

Water temperature and fish growth: otoliths predict growth patterns of a marine fish in a changing climate

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Abstract

Ecological modeling shows that even small, gradual changes in body size in a fish population can have large effects on natural mortality, biomass, and catch. However, efforts to model the impact of climate change on fish growth have been hampered by a lack of long-term (multidecadal) data needed to understand the effects of temperature on growth rates in natural environments. We used a combination of dendrochronology techniques and additive mixed-effects modeling to examine the sensitivity of growth in a long-lived (up to 70 years), endemic marine fish, the western blue groper (*Achoerodus gouldii*), to changes in water temperature. A multi-decadal biochronology (1952–2003) of growth was constructed from the otoliths of 56 fish collected off the southwestern coast of Western Australia, and we tested for correlations between the mean index chronology and a range of potential environmental drivers. The chronology was significantly correlated with sea surface temperature in the region, but common variance among individuals was low. This suggests that this species has been relatively insensitive to past variations in climate. Growth increment and age data were also used in an additive mixed model to predict otolith growth and body size later this century. Although growth was relatively insensitive to changes in temperature, the model results suggested that a fish aged 20 in 2099 would have an otolith about 10% larger and a body size about 5% larger than a fish aged 20 in 1977. Our study shows that species or populations regarded as relatively insensitive to climate change could still undergo significant changes in growth rate and body size that are likely to have important effects on the productivity and yield of fisheries.

Keywords: *Achoerodus gouldii*, additive mixed models, Australia, climate change, fish growth, otolith, sclerochronology, sea surface temperature

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Introduction

Determining the sensitivity of marine species to climate change is an important part of the development of mitigation and adaptation strategies for the management of marine ecosystems (Rowland *et al.*, 2011), and to date, sensitivity has largely been defined in terms of changes in species distributions. When the rate of climate change exceeds the rate at which a species can adapt to the changing environment, distribution change is a likely response (VanDerWal *et al.*, 2013). If new suitable habitats are unavailable or unreachable for a species, then it may be at higher risk of extinction, and thus, it could be characterized as sensitive. Niche modeling has often been used to predict changes in distributions

under future conditions (based on some assumptions; García-Valdés *et al.*, 2013), and predicted range loss has been used as an indicator of sensitivity (Thuiller *et al.*, 2005). However, species that appear robust using this criterion may still be strongly affected by changing climate conditions.

The distributions of organisms are determined by habitat preferences (physical parameters and biotic interactions), dispersal ability, and history (Pearson & Dawson, 2003; Araújo & Pearson, 2005). The relative importance of these factors can vary spatially and temporally, and it is possible that large parts of a range could be suboptimal (e.g. for growth) in one or more parameters due to other more limiting factors such as dispersal barriers or human exploitation. In these cases, a shift toward the optimal value of an environmental parameter, such as temperature, may or may not cause changes in distribution. However, it could influence

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biotic interactions or have physiological impacts that would be ecologically relevant within the current species range. For example, some fish species are distributed so that many individuals live permanently below their experimentally determined optimum growth temperature (Brodte *et al.*, 2006). Warming could lead to increased growth rates with concomitant changes in size-at-age for such species, and even small gradual changes in fish body size can have large effects on natural mortality, biomass and catch (Audzijonyte *et al.*, 2013). Such effects would not be apparent in a predicted-range-loss indicator of sensitivity, but they require consideration.

There has been success in modeling the relationship between temperature and fish growth on a global scale using dynamic bioclimatic envelope modeling, which accounts for dispersal and aspects of physiology, but such approaches do not account for changes in food availability or trophic interactions (Cheung *et al.*, 2012). Furthermore, for cases in which many individuals are living at nonoptimal temperatures, the modeled environmental preferences of the species may be inaccurate. Controlled experimental studies can also aid in determining the impacts of temperature on growth, but they are of limited value in assessing the impacts of temperature changes in the natural environment because they generally cannot account for the possibility that temperature variations may also drive changes in many other factors (e.g. food supply, competition, etc.) that simultaneously impact growth. Thus, analyses complementary to global modeling efforts and experimental studies, such as those based on observations of past variations of growth rate in nature, can help provide a clearer picture of the impact of climate change on fishes.

