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Extracting a time-varying climate-driven growth index from otoliths for use in stock assessment models

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ABSTRACT

Understanding the characteristics of individual growth is a critical component of population assessment. Most fisheries stock assessments assume constant values for each life history parameter, despite growing evidence that growth is variable at individual, temporal, and spatial scales. Otoliths contain important information pertaining to age and growth, among other things, and otolith increment data correlate with climate indices on a decadal scale. We expand on this concept to include individual- and year-level variation, and develop a nonlinear mixed-effects model to analyze otolith increment data. We then fit the model to otolith increment data for splitnose rockfish, and simulation-test the ability to precisely estimate year effects without bias. Generally, given a sample size of at least 50 otoliths, the model performs well at estimating year effects. With this method, species-specific indices of growth can be extracted from otolith increment data, and potentially be used in stock assessments to detect the effects of climate change on fish growth.

1. Introduction

Climate can have varying degrees of impact on a population depending on life history stage, and these impacts are often highly complex and difficult to isolate (Black, 2009). Understanding variability in life history characteristics in space and time also helps determine the most appropriate assessment model structure (Gertseva et al., 2010), although time-variation in biological rates adds complexity to the definition of management targets (Thorson et al., 2015). Estimating the growth of individual fish is important to stock assessment modelling, as growth is one component of the productivity of a stock. Currently, most stock assessments assume time-invariant mean growth rates (Lorenzen, 2016), even though there is an increasing number of studies that show that growth actually varies over time (e.g., Black, 2009; Stawitz et al., 2015; Thorson and Minte-Vera, 2016), particularly in response to environmental factors such as temperature and food availability (Brett, 1979; Weatherley, 1990).

Collecting long-term (multiple decades) growth data on marine fish populations is often a lengthy and costly process, which makes mechanistic understanding of growth drivers difficult, and indices of growth variation hard to obtain. Stawitz et al. (2015) describe a state-space Bayesian modelling approach that uses fishery-dependent and −independent data to detect the presence of growth variation. However, sampling procedures (such as selectivity) could potentially be confounded in the annual growth anomalies, as acknowledged by the authors. Measurement of annually-formed growth increments, using a method known as dendrochronology, has been proposed as an alternative to direct measurements for the reconstruction of time series of environmental variation in growth (Black et al., 2005; Strom et al., 2004; Weisberg, 1993). Dendrochronology may be costly and time-consuming (Stawitz et al., 2015), but represents a fishery-independent source of data as back-calculation would allow for observations for ages that are rarely sampled, perhaps due to gear selectivity (Ballagh et al., 2011; López-Abellán et al., 2008). Additionally, otoliths contain historical information about growth that would allow of reconstruction of growth time series potentially dating back to before size-at-age data were available (Begg et al., 2005).

In terrestrial forested ecosystems, tree ring data have been widely used to reconstruct various aspects of climate, disturbance, and community dynamics, and are accepted as a way to capture changes in the environment (e.g., measuring a species' sensitivity to climate). Similarly, bony fish are known to deposit annual rings on their otoliths, much like tree rings (Pannella, 1980). Studies have previously examined the application of dendrochronology techniques to reconstruct time series of ocean conditions (Black, 2009; Strom et al., 2004). Widths between each ring on otoliths of splitnose rockfish (*Sebastes diploproa*) were measured, and detrended using cubic splines and autoregressive models to remove any age-related trends in the data (Black et al., 2005). The resulting time series was averaged to create an environmental index for the species, which was then found to be strongly

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correlated with various productivity indicators in the California Current Ecosystem and other dendrochronology indices obtained from trees and other marine species in the area (Black, 2009). However, early years of growth data for each otolith − particularly critical in short-lived species (Weisberg et al., 2010) − were removed from the study to allow for better model fit, which could affect the strength of the relationship between growth and the environment, as well as the precision of the resulting indices.

Rather than the use of cubic splines by Black et al. (2005), fish growth is often described using a nonlinear model such as the von Bertalanffy growth curve (Essington et al., 2001; Von Bertalanffy, 1957). Mixed effects models − where fixed effects describe the entire population, and random effects are associated with randomly-selected experimental units within the population (Pinheiro and Bates, 2000) − are often used to describe incremental growth data, repeatedly measured on the same individuals over a period of time ("longitudinal data", Liang and Zeger, 1986; Zeger and Liang, 1986). This method originated from a study on bacon pigs (Wishart, 1938), and followed by studies on emus (Palmer et al., 1991), clams (Escati-Peñaloza et al., 2010), and tree rings (Xu et al., 2014). Bayesian hierarchical von Bertalanffy growth curves have been used in meta-analyses to model overall fish length across similar species (Helser et al., 2007) and across geographic environments (Helser and Lai, 2004). They have also been used in tag-recapture studies on fish growth (e.g., Eveson et al., 2015; Zhang et al., 2009; Zhu et al., 2016), but, as mentioned previously, these data might not be readily available for many species. Pilling et al. (2002) fit a random effects von Bertalanffy growth model to length-at-age information back-calculated from otolith increment data for tropical emperor, *Lethrinus mahsena*, specifically incorporating individual (but not annual) growth variability. Similarly, Alós et al. (2010) fitted von Bertalanffy growth curves to back-calculated length-at-age data from otoliths for painted comber *Serranus scriba* using a Bayesian approach, using growth parameters specific to the individual. However, these studies did not specifically incorporate year effects, and assumed a direct relationship between otolith increment growth and somatic (body) growth. Weisberg et al. (2010) described additive linear mixed effects models that were empirically used with otolith increment data for Pacific halibut (*Hippoglossus stenolepis*) and smallmouth bass (*Micropterus dolomieu*) respectively, where year and individual effects were treated as random. A modified von Bertalanffy curve (Von Bertalanffy, 1957) was also fit to the data, although it did not perform well with this parameterization, and only age (and not year or individual) effects were estimated. Furthermore, the methods applied by Weisberg et al. (2010) were not simulation-tested, nor were the year effects cross-validated with other local species, as was done in Black (2009).

