Leeuwin Current is the dominating boundary current off the coast of Western Australia and flows poleward, suppressing productivity and creating an oligotrophic marine environment (Feng *et al.*, 2009). This contrasts with the highly productive eastern boundary currents that flow to the Equator in other parts of the world (Canary, California, Humbolt and Benguela currents), all of which contribute significantly to global catches of marine fishes (Fréon *et al.*, 2009). The Leeuwin Current extends more than 2000 km transporting warm, nutrient-poor water southward along the continental shelf from the tropics to cool temperate coasts. It is ecologically important for the recruitment, growth and survivorship of many species in the region (Caputi *et al.*, 1996, Caputi, 2008) and extends the distribution of some tropical taxa southward (Maxwell & Cresswell, 1981). Although the Leeuwin Current typically suppresses productivity, it is also associated with mesoscale eddies that can increase primary productivity over short periods of time (Koslow *et al.*, 2008). The Holloway Current is a south-westward flowing current that was described in 2009 (D'Adamo *et al.*, 2009). It has been suggested to be a strong contributor to the Leeuwin Current (Holloway & Nye, 1985) with seasonal flows occurring from February to July (D'Adamo *et al.*, 2009) that are stronger in La Niña years (Wilson, 2013).

Earlier studies of otolith chronologies of fishes along the coast of Western Australia have shown that growth of some shallow-water, temperate species respond positively to SST (Coulson *et al.*, 2014, Rountrey *et al.*, 2014). In contrast, the growth of tropical fishes is positively correlated with ENSO variability (Ong *et al.*, 2015, Ong *et al.*, 2016), whereas the growth of a deep-water fish off the coast of the southwest is positively correlated with the strength of the Leeuwin Current (Nguyen *et al.*, 2015). Given that these observed drivers are inter-related, the growth patterns of fishes might be similar across relatively large spatial scales, from tropical to temperate zones off Western Australia. Thus, the effects of climate change could manifest simultaneously and synoptically across environments where fishes share connected drivers of growth. We predict that strength of the Leeuwin Current, which is strongly correlated to ENSO fluctuations and determines regional environmental variables such as temperature, will be an important driver of the growth in adults of six species throughout the coastal marine waters of Western Australia. We examine the implications of this link for growth and productivity of fish populations under scenarios of future climate change.

Materials and methods

The otoliths of fishes grow in proportion to body size and thus provide a proxy for measures of somatic growth (Rowell *et al.*, 2008, Neuheimer *et al.*, 2011, Stocks *et al.*, 2011, Black *et al.*, 2013). Existing increment data from the otoliths of five coastal fishes (*Lutjanus argentimaculatus*, *Lutjanus bohar*, *Lethrinus nebulosus*, *Achoerodus gouldii* and *Polyprion oxygeneios*) in Western Australia were obtained from earlier studies and a new chronology for *Scorpis aequipinnis* was constructed (Supplementary Table S2). These six species, which all have relatively long lifespans, were sampled in different climatic zones (Fig. 1) and depth ranges (Supplementary Table S1). *Scorpis aequipinnis* were sampled between 2008 and 2011 using both spear fishing methods (up to 20m depth) and commercial catches (up to 50m depth) and otoliths were sectioned transversely through the primordium, see Coulson *et al.* (2012) for more details. Image analysis methods are described in the Supporting Information. Raw otolith increment widths for all individuals from each species were obtained and detrended using the method of Black *et al.* (2013), where increment widths were first aligned by age and the mean increment width for each age calculated. Each series was then divided by the mean to obtain detrended values. The quality of the detrended increment series (for fish of the same species) was then assessed using the mean of pair-wise series correlations ($\bar{r}$), an estimate of fractional common variance, and the expressed population signal (EPS), a

measure of how well the chronology represented the theoretical population chronology (Wigley *et al.*, 1984). To ensure that the chronologies contained only synchronous growth signals, bootstrapped 95% confidence intervals for $\bar{r}$ (with 15 year intervals) were estimated following the methods of Rountrey *et al.* (2014). These were calculated using a modified version of the package "dpIR"(Bunn, 2008) in R software (R Core Team, 2015). Only periods with $\bar{r} > 0$ and EPS > 0.50 were used to construct the growth chronology. If the detrended increment series for any species did not contain periods with $\bar{r} > 0$ and EPS > 0.50, the detrending methods used in the original publications were adopted to retain the aspects of the growth chronology that contributed to shared variance among sampled individuals. The growth series for *L. argentimaculatus*, *L. bohar*, *L. nebulosus* and *S. aequipinnis* were detrended following Black *et al.* (2013), as described earlier. *Achoerodous gouldii* was detrended using the double-detrending technique in the original publication (Rountrey *et al.*, 2014), where each series was detrended first with a modified negative exponential function followed by a spline with rigidity set to 67% of the series length. *Polyprion oxygeneois* was detrended using a spline rigidity with a 50% frequency cut-off of nine years, following the original publication (Nguyen *et al.*, 2015). The double-detrending and spline methods may have been more successful in emphasizing signal and removing noise for *A. gouldii* and *P. oxygeneois*, respectively, due to higher levels of individual variation in year-adjusted mean increment width and/or more medium frequency variance caused by local factors rather than regional drivers. However, explicit testing of detrending methods was beyond the scope of this study. The final growth chronologies for each species were constructed from the average of all detrended increment series for all individuals within each species. The time span of overlap of chronologies for all six species covered 16 years, from 1988 to 2003.