Efforts to model fish growth under climate change have been hampered by a lack of the long-term (multi-decadal) data sets needed to understand the effects of temperature and associated covariates on growth rates in natural environments (Morrongiello *et al.*, 2012). For most fish species, profiles of growth responses to temperature under experimental conditions are not known. However, the information on growth rate held within otoliths can be used to develop biochronologies that reflect interannual variations in growth rate over long periods (Morrongiello *et al.*, 2012). Growth rate is an integrative measure (Del Toro-Silva *et al.*, 2008) that reflects the (direct) impacts of temperature variation as well as the associated ecological changes (e.g. temperature might also affect prey abundance), regardless of whether or not the distribution of the study species is in equilibrium with environmental conditions. Thus, changes in growth rate that correlate with changes in temperature result from the net effects of direct and

indirect factors. Historical growth records offer a window on the results of the complex processing of parameter changes by ecosystems, but it is difficult to make mechanistic interpretations of the records without ancillary data. While there are reasons to prefer mechanistic or process-based models for predicting the responses of organisms to climate change, the data required for these models are not available for many systems (Morin & Thuiller, 2009; Morrongiello *et al.*, 2012), and they may not be available before species are significantly impacted. Otolith analysis allows the description of net growth response in many individuals over many past years, perhaps making this technique one of the most powerful and efficient means of estimating the impact of environmental conditions on growth at the population level in systems that have not been studied in detail sufficient for the development of mechanistic models.

Modeling the potential impact of climate change may be particularly important for endemic species because they tend to have relatively narrow geographic ranges and are often more ecologically specialized than widespread species. These factors contribute to increased risk of extinction for endemics (Brook *et al.*, 2008), but this does not necessarily imply that such species are highly sensitive to temperature change. Here, we use a novel approach to examine the sensitivity of the growth of a southwestern Australian endemic marine fish, the western blue groper (WBG, *Achoerodus gouldii*), to temperature. We use a hybridization of dendrochronology techniques and additive mixed-effects modeling to determine the impact of past environmental variation on otolith and body growth of this long-lived (up to 70 years) labrid near the center of its range. The resulting model is used to predict growth responses (including uncertainty estimates) under a climate change scenario.

Our approach allows us to estimate the sensitivity of WBG to climate change in a region of its distribution with conditions substantially removed from critical thresholds (based on the range of temperatures found in the present distribution). We show that although the growth of this species appears relatively insensitive to temperature, climate change could create changes in growth rate sufficient to affect mortality and biomass of stocks.

Materials and methods

Western blue groper are found in shallow depths (generally <60 m) along the western and southern coasts of Australia from the Houtman Abrolhos Islands of Western Australia to Portland, Victoria (Coulson *et al.*, 2009; Bryars *et al.*, 2012). Much of this area is under the influence of the Leeuwin

Current, which brings warm water south along the west coast, then east across the southern coast, making it unusually warm compared to similar regions at the same latitudes (Feng, 2003). Western blue groper are site attached, and average home range is small at 0.04 km² (Bryars *et al.*, 2012). Individuals feed on large invertebrates such as crabs, urchins, and abalone, as well as smaller epifaunal crustaceans and molluscs (Shepherd, 2005).

Most of the otoliths (54 of 56) used in this study came from fish caught by a commercial gill net fishery in 20–100 m water depths between Albany and Esperance in Western Australia (Fig. S1). The remaining two adult otoliths came from recreational fishers in the same region. In addition, some juveniles used in an otolith size/fish size calibration were collected by spearfishing in this region. Based on HadISST data (Rayner *et al.*, 2003), mean annual sea surface temperature in the study region (17.4 °C) is near the median of mean annual temperatures (17.6 °C, min = 14.8 °C, max = 21.4 °C) experienced throughout the species range (also see Fig. S2). The otoliths were collected between 2004 and 2007 as part of an earlier study that also details sectioning and photomicrography procedures (Coulson *et al.*, 2009).

