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Determining climate-growth relationships in a temperate fish: A sclerochronological approach

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ABSTRACT

Otoliths of fish can provide long-term chronologies of growth. Differences in the width of the annual growth increments can reflect the effects of environmental variability on somatic growth rate. We used generalized linear mixed models (GLMM) to evaluate the influence of region, sea surface temperature (SST), El Niño–Southern Oscillation events, and recruitment on the otolith growth of King George whiting (*Sillaginodes punctatus*), a commercially and recreationally important fish species in southern Australia. Growth increment data spanned 25 years (1985–2010). The optimal model demonstrated that mean winter SST was negatively correlated to growth, and as the winter SST increased the average width of the growth increments declined. However, the temperature effect was very weak ($r^2: 0.0006$). There were no regional growth differences and recruitment was not correlated with growth. Understanding long-term temperature-growth relationships is crucial for disentangling the effects of climate change and other parameters on fish growth, and thus predicting how populations will change in the future.

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1. Introduction

Climate change is a major threat to global biodiversity and ecosystem functioning (Solomon et al., 2007), and its effects are already evident across a range of marine environments and biota (Parmesan and Yohe, 2003; Hobday and Lough, 2011). Understanding how fish populations respond to a changing environment is essential for predicting the future effects of climate on fish growth and survival (Morrongiello et al., 2012). Despite this, there is still a paucity of long-term ecological data available for marine fish species (Thresher et al., 2007), especially in the southern hemisphere. Regions such as Australia, are experiencing relatively rapid rates of global warming (Hobday and Lough, 2011). All fish species have a temperature range at which growth and survival are optimal (Pörtner and Farrell, 2008), hence a detailed understanding of the effects of temperature on individual fish species is important for predicting how they may change in the future (Thresher et al., 2007; Neuheimer et al., 2011; Gillanders et al., 2012).

An approach for measuring long-term changes in temperature may be the use of otoliths or ear bones of fish. Otoliths have annual ever, detecting and assigning environmental/ecological factors to growth chronologies is difficult due to different factors driving growth responses (Parmesan et al., 2011). A number of approaches have been used to analyze growth biochronologies in the hard parts of aquatic organisms (e.g. otolith, teeth and shells). These approaches include master chronology (Black et al., 2011), generalized linear models (GLMs; Weisberg, 1993), generalized linear mixed models (GLMs; Weisberg et al., 2010; Kendall et al., 2010; De'ath et al., 2009) and age-/stage-specific regression (Thresher et al., 2007). Biochronological data such as growth are usually hierarchical and consist of a repeated measurement from individuals of different years and populations (Morrongiello et al., 2012). Factors that can externally affect the species growth rate include extrin-

growth increments (bands) that can be used to reconstruct growth histories of individuals and populations (Black et al., 2008a,b). How-

sic and intrinsic factors. Intrinsic factors are the age-dependent or individual specific factors influencing growth; extrinsic factors are related to environmental conditions (e.g. temperature) or biological interactions (e.g. competition). Dendrochronological approaches rely on crossdating method to ensure that all increments are assigned to the correct calendar year of formation. The crossdated data can be then analyzed to generate chronologies using different techniques, such as mixed modelling approaches (Morrongiello and Thresher, 2014), individual de-trending (Black







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et al., 2011) and Bayesian approaches (Helser et al., 2012). In individual detrending approaches otoliths are first visually crossdated to make sure growth increments have been assigned to the correct calendar year (Black et al., 2005; Gillanders et al., 2012) and then the increment width are measured. Crossdating is then statistically validated (e.g. using a program like COFECHA; Holmes, 1983). Low-frequency variability is removed via detrending (Black et al., 2008b). One of the methods for detrending is that, each measurement time series are fit with a cubic smoothing spline with a 50% frequency response and then dividing by the values predicted by the spline and finally removing the low-frequency variability by weighting each set of measurements to a mean of one. This process enhances high-frequency growth variation. Detrended time series are correlated with the average of other standardized/detrended time series (Black et al., 2008b). Lastly, the detrended increment measurements return to the original data and can be used by different techniques (e.g. individual detrending, mixed effects modeling, Bayesian approaches) to generate chronology.

Mixed modeling approaches have been utilized as a flexible tool for representing hierarchy within and among individuals (Morrongiello and Thresher, 2014). Such models can also analyze the effect of intrinsic and environmental variability on otolith growth increments across species and through time (Morrongiello and Thresher, 2014). In age stage specific regression, growth variation and the extrinsic drivers are examined at specific life history stages (Neuheimer et al., 2011; Thresher et al., 2007). This approach maximizes accuracy of measurements but results are restricted to the age classes examined (Morrongiello et al., 2012).