Each of the six chronologies, one per species, were standardized (mean = 0, variance = 1) and analysed using principal components analysis (PCA), to reduce the number of response variables. The scores from the principal components that accounted for majority of the variance were subsequently included as response variables (in the form of time-series data, similar to the original chronologies) in separate linear regression models based on information-theoretic methods. These models enabled us to assess the influence of the Leeuwin Current (measured by the Fremantle sea level) and climate indices including the multivariate El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and Dipole Mode Index (DMI; see Supporting Information for justification and details on datasets obtained) on the growth chronologies. Collinearity between environmental variables ($|r| >$

0.5, p < 0.01) was evaluated to ensure that collinear variables were not included in the same model. Due to collinearity among the environmental variables and the low number of observations (n = 16 years), only one variable was used in the construction of each model, resulting in the evaluation of five models (one for each of the four environmental variables and an intercept-only model) for each response variable. The R package "MuMIn" (Barton, 2015) was used for model selection using the second-order Akaike information criterion (AIC_C) based on Kullback-Leibler information loss and accounting for small sample sizes (Burnham & Anderson, 2004). Differences in AIC_C values (ΔAIC_C), model probabilities (Akaike weights) and relative variable importance (using the sum of Akaike weights over all models) were used to assess the models. Adjusted R^2 values, F-statistics and p-values were reported for the top-ranked models. All top-ranked models identified in the model selection process were validated to ensure that assumptions of homogeneity, normality and temporal autocorrelation were not violated. Linear dependence was assumed for the environmental variables because the use of smoothers for the variables did not improve the fit of the models. All statistical analyses were completed in R software (R Core Team, 2015).

After the model selection process, spatial correlation maps of the first principal component with quarterly ocean heat content and ocean mean temperatures (see Supporting Information for further details) were constructed to illustrate the spatial relationships, in addition to the temporal resolution that the linear models (described above) provides. Ocean heat content was selected because it has been identified as a predictor of the strength of the Leeuwin Current (Hendon & Wang, 2010) and has strong correlations with Fremantle sea level (Supplementary Figure S1). Ocean mean temperatures up to 700 m depth were selected to encompass the depth ranges of all study species and because it also shows strong correlations with Fremantle sea level (Supplementary Figure S1). Individual correlations of each chronology with the environmental variables were also carried out to confirm the importance of the various environmental variables on each species and to corroborate the results of the PCA and the linear regression models.

Results

Similarities in the otolith chronologies

We show that among the individuals for each of the six species of fish, there were synchronous signals of growth at certain periods of the chronologies (Supplementary Table S3). The period of overlap for all species was 1988–2003, a 16-year period. Similarities

between the six otolith chronologies (one for each species) were then assessed using a principal components analysis. The first two principal component (PC) scores accounted for 65% of the total variance in the data set. Of these, the first accounted for 41% of the variance, and the second, 24%. The remaining principal components were not included in further analyses. Growth of three of the species (*Lutjanus argentimaculatus*, *Achoerodus gouldii* and *Polyprion oxygeneios*) had negative loadings on PC1 (Table 1) and displayed similarities in temporal patterns of growth (Fig. 2a). Chronologies of two of the remaining species (*Scorpis aequipinnis* and *Lethrinus nebulosus*) also had negative loadings on PC1, whereas *Lutjanus bohar* had a positive loading (Table 1). Chronologies for *L. bohar* and *S. aequipinnis* had the most negative loadings on PC2 (Table 1) and displayed similar temporal patterns in growth (Fig. 2b). Inverse values of PC1 ($PC1_{inv}$) and PC2 ($PC2_{inv}$) scores were used in further analyses.

Influence of boundary current on fishes

Collinearity among the four environmental variables are shown in Supplementary Table S4. The model selection process involving $PC1_{inv}$ found that the first-ranked model (i.e. lowest AIC_C) was one that related $PC1_{inv}$ with Fremantle sea level, and it was estimated to be approximately six times more likely (Akaike weight = 0.82) than the second-ranked model (Akaike weight = 0.13, ΔAIC_C = 3.64; Table 2). The first-ranked model showed a positive relationship between $PC1_{inv}$ and Fremantle sea level, and it explained 48% of the variance in $PC1_{inv}$ (adjusted R^2 = 0.48, F-statistic = 14.81, p-value = 0.002).