To obtain a long growth chronology from fish collected over only a few years, we preferentially selected otoliths from older individuals (age 29–69). This sampling scheme is not ideal because earlier years of the chronology are constructed only from records of unusually old individuals, and fish surviving to very old age may have nonrepresentative growth patterns (e.g. slow growers might be less susceptible to fishing mortality) (Morrongiello *et al.*, 2012). However, complete avoidance of this problem would only be possible if samples had been collected over many years, which unfortunately is not the case for this species or many others of interest. We partly accounted for bias within our sample by using individually standardized growth indices in our chronology and by including an 'individual' random effect in our mixed-effects model. Both of these strategies decrease the influence of differences in mean growth rates among individuals.

The thicknesses of annual growth increments were measured on digital images using a plug-in written for ImageJ ('IncMeas'; Rountrey, 2009). Polyline were drawn dorsal to the margin of the *sulcus acusticus*, and they remained locally parallel to the direction of growth (i.e. perpendicular to otolith increments; Fig. S3). Otolith growth rate in WBG is highest from November to May, and opaque zones, which were used as increment boundaries, form in austral winter (Coulson *et al.*, 2009). Assignment of measurements to calendar years was aided by cross-dating. This method has been shown to reduce errors in yearly increment assignments (Kastelle *et al.*, 2011), and we suggest that it has been underutilized (with notable exceptions, e.g. Black *et al.*, 2005; Gillanders *et al.*, 2012) in otolith-based studies (see Data S1). We used the date of capture to anchor each increment measurement series, and statistical cross-dating was performed using COFECHA software (Holmes, 1983; see Data S1). Some otoliths that had areas in which increments could not be confidently identified (likely due to nonoptimal section orientation) were excluded from the database. The final set included otoliths from 56 fish

ranging in age from 29 to 69 years (median = 41.5). These were representatives of year-classes between 1934 and 1974.

Growth chronology development

To construct the biochronology, we employed the double detrending method outlined by (Cook, 1985) in which each series was detrended using a modified negative exponential function and then the resulting indices were detrended once more using a spline with the rigidity parameter equal to 67% of the series length. The negative exponential detrending effectively removed the rapid ontogenetic decline in growth rate that occurs in early life, while the subsequent spline detrending removed other low frequency variation including departures from the negative exponential fit. The R package 'dplR' (Bunn, 2008) was used for detrending and analysis. A mean index chronology was calculated from all the series using Tukey's biweight robust mean (Bunn, 2008), and chronology quality was evaluated using the mean of pairwise series correlations (\bar{r}), which is approximately equivalent to fractional common variance (Wigley *et al.*, 1984).

Previous studies have shown correlations between growth and temperature, El Niño/Southern Oscillation (ENSO), and upwelling (Black *et al.*, 2005; Gillanders *et al.*, 2012). We hypothesized that growth rate of WBG might be affected by: (i) temperature, (ii) the strength of the regionally important Leeuwin Current, which influences productivity and is modulated by ENSO (Feng *et al.*, 2009), (iii) ENSO, and/or (iv) the Indian Ocean Dipole, which affects winds and precipitation in western Australia (Ashok *et al.*, 2003). Thus, we tested for correlations between the mean index chronology and detrended sea surface temperature (SST) from the Met Office HadISST set (Rayner *et al.*, 2003), the Multivariate El Niño/Southern Oscillation Index (MEI; Wolter & Timlin, 1993), detrended Fremantle sea level (FSL, a proxy for Leeuwin Current strength (Feng, 2003); data from the Permanent Service for Mean Sea Level, www.psm.org), and the Dipole Mode Index (DMI, reflecting the status of the Indian Ocean Dipole; Saji *et al.*, 1999); data from the Japan Agency for Marine-Earth Science and Technology). In addition, we tested for correlations with WBG catch per unit effort in Western Australia (from Department of Fisheries, Western Australia). Fremantle sea level was linearly detrended to remove the long-term global increase in sea level. To account for a possible lag in response, correlations with environmental variables from the year prior to the year in which growth occurred were also tested.