GLMs have been used to correlate growth increment width with environmental and fishery covariates at the time of the growth increment formation (Weisberg, 1993). GLMs can account for both intrinsic and extrinsic environmental parameters and the change in increment width with age can be explicitly represented in the model (Weisberg et al., 2010; Ostazeski and Spangler, 2001). A shortcoming of the application of GLMs for this purpose is that multiple measurements from individual fish are treated as independent measurements, violating an assumption of the model. This is referred to as temporal pseudo-replication, the failure to acknowledge the sequential measurement of multiple observations on the same treatment replicate (Millar and Anderson, 2004).

The development of GLMMs (Lindstrom and Bates, 1990; Pinheiro and Bates, 2000) has permitted temporal pseudoreplication to be accounted for by treating each unique fish as a random effect in a GLMM (Weisberg et al., 2010). Mixed modelling methods provide an ecologically robust understanding of how fish may respond to climate variability (Black et al., 2008a; Matta et al., 2010; Thompson and Hannah, 2010). Ecologists usually use GLMMs for analyzing both parametric and non-parametric data which involve random effects and rely on large samples approximation (Bolker et al., 2009). Random effects in mixed modeling can also represent repeated measurements from individuals (Morrongiello et al., 2012). However, GLM is sometimes challenging as it is limited by the assumptions that errors are normally distributed and is statistically complex (Guisan et al., 2002).

A growing number of studies have used otoliths to elucidate long-term patterns in fish growth in response to biological (e.g. age, gender) and external (e.g. environmental variables) factors (Hagen and Quinn, 1991; Black et al., 2008a; Morrongiello and Thresher, 2014). Time-dependent changes in otolith growth increments have been investigated for a number of species using GLMMs including, golden perch (*Macquaria ambigua*) (Morrongiello et al., 2011), tiger flathead (*Platycephalus richardsoni*) (Morrongiello and Thresher, 2014) and smallmouth bass (*Micropterus dolomieu*) (Weisberg et al., 2010). Otolith growth analysis using a mixed modelling approach can help with predicting the growth responses of individual fish species to environmental parameters (Morrongiello and Thresher, 2014).

King George whiting (Sillaginodes punctatus; Sillaginidae), is an important commercial and recreational fish species found in temperate southern Australia (Kailola et al., 1993; Hyndes et al., 1998). King George whiting spawn in offshore areas and the post-larvae are transported to shallow protected embayments that are the nursery areas. The juveniles grow and develop and as sub-adults migrate back to deeper water (Fowler et al., 2002). There is little known about the effects of climate change and recruitment on King George whiting growth. We reconstructed historical climate growth relationships for this species using otolith growth chronologies (Weisberg et al., 2010; Morrongiello and Thresher, 2014). The objectives were addressed using a mixed modelling approach to examine: 1) inter-annual variation in growth and; 2) the influence of a number of environmental variables including, sea surface temperature (SST), El Niño-Southern Oscillation events, and recruitment on growth variation.

2. Materials and methods

2.1. Sample collection

Transverse otolith sections from King George whiting were sourced from archived collections held at the South Australian Research and Development Institute (SARDI), Aquatic Sciences. The samples had been collected from Spencer Gulf (SG) (-34.30°N, 136.98°E), Gulf St Vincent (GSV) (-34.92°N, 138.59°E) and the northern coastline of Kangaroo Island (KI) (-35.65°N, 137.63°E) in South Australia between 1995 and 2010 (Table 1). Fish were obtained from recreational fishers, commercial catch, and scientific surveys. They ranged in length from 324 to 563 mm (Table 1).

2.2. Otolith preparation and growth estimation

The transverse sections had been previously prepared for age analysis. Each otolith had been embedded in clear, polyester resin and allowed to cure overnight before being sectioned through the core. The transverse section was mounted on a microscope slide using resin, and viewed using a dissecting microscope (Leica[®] DMLB) with transmitted light and 25x magnification. The section was lightly coated with immersion oil to accentuate the otolith macrostructure and aged by counting annual increments (opaque zones) from the core to the edge. To ensure a sufficiently long growth chronology, the study was restricted to fish aged six years and older. Growth increment widths were measured using 'Image-Pro[®] Plus software' (version 7.0), along a transect towards the proximal edge from the core to the last complete increment (Fig. 1).

In South Australia, King George whiting spawn in autumn, with a birth date in May and a larval phase of approximately 5 months (June-November) (Fowler and Short, 1996, 1998). They lay down their first opaque zone in October of the following year (Fowler and Short, 1996), representing the first 16 months of life rather than 12 months. Therefore, the first growth increment from the core was not included in the analysis. Based on the timing of growth increment formation, the biological growth year of King George whiting was defined from the 1st October of each year to 30th September of the following year (i.e. 2007/08 was therefore referred to as 2007). To ensure the correct calendar year was assigned to each growth increment, marginal increments were classified visually, as narrow, wide, or intermediate and subsequent rules applied depending on the month of capture (Table 2). The 1st October was assumed to be the formation date of each increment, and, for most fish, one year was subtracted from year-of-capture, as the marginal increment was not included in the analysis. This approach helps to ensure the Download English Version:

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