The strong, positive relationship between the Leeuwin Current and the western Pacific warm pool (via the Indonesian through-flow) were evident in the spatial correlation maps of $PC1_{inv}$ with ocean heat content from January to March (Fig. 3a; see Supplementary Fig. S2 for spatial correlation maps of the other months). The spatial correlation map of $PC1_{inv}$ and ocean temperatures from January to March (Fig. 3b; see Supplementary Fig. S3 for the other months) showed that higher temperatures were correlated with wider otolith increments for five of the six study species, represented by negative loadings on $PC1_{inv}$. This result was consistent with the results for ocean heat content, which also showed positive correlations with growth when higher amounts of heat were stored in these waters. Both the PCA results and the spatial correlation maps showed the influence of the Leeuwin Current, itself modulated by ENSO, on five of the six study species (as indicated by the PC1 loadings). In addition to the influence of the Leeuwin Current on the shared variance of the five species using $PC1_{inv}$, individual correlations of each chronology (all six study species) are shown in

Table 3. The importance of the Leeuwin Current (as measured by Fremantle sea level) was re-affirmed on at least three of the species (*L. argentimaculatus*, *S. aequipinnis* and *A. gouldii*), with again five species having similar positive signs. Significant correlations were also seen between measures of ENSO (MEI and PDO) and some of the species, while the DMI was significantly correlated to one species (Table 3).

Influence of Pacific Decadal Oscillation on fishes

The first-ranked model for $PC2_{inv}$ identified a possible relationship between growth and the PDO (Table 2). It was only approximately twice as likely (Akaike weight = 0.55) as the second-ranked, intercept-only model (Akaike weight = 0.24, ΔAIC_C = 1.65) and was not considered to be a substantial improvement, as the ΔAIC_C was less than 2 (Burnham & Anderson, 2004). The relative variable importance of the PDO was 0.56, which was much greater than other variables (0.06–0.07). The linear model showed that the negative relationship between $PC2_{inv}$ and the PDO was marginally significant (F-statistic = 4.81, p-value = 0.05) and explained 20% of the variation in $PC2_{inv}$ (adjusted R^2 = 0.20), which largely reflected the growth chronologies of *L. bohar* and *S. aequipinnis* (Table 1).

Discussion

The strength of the Leeuwin Current, linked to inter-annual variations of ENSO (Feng *et al.*, 2009), was a key driver of the growth of adult fishes across more than 3000 km of coastline in the eastern Indian Ocean. These fishes were collected from a shelf that encompassed tropical, subtropical, warm temperate and cool temperate environments over ~23° of latitude and from both shallow coastal waters and deeper continental slopes. Fremantle sea level (a proxy for strength of the Leeuwin Current) and composite growth of five of the six species were positively correlated, indicating that in years of high flow (La Niña phases of ENSO), growth rates of adult fishes tended to increase, whereas in years of low flow (El Niño phases of ENSO), growth declined. Overall, current strength accounted for almost half of the variability in the composite growth chronologies, which represented the shared variance among the sampled individuals.

Our work is the first to provide evidence of a link between the growth patterns of adult fishes, flow of a boundary current and ENSO at spatial scales that include multiple climate zones, habitat types and depth ranges. Earlier studies have found strong relationships between growth and ENSO indices for single species in north-western Australia (Ong *et al.*, 2015,

Ong *et al.*, 2016). Other studies using growth chronologies in the Southern Hemisphere have focussed on relationships between growth of single species of fishes and temperature (Thresher *et al.*, 2007, Morrongiello & Thresher, 2015, Izzo *et al.*, 2016). However, our results show that links between growth and ENSO indices can occur for multiple species along both tropical and temperate coasts and across the shelf in waters influenced by the Leeuwin Current, an area encompassing a third of the entire coastline of the Australian continent. Other studies on synchronous patterns among marine populations commonly use metrics of recruitment (Megrey *et al.*, 2009), abundance (Defriez *et al.*, 2016) or biomass (Vasseur & Gaedke, 2007), which tend to be population-level estimates that may or may not be fishery-dependent. In contrast, our research uses individual-level growth data to infer growth variation and the subsequent effects of climate on somatic growth rates. Hence, our study provides a different yet valuable approach to the historic effects of climate on population dynamics and its consequences.