Because precise capture locations of fish were not available, we included SST data from two representative grid cell locations along the coast ('western south' –35.5°, 116.5°, and 'eastern south' –34.5°, 121.5°; Fig. S1) in analyses. A regional SST (detrended) correlation map was also produced. Detrended SST was used in correlational analyses because otolith measurements were detrended during chronology construction; this removed long-term trends in growth that might be associated with long-term trends in SST. Mixed layer depth in the region varies seasonally from approximately 30 to

80 m (de Boyer Montegut *et al.*, 2004), so surface temperatures should be representative of temperatures experienced by the fish.

Modeling future growth

Predictions of annual increment thicknesses under specific conditions were developed using the R packages 'gamm4' (Wood, 2012) for generalized additive mixed modeling and 'MuMIn' (Barton, 2013) for model selection. This approach was separate from our initial biochronology development, and detrending to remove the influence of ontogeny was not necessary because age was a covariate in the model. This permitted improved assessment of the influence of environmental factors that had long-term trends in addition to high-frequency variations. The utility of similar Bayesian hierarchical models and linear mixed models has been shown in other studies in which the influences of environmental parameters on growth rates recorded in hard parts were estimated (Weisberg *et al.*, 2010; Helser *et al.*, 2012). In this case, our use of an additive mixed model allowed for the linear predictor to depend upon unknown smooth functions of covariates (Wood, 2012), and because the relationship between age and otolith growth rate was complex for WBG, a smooth was appropriately used for the age covariate. Simple linear dependence was assumed for all other covariates (in trials, the use of smooths of other covariates did not improve the models). Model selection (see Table S2) was based on minimization of the corrected (for small sample size) Akaike Information Criterion (AICc; Burnham *et al.*, 2002). The mixed-effects models were based on log-transformed, nondetrended growth increment and age data from the same 56 individuals used in construction of the mean increment chronology, along with environmental data (1959–2003, temporal range limited by availability of complete environmental data series). All evaluated models included a random effect to account for intraindividual correlations in growth rate. All possible models were evaluated with covariates limited to age, mean November–May SST in the western-south grid cell (correlation of growth and SST was higher in this grid cell), mean annual MEI, mean annual DMI, and detrended mean annual FSL. One-year-lagged environmental series were also included. Catch data were not included as the series was of inadequate length. After model selection, we used historical data (HadISST) and output from the National Oceanic and Atmospheric Administration/Geophysical Fluid Dynamics Laboratory coupled model CM2.1 (Delworth *et al.*, 2006) under the SRES A1B scenario to estimate otolith growth under past and future conditions.

To translate environmental effects on otolith growth to effects on fish growth, we determined the relationship between otolith size and fish length. Otolith size was defined as the distance from the first opaque zone, which forms in the first postlarval winter, to the medial surface of the otolith, measured ventral to the *sulcus acusticus*. Otolith size was measured for 82 otoliths from fish of known length aged between 3 and 20 years. We did not include fish over 20 years of age because around this age the corre-

lation between fish length and otolith size weakens as fish reach asymptotic body length and the otoliths continue to grow. Fish could continue to increase in mass beyond this age, but we did not have sufficient data on mass to include it in the analysis. The R function 'nls' (R Development Core Team, 2011) was used to fit a power function relating total fish length to otolith size (Fig. S4). This model was used in conjunction with estimates of otolith growth from the additive mixed model to estimate fish length under specific conditions.

Results

Growth chronology development

Signal strength (relative magnitude of common variance among individuals; as indicated by \bar{r}) was low, but sample depth (number of individual measurements per year) was adequate to reveal a common signal that was statistically significant (Fig. S5). Sample depth was at a maximum of 56 individual increment measurements per year for the period from 1976 to 2002. In this period, \bar{r} was 0.022 (s.e. = 0.005), and the interseries correlation, or mean correlation of each detrended individual series with the mean of all others was 0.112.