There are several possible mechanisms that could account for the positive relationship between growth (as measured by the $PC1_{inv}$ index) and the strength of the Leeuwin Current. Firstly, an increase in current flow results in a greater input of warmer and lower salinity waters from the western Pacific to the Western Australian coast (Meyers *et al.*, 2007). As fish are poikilotherms, these warmer waters may increase metabolic rates and aid growth (Rountrey *et al.*, 2014), provided individuals do not exceed thermal limits and sufficient food is available to support energy demands. Secondly, stronger flows of the Leeuwin Current may create intense mesoscale eddies that draw nutrient-rich water from depth into the photic zone, increasing primary production (Koslow *et al.*, 2008) that then flows up the food chain to fishes at higher trophic levels (Nguyen *et al.*, 2015). Finally, a stronger Leeuwin Current is also associated with higher rainfall over north-western Australia due to the influences of La Niña over SST, winds and convection north of the continent (Wang *et al.*, 2003). The input of terrestrial nutrient via runoff at these times might be an important factor for the growth of fish that live in or near large embayments or estuaries such as *L. nebulosus* (Ong *et al.*, 2016) or young *L. argentimaculatus* (Ong *et al.*, 2015).

The Pacific Decadal Oscillation (PDO) was identified as a driver of adult growth of *L. bohar, S. aequipinnis* and, to a lesser extent, *P. oxygeneios*. Although it might seem incongruous that the physical oceanography of the northern Pacific could influence growth of fishes in the eastern Indian Ocean, this teleconnection (linked, large-scale variability at long timescales; e.g. Lehodey *et al.*, 2006, Kilduff *et al.*, 2015, Newman *et al.*, 2016) is not without precedent.

The PDO describes a combination of oceanographic processes that span both the tropics and the extratropics and is strongly linked to the oceanography of the tropical western Pacific (Chen & Wallace, 2015, Newman *et al.*, 2016). It is also regarded as a reddened/delayed response to ENSO where the ENSO signal re-emerges in the PDO in the subsequent year (Newman *et al.*, 2003, Shakun & Shaman, 2009). Hence, correlations with the PDO might have occurred via two mechanisms. Firstly, growth variations in the three species could be linked to the lagged ENSO signal. Alternatively, the growth patterns were responding to low-frequency (i.e. decadal) variations of SST anomalies in the tropical Pacific (Chen & Wallace, 2015). In support of the second explanation, multi-decadal variations of the PDO in the tropical Pacific have been found to influence low-frequency variability of the Fremantle sea level, a proxy for the strength of the Leeuwin Current (Feng *et al.*, 2003), and this process has also been recorded in the growth patterns of corals along the Western Australian coast (Zinke *et al.*, 2014).

We acknowledge that although our study has focused on the effects of climate, other external factors such as the effects of fishing pressure can also induce synchronous changes in population dynamics (Frank *et al.*, 2016). However, in our study system, the exploitation of fish populations are of relatively minor commercial importance compared to invertebrate species such as prawns, abalone and lobster (Fletcher *et al.*, 2017). Furthermore, the species we have chosen in this study tend not to be the main targets of the commercial fisheries in their respective regions. Even though *A. gouldii* and *L. nebulosus* have the highest commercial catches compared to the other species (maximum 60 tonnes in a year), their catches are still a small fraction (< 3%) of the total commercial catches in their respective regions (Fletcher *et al.*, 2017). Hence, commercial exploitation is less likely to be a major driver of fluctuations in the population dynamics of fishes along this coastline. We also acknowledge that because of our attempts to compare multiple time series of growth data, the number of years of overlap among the biochronologies is not large (16 years), however, this is an inevitable consequence of using datasets that were not originally constructed for our purpose.

The importance of ENSO and the Leeuwin Current to the settlement and recruitment of marine invertebrates and fishes along parts of the coastline of Western Australia is well-recognised (Caputi *et al.*, 1996). The strength of the current also influences the presence and persistence of corals and their symbionts at high latitudes (Collins *et al.*, 1993, Silverstein *et al.*, 2011) and the abundance of very large planktivores, such as whale sharks (Sleeman *et al.*,

2010). Our study shows that the growth of adult fishes is also driven by these large-scale atmospheric and oceanographic phenomena, irrespective of the thermal range of a species (tropical or temperate), the depth of habitat or trophic role it occupies. This result has important implications for the potential scale and ubiquity of climate change impacts along the Western Australia coast. Climate forecasts suggest that El Niño and La Niña events are likely to become more frequent and intense (Cai *et al.*, 2014, Cai *et al.*, 2015). Strong El Niño events slow the flow of the Leeuwin Current (Feng *et al.*, 2009) and our study shows that such conditions may lead to concurrent declines in the growth of many fishes along the entire coastline of Western Australia. This has the potential to alter key life history traits, e.g. size at age (Rountrey *et al.*, 2014), with subsequent impacts on population demography. Although moderate La Niña conditions are likely to positively affect growth rates, as demonstrated by our study, extreme events can produce anomalous water temperatures that may surpass the thermal limits of fishes. For example, the marine heat wave that occurred in the summer of 2011 on the coastline of Western Australia was driven by an unusually strong Leeuwin Current, itself a result of a strong La Niña event (Feng *et al.*, 2013). The marine heat wave caused major fish kills along the coast (Pearce *et al.*, 2011), reductions in abundances of commercially important invertebrates such as the abalone *Haliotis roei* and scallops *Amusium balloti* (Caputi *et al.*, 2016), reductions in habitat-forming seaweeds (Wernberg *et al.*, 2013) and coral bleaching (Depczynski *et al.*, 2013). Thus, extreme phases of both El Niño and La Niña are likely to negatively impact fish populations in a synoptic manner along the entire coastline of Western Australia, across a variety of distribution ranges, thermal limits, depth ranges and trophic levels.