Despite apparently low sensitivity, statistically significant, positive \bar{r} were found for all 15-year windows with midpoints from 1976 to 1996 (i.e. the period from 1969 to 2003; Fig. S5) indicating that the chronology covering this period carried a signal of synchronous regional variation in growth. Earlier 15-year windows also showed significant positive \bar{r} (those with midpoints from 1959 to 1962, and 1965 to 1968). To determine the effect of including earlier years, we first constructed a chronology using data from 1969 to 2003. This chronology was positively correlated with mean November–May sea surface temperature at the 'western-south' grid cell near Albany ($r = 0.61$, $P = 0.0001$), suggesting temperature in the region may have been a driver of growth. We then constructed a second chronology covering the period from 1952 to 1968. This chronology also showed a positive correlation with November–May sea surface temperature at the 'western-south' grid cell ($r = 0.50$, $P = 0.04$), giving some indication that the chronologies from both time intervals captured a dependence of growth on regional temperature.

As an additional check, we calculated the bootstrap 95% confidence interval for \bar{r} in the 52-year period from 1952 to 2003 (requiring that an individual series overlap another series by at least 30 years – the default in the dplr package – for the correlation to be included in calculation of \bar{r}). The calculated \bar{r} was 0.019, and the 95%

confidence interval did not include 0 (0.009–0.029). Based on this result and the persistence of correlation with temperature over the entire period, we chose to use the chronology encompassing the years from 1952 to 2003.

Correlations with environmental variables

A map of the correlation between the chronology and detrended SST around Australia (Fig. 1) reveals that growth was positively correlated with SST along the west and south coasts (fish were collected on the south coast) of Australia from November to May, the part of the year during which otolith growth rate is highest. The spatial pattern of correlations (i.e. positive correlations in the southwest) also shows the influence of the Leeuwin Current on SST in the region. The occurrence of relatively high correlations with SST in this region was taken as additional evidence that the weak signal, as expressed through synchronous patterns in growth, was not spurious.

Of the two selected SST grid cells on the south coast, the record from the ‘western-south’ (WS, Fig. S1) cell exhibited higher correlations with the chronology. Significant (with Bonferroni–Holm adjustment for multiple tests) positive correlations were found with mean SST in January–March ($r = 0.48$, $P = 0.0003$), April–June ($r = 0.52$, $P < 0.0001$), and November of the previous year through May of the current year (the season of rapid growth) ($r = 0.55$, $P < 0.0001$). The

other cell, ‘eastern south’ (ES, Fig. S1), showed slightly weaker correlations for mean November through May SST (Table S1), but the correlations were not significantly different (Williams test, $P = 0.95$). There were no significant correlations with MEI, DMI, detrended FSL, or catch per unit effort (Table S1). We also found no significant lagged (1 year) correlations between the chronology and environmental series (Table S1).

Modeling future growth

To quantify the impact of projected climate conditions on body growth, we first developed an additive mixed model to predict annual otolith growth given environmental conditions, then determined the relationship between otolith size and fish size (length) for WBG. The model that included a smooth of age and the mean November–May SST in the WS grid cell was stronger than other possible models ($\Delta\text{AICc} > 5$), and age and mean November–May SST were present in nine of the top ten models identified (see Table S2). A significant positive response of increment thickness to temperature (estimate = +0.0461, SE = 0.0093; see Fig. S6 for additional model details) was indicated. The otolith-size/fish-length relationship (Fig. S4) was significant ($r^2 = 0.77$, $P < 0.001$), with

$$L = 23.61O_s^{0.51}$$

where L = total length (mm) and O_s = otolith size (μm).

We predicted the response to climate change by using the model to calculate otolith growth from age 2 to 20 under historical SST from 1959 to 1977 and projected SST from 2081 to 2099 (from the NOAA GFDL CM2.1 model under the A1B scenario (Delworth *et al.*, 2006); Fig. 2c). Growth increment thickness and uncertainty were calculated for each year, and the cumulative sums provided the estimated otolith sizes and uncertainty at a given age, which were then used to determine fish size. The model results suggested that fish aged 20 in 2099 would have otoliths about 10% larger than those of the same age in 1977 (794 μm , 1-SE interval = 773 to 817 vs. 720 μm , 1-SE interval = 706 to 734) (Fig. 2a), and the differences in estimated otolith size were significant ($P < 0.05$) at all ages. However, due to the allometric relationship between otolith size and fish size for WBG, this did not mean that body size would also increase by 10%. The models predicted that fish growing near the end of this century would be between 5% and 6% larger than their twentieth-century counterparts (Fig. 2b). To assess this difference given the uncertainties, we ran 10 000 simulations drawing from the error distributions in both models under