The recent marine heat waves highlight the way in which the ENSO signal can introduce extreme variability in physical environments inhabited by marine fishes. The degree of entrainment to the ENSO signal and the consistency of relationships among a diverse range of fishes show that there is likely to be only a limited variety of responses to stressful climate incidents by these faunas across large areas of the Western Australian coastline. This implies that these ecosystems may be extremely vulnerable to and have limited capacity to recover from the threat of extreme La Niña and El Niño events.

Acknowledgements

Conflict of interests

The authors declare no conflict of interests.

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Tables

Table 1. Loadings of the otolith biochronologies of six marine fishes on the first and second principal component (PC) scores. Fishes were sampled from coastal Western Australia and the otolith growth chronologies were from the years 1988 to 2003.

Species	PC1	PC2
Lutjanus argentimaculatus	-0.55	-0.09
Lutjanus bohar	+0.17	-0.66
Lethrinus nebulosus	-0.37	-0.15
Scorpis aequipinnis	-0.32	-0.60
Achoerodus gouldii	-0.49	-0.01
Polyprion oxygeneios	-0.44	+0.43

Table 2. List of models with one explanatory variable that went into the model selection process. Explanatory variables consisted of annual means over the years 1988 to 2003. The response variables were the first two principal components (PC) scores from six marine fishes in Western Australia. Model 1 shows the first-ranked model for $PC1_{inv}$ and model 2 is the first-ranked model with $PC2_{inv}$. The inverse of PC1 and PC2 were used because the respective taxa were negatively loaded on both principal components. ENSO = El Niño-Southern Oscillation, ΔAIC_C = difference in second order Akaike information criterion.

Model	Explanatory variable	ΔAIC_C for $PC1_{inv}$	ΔAIC_C for $PC2_{inv}$
1	Fremantle Sea level	0.00	4.13
2	Pacific Decadal Oscillation	6.11	0.00
3	Dipole Mode Index	11.53	4.16
4	Multivariate ENSO Index	3.64	4.41
5	Intercept only	8.47	1.65