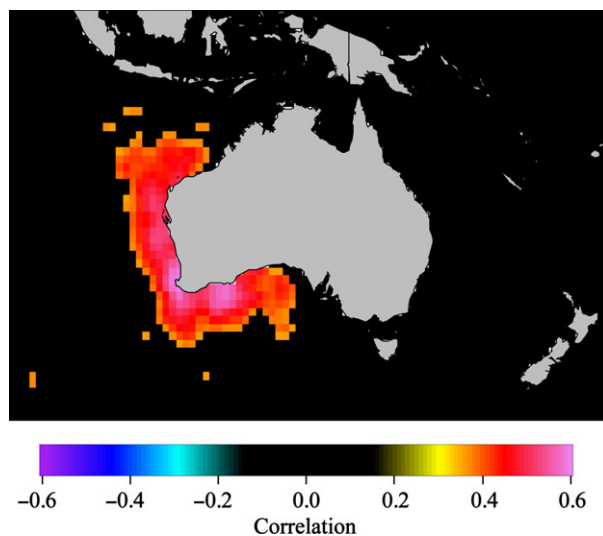


Fig. 1 Map depicting significant correlations ($P < 0.01$) between the western blue groper otolith increment chronology and linearly detrended mean November to May sea surface temperature from 1952 to 2003. Strong positive correlations occur off south-western Australia where the fish were captured.

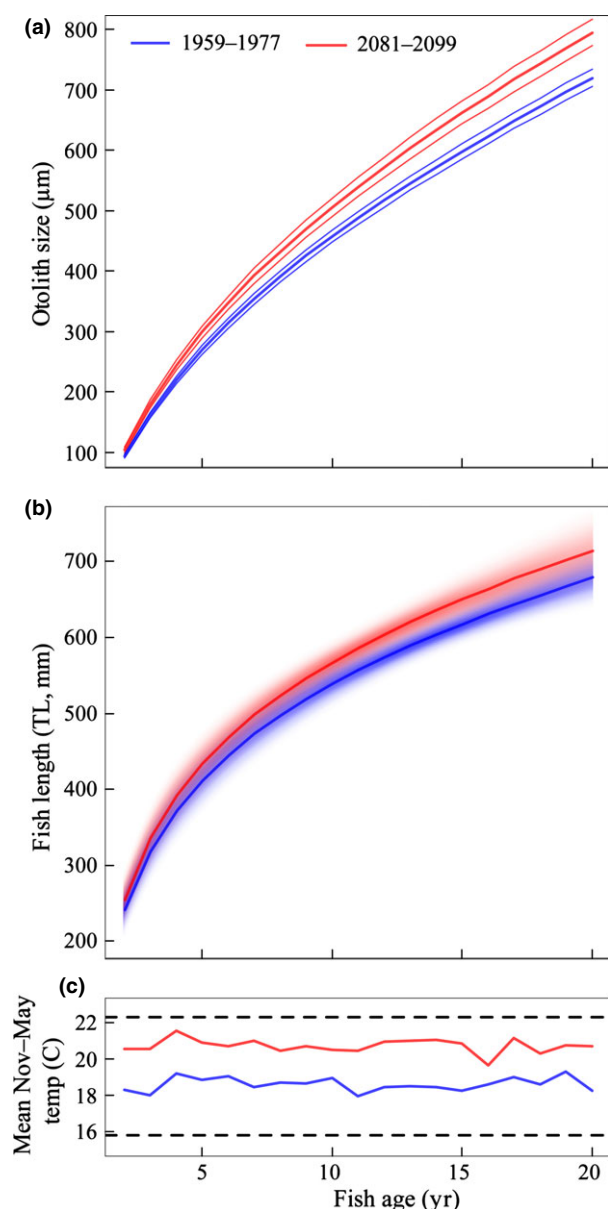


Fig. 2 Model results showing otolith size and fish length under historical (blue) and future (red) sea surface temperature (SST). (a) Predicted otolith size (heavy lines) \pm 1 SE (fine lines) for fish aged 2–20 years. (b) Predicted fish length (lines) and density of simulations resulting from sampling the error distributions in both models (shading). (c) Mean November–May SST series used for historical (blue) and future (red) model predictions; dashed lines indicate the maximum and minimum long-term (1952–2003) mean November–May HadISST in grid cells representing the approximate range of this species.

1959–1977 conditions and 2081–2099 conditions. For age-2 to age-7 fish, predicted sizes under future conditions were greater than those under historic conditions in at least 75% of simulations. For age-8 to age-20 fish, this value was greater than 91%.

Discussion

We showed that growth rates of WBG in this region may be higher under conditions predicted to occur later this century, assuming other factors are not limiting and that the response to temperature in the future is similar to the response in the past. Our analysis identified relatively weak (as shown by the low \bar{r} of 0.019) but significant influences of regional temperature on otolith growth in WBG, and the biochronology showed that growth in this region has tended to respond positively to increased temperatures in the past. Temperatures in November to May predicted for the end of this century in the sampled region do not exceed historical temperatures from the warmest part of the present species distribution (Fig. 2c), indicating the predicted thermal conditions are likely to be within the range required by the species (Fig. S2).

It was not clear if the observed response of WBG to temperature variation was due to a direct physiological effect, such as an increase in aerobic scope (Pörtner & Knust, 2007), an indirect effect related to prey availability or other biotic interactions, or a combination of both. It is notable that the abundances of several other marine invertebrate and fish species found off southwestern Australia appear to be influenced by the strength of the regionally important Leeuwin Current, principally through effects on larval phases (Caputi *et al.*, 1996). If abundances of prey species for WBG were also affected by the strength of the Leeuwin Current, and this drove changes in growth rate, we might expect to see a strong correlation between WBG growth and Fremantle sea level (a proxy for Leeuwin Current strength), perhaps with a lag, but this was not the case (Table S1). Growth of WBG in the study region seemed most closely tied to SST in the warmer parts of the year (Table S1), which may indicate a physiological effect, but we do not know the impacts of temperature on WBG prey abundance or availability, and the experimental optimum growth temperature has not been determined for this species.

Endemism at the scale presented by this species did not appear to be associated with heightened sensitivity of growth to temperature. Other studies that have used dendrochronology techniques to analyze otoliths have shown more acute influences of environmental factors on growth. For example, Black *et al.* (2005) found an interseries correlation (the mean of the correlations between individual detrended series and the chronology – a measure related to common variance and signal strength) of 0.523 for splitnose rockfish (*Sebastes diploproa*) off the west coast of the United States, while Gillanders *et al.* (2012) found an interseries correlation of 0.512 for luderick (*Girella tricuspidata*) in New Zealand waters. In contrast, we found an interseries correlation

of 0.112 for WBG suggesting that this species is relatively insensitive to regional environmental variations in the study area.

Despite this result, our model still predicted that WBG in the region can be expected to increase in size by about 5% by the end of this century due to increasing November–May (growing season) water temperatures. While such a change in length may seem insignificant, recent modeling work by Audzijonyte *et al.* (2013) showed that small, gradual, changes in length-at-age (4% over 50 years) can have disproportionately large impacts on predation mortality, biomass, and catch. These impacts occur due to complex ecosystem feedback loops, and changes in the size of one species can influence others (Audzijonyte *et al.*, 2013). The results have important implications since they suggest that climate change may have major impacts on species and/or ecosystems even when regional changes in temperature are only a minor driver of variance in growth. Brander (2007) suggests that management of fisheries should, where possible, take into account the effects of climate change on growth and other variables, and our study provides an example of an approach that can be used to assess the sensitivity of growth to climate change in species that have not been the focus of long-term monitoring efforts. Such analyses, in combination with other techniques such as ecosystem modeling, could allow for additional exploration of the complex effects of temperature change in marine systems.