Table 3. Pearson's correlations of the otolith biochronologies of six marine fishes from coastal Western Australia with environmental variables. Otolith chronologies of each species included all periods with synchronous growth signals. SL = sea level, MEI = Multivariate El Niño-Southern Oscillation Index, PDO = Pacific Decadal Oscillation, DMI = Dipole Mode Index. ** indicates a p-value < 0.01, * indicates a p-value < 0.05.
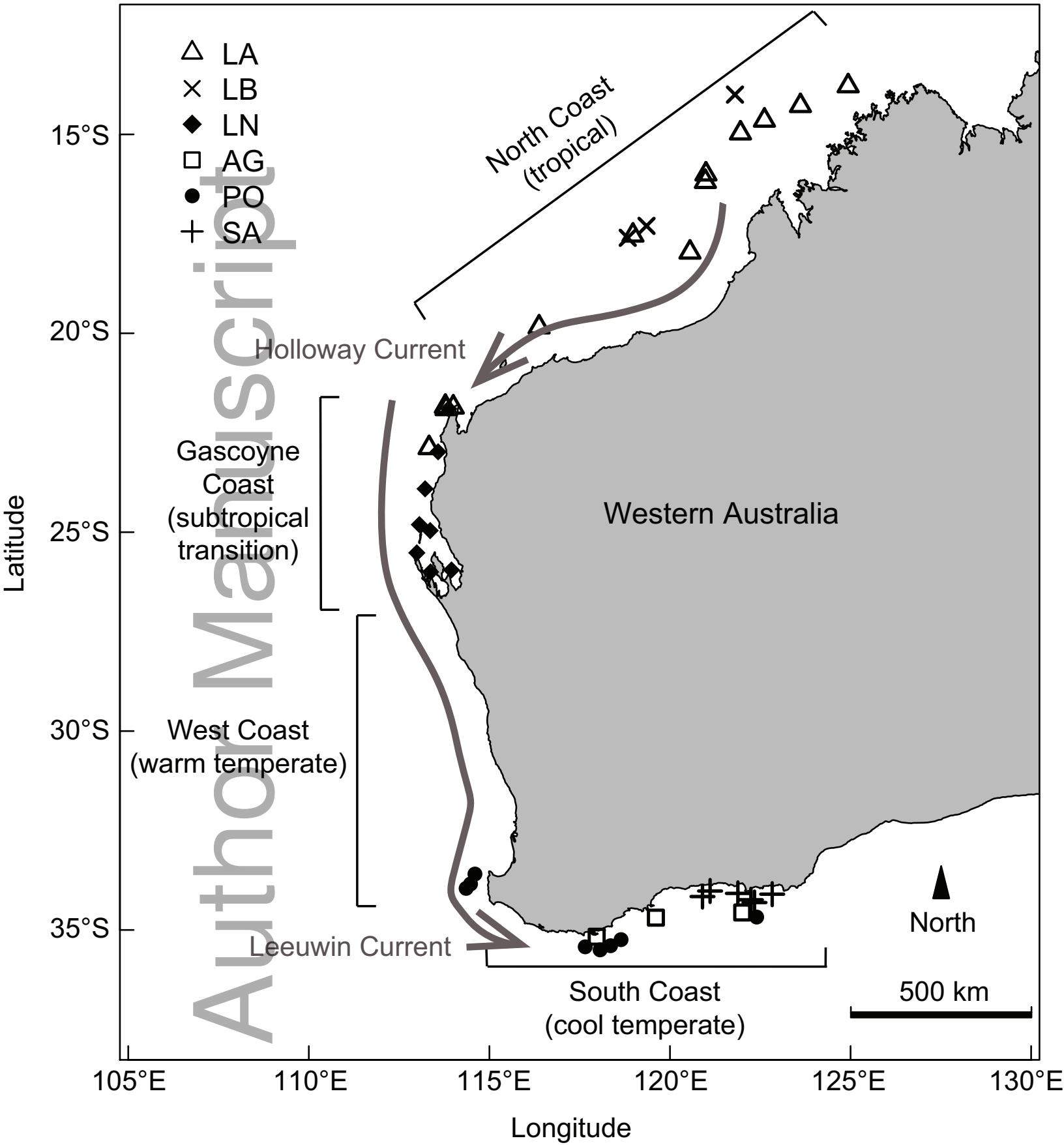
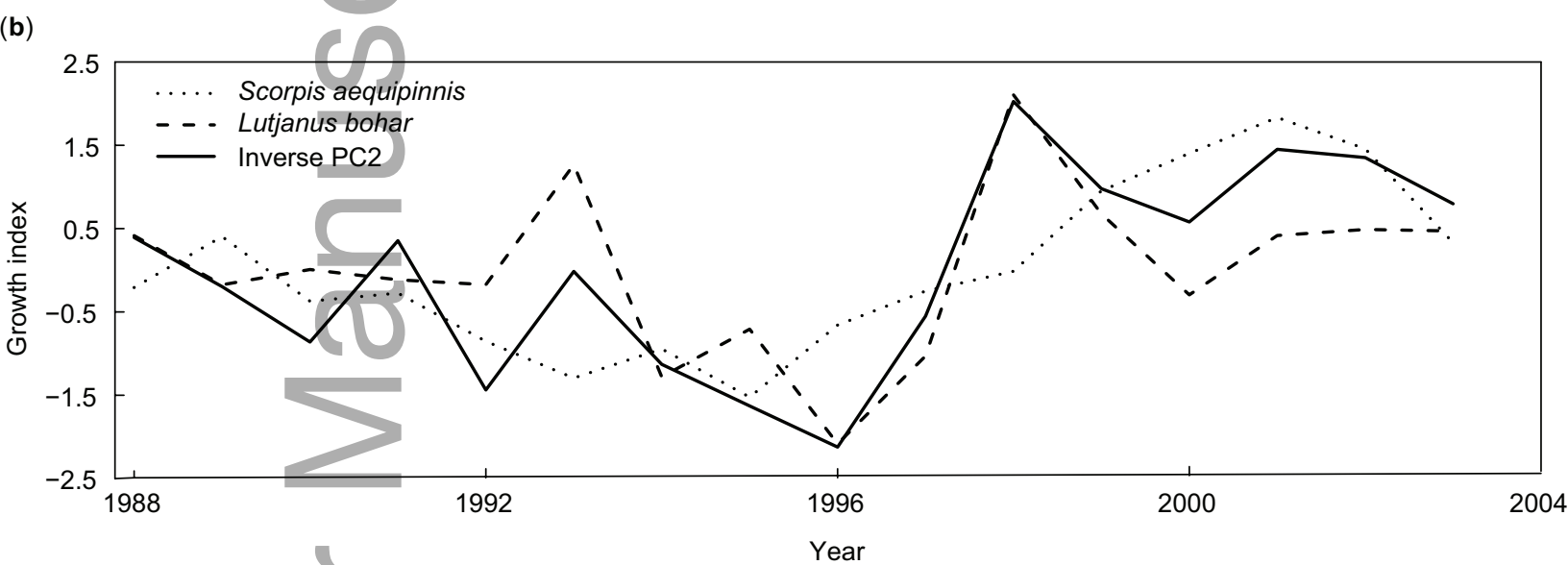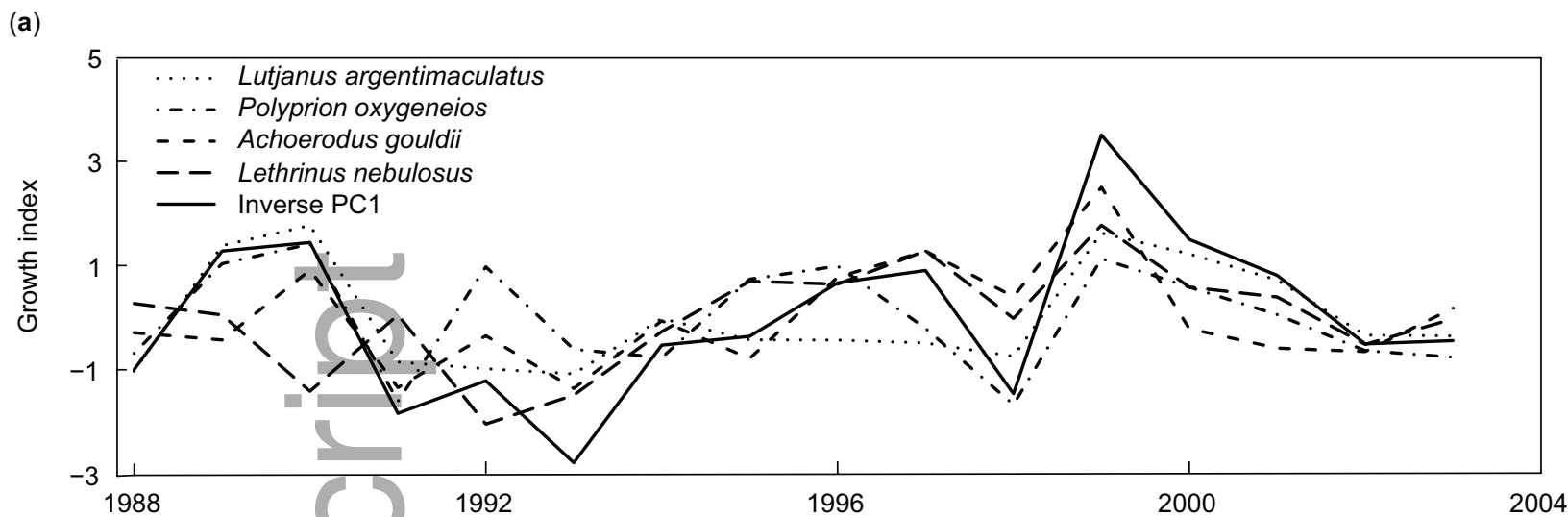| Species	Fremantle SL	MEI	PDO	DMI
Lutjanus argentimaculatus	+0.46**	-0.48**	-0.46**	-0.06
Lutjanus bohar	-0.04	-0.16	-0.26	-0.09
Lethrinus nebulosus	+0.21	-0.01	-0.03	+0.14
Scorpis aequipinnis	+0.56**	-0.44*	-0.63**	+0.11
Achoerodus gouldii	+0.49**	-0.27	-0.06	-0.16
Polyprion oxygeneios	+0.42	-0.43	-0.11	-0.51*

Figure captions

Figure 1. General sampling locations of the six species of adult fishes collected along the coast of Western Australia. LA (Δ) = *Lutjanus argentimaculatus*, LB ($\times$) = *Lutjanus bohar*, LN ($\blacklozenge$) = *Lethrinus nebulosus*, AG ($\square$) = *Achoerodus gouldii*, PO ($\bullet$) = *Polyprion oxygeneios*, SA ($+$) = *Scorpis aequipinnis*. The marine regions and the major current flows along the coastline are also indicated.

Figure 2. Otolith growth chronologies of six marine fishes from Western Australia with the respective leading principal component (PC) scores. Chronologies were detrended (see methods) and standardized (mean=0, variance =1). (a) *Lutjanus argentimaculatus*, *Polyprion oxygeneios* and *Achoerodus gouldii* chronologies with $PC1_{inv}$ and (b) *Scorpis aequipinnis* and *Lutjanus bohar* chronologies with $PC2_{inv}$. The inverse of PC1 and PC2 were used because the respective taxa were negatively loaded on both principal components.
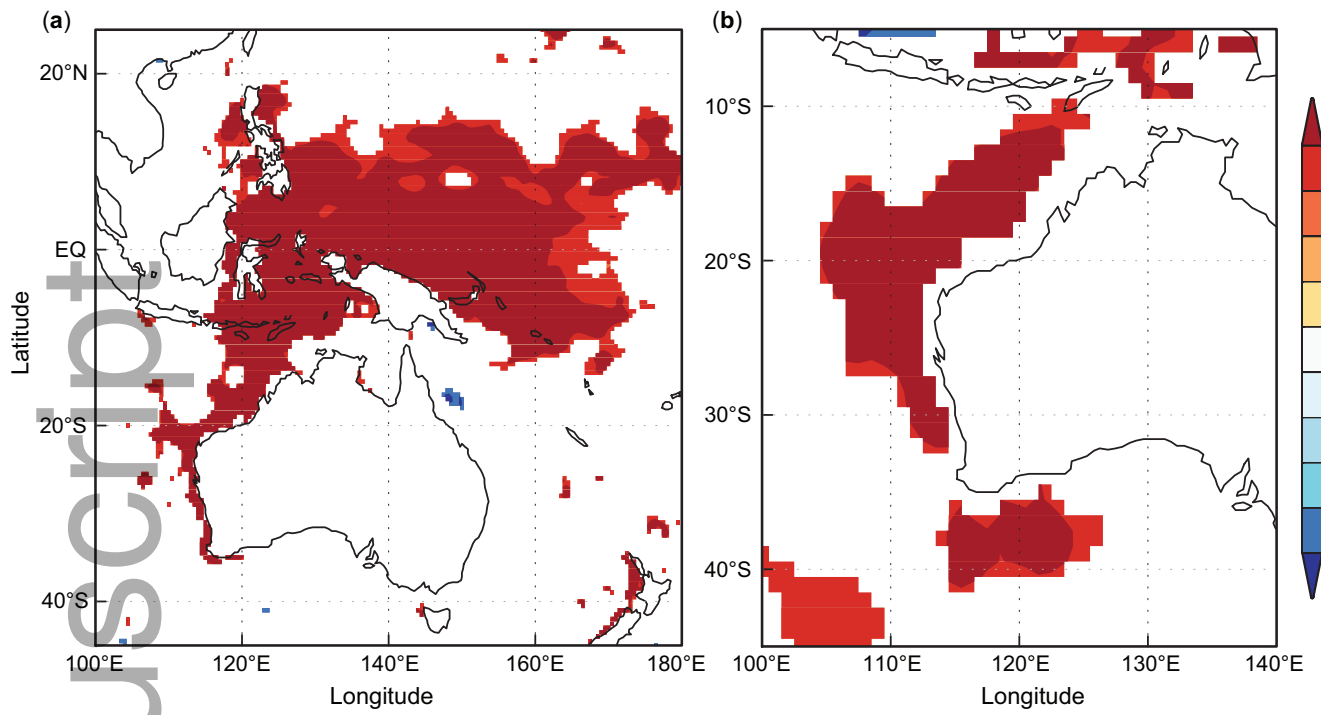
Figure 3. Significant correlations ($p < 0.05$) between the inverse of the first principal component ($PC1_{inv}$) and environmental variables averaged between January and March. $PC1_{inv}$ was constructed from the detrended and standardized growth chronologies of six fishes from Western Australia and inverse values were plotted as five of the six species were negatively loaded on PC1. (a) $PC1_{inv}$ and ocean heat content (0–750 m depth) and (b) $PC1_{inv}$ and ocean mean temperature (0–700 m depth). Warmer colours indicate positive correlations, cooler colours indicate negative correlations. All data were from the years 1988 to 2003 and spatial correlation maps were obtained and modified from KNMI Climate Explorer.

Legend:
△ LA
✕ LB
◆ LN
□ AG
● PO
✚ SA

North Coast
(tropical)

Holloway Current

Gascoyne
Coast
(subtropical
transition)

Western Australia

West Coast
(warm temperate)

Leeuwin Current

South Coast
(cool temperate)

North

500 km

Latitude

Longitude

gcb_14083_f1.eps

(a)

Growth index

- .... *Lutjanus argentimaculatus*
- ·—·— *Polyprion oxygeneios*
- ––– *Achoerodus gouldii*
- —— *Lethrinus nebulosus*
- —— Inverse PC1

(b)

Growth index

- .... *Scorpis aequipinnis*
- ––– *Lutjanus bohar*
- —— Inverse PC2

Year

gcb_14083_f2.eps

gcb_14083_f3.eps