The biochronology that we developed using classical dendrochronology methods (detrending and averaging) captured the dependence of the growth of WBG on interannual variation in water temperature. However, detrending also removed low frequency variance, some of which may have related to low frequency variance in environmental parameters. Recognition of this issue by dendrochronologists has led to the development of methods that retain more low frequency variance such as Regional Curve Standardization (RCS; Briffa & Melvin, 2011). As pointed out by Helser *et al.* (2012), a multilevel modeling approach can be similar to RCS in that ages and increment thicknesses are used to estimate the influence of ontogeny. However, it differs from RCS in that the model may account for intraindividual correlations (e.g. consistent offset from the expected growth rate) through a random effect. This helps to mitigate one of the potential problems with the RCS technique – some individual-level differences in growth rate may be due to site-specific factors, such that differences from the expected growth trend are partly forced by drivers other than regional climate (Fritts, 1976). In WBG, some variation in otolith growth rate was likely due to local drivers and/or genetic factors that were unrelated to regional environmental variation, but data

were not available to characterize individual-level influences, so use of an individual-level random effect was appropriate. Furthermore, using our approach, estimation of the parameters for the smooth function (of age) was part of the model fitting process, so that it was not necessary to choose a function or spline rigidity in estimation of the general growth profile.

Earlier research often focused on the edges of species ranges as these areas are expected to be strongly influenced by climate (Parmesan & Yohe, 2003). However, the effects of climate change may vary across a species range, so knowledge of impacts occurring away from edges is also required. Our results show that, despite a potentially weaker influence, ecologically relevant impacts of climate change are still detectable in regions distant from the edges of species distributions. For WBG, the consequences of increased temperatures in the warmer northern-most part of the range are unknown, since temperatures are predicted to exceed those experienced historically over the range of the species. Growth rates may increase, but temperatures could also exceed the temperature at which aerobic scope is maximized, resulting in negative impacts on growth and reproduction (Neuheimer *et al.*, 2011). In the absence of other limiting factors, individuals in the region of sampling (near the center of the distribution) are likely to benefit from warming, suggesting that they may currently be living at suboptimal temperatures for growth. Similar observations have been made in other studies. For example, Neuheimer *et al.* (2011) showed that populations of banded morwong (*Cheilodactylus spectabilis*) in the Tasman Sea near the center of the species range showed acceleration of growth with increasing temperature, while those at the warm margin of the range showed decreased growth rates that might indicate a coming range contraction. Luderick (*Girella tricuspidata*) in New Zealand (Gillanders *et al.*, 2012) and redfish (*Centroberyx affinis*) and jackass morwong (*Nemadactylus macropterus*) in the southwest Pacific (Thresher *et al.*, 2007) have also shown positive growth responses to increases in temperature in the past, suggesting that these populations occur in regions with temperatures that are suboptimal for growth.

Given the complexities of marine ecosystems, it is difficult to predict how species and individuals will respond to future increases in temperatures. Of concern is the fact that, even for a species such as WBG, in which regional signals of water temperature appeared to play only a minor role in driving growth, predicted outcomes for size-at-age under scenarios of climate change are likely sufficient to have important impacts on the productivity and yield of stocks. For this reason, additional studies that broaden the picture of likely responses for other marine species, including those at higher and lower trophic levels in the same system, are

needed. By combining classical dendrochronology methods with mixed-effects models, important insights regarding the potential responses of understudied species or populations can be obtained in a relatively fast and efficient manner.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supporting Notes.

Figure S1. Map showing WBG distribution, sampling area, and SST locations.

Figure S2. Monthly mean SST within the range of WBG.

Figure S3. Sectioned WBG otolith.

Figure S4. Relationship between otolith size and fish length.

Figure S5. \bar{r} with bootstrap confidence intervals and sample depth.

Figure S6. Details of the selected additive mixed model.

Table S1. Correlations between 1952–2003 mean increment chronology and environmental variables

Table S2. Model selection table for mixed models ranked by AICc (only top ten shown). The highest ranked model was used for predictive modeling.