The main purpose of this study is to develop a mixed effects model using a von Bertalanffy curve – the most commonly used growth model in stock assessment – that incorporates both random individual effects and random year effects, with the aim of obtaining a time-varying index of growth directly from otolith increment data (i.e., the otolith increment data were not converted to length-at-age data). The model was tested in terms of its ability to accurately detect and estimate year effects from simulated otolith increment data, given various samples sizes, life histories, and levels of process and measurement error. To our knowledge, this method (and its parameterization) has not been applied previously for the analysis of otolith band widths for use in estimating climate indices, and has only been made more accessible due to recent developments in nonlinear minimization software.

2. Methods

2.1. Model description

There were three sources of random variation in the model − the year effects, individual within-fish variation, and process error. Year effects could come from any environmental factor or time-varying factor, while individual effects could potentially come from genetic, environmental or behavioral differences. Cohort effects were also considered for the model, but a meta-analysis by Thorson and Minte-Vera, (2016) found they only explained variability of weight-at-age data in about 10 of 91 stocks examined, whereas year effects explained variability in 69 stocks. Process error could come from unknown processes leading to stochasticity and variability in the population dynamics (Rosenberg and Restrepo, 1994). Otolith widths were defined as the distance from the distal dorsal surface to the proximal dorsal surface of an otolith thin section, which is cut along the dorsal-ventral axis, perpendicular to the sulcus, and passing through the focus of each otolith. More details of the data on which this study was based can be found in Black et al. (2005). Otolith width (w) for individual i at year t was modelled using a von Bertalanffy growth function (Von Bertalanffy, 1957):

$$w_{i,t} = \begin{cases} w_{\infty,i,t}(1 - e^{(-K_{i,t}(a_t - a_0))}) + \varepsilon_{inc} & for\ t = 1 \\ w_{i,t-1} + (1 - e^{-K_{i,t}})(w_{\infty,i,t} - w_{i,t-1}) + \varepsilon_{inc} & for\ t > 1 \end{cases} \quad \varepsilon_{\mathrm{inc}} \sim Normal(0,\ \sigma_{inc}^2) \tag{1a}$$

where w_∞ is the asymptotic width of the otolith along the dorsal-ventral axis, K is the intrinsic growth rate, $\mathrm{a_t}$ is the age at year t, a_0 is age for which size is zero, ε_{inc} is the process stochasticity, and σ_{inc} is the standard deviation of the process error. a_0 was not estimated within this model because initial length of the otolith is measured, removing the need for said parameter. Eq. (1a) can also be modified to model otolith growth increments, as opposed to overall widths:

$$w_{i,t} - w_{i,t-1} = (1 - e^{-K_{i,t}})(w_{\infty,i,t} - w_{i,t-1}) + \varepsilon_{inc} \quad \varepsilon_{\mathrm{inc}} \sim Normal(0,\ \sigma_{inc}^2) \tag{1b}$$

Environmental factors can sometimes have effects on both w_∞ and K, often with inverse effects (Brunel and Dickey-Collas, 2010; Kimura, 2008). Normally-distributed random individual effects $\varepsilon_{w_\infty,i}$ and $\varepsilon_{\mathrm{K},i}$ and year effects ε_t were added to the K and w_∞ parameters, i.e.:

$$\begin{aligned} K_{\mathrm{i,t}} &= K_{base} \cdot e^{\varepsilon_{\mathrm{K},i} + \beta_{\mathrm{K}} \cdot \varepsilon_t} & \varepsilon_{\mathrm{K},i} &\sim Normal(0,\ \sigma_{\mathrm{K}}^2) \\ w_{\infty,i,t} &= w_{\infty,base} \cdot e^{\varepsilon_{w_\infty,i} + \beta_{w_\infty} \cdot \varepsilon_t} & \varepsilon_{w_\infty,i} &\sim Normal(0,\ \sigma_w^2) \\ & & \varepsilon_t &\sim Normal(0,\ 1) \end{aligned} \tag{2}$$

where K_{base} and $w_{\infty,base}$ are the base, mean growth parameters, β_{K} and β_{w_∞} are parameters linking the growth parameters to the year effects, scaling the year effects accordingly, and σ_{K} and σ_w are the standard deviations of the individual effects. The year effects were modelled as a single factor identical between the$K$ and w_∞ parameters – a model that also describes the covariance between the two growth parameters over time (Warton et al., 2015), as determined by the β values. Year effects were presumed to be normally-distributed with a mean of 0 so the mean growth parameters were identifiable, and the population generally following an overall mean growth curve.

2.2. Estimation method

Using Eqs. (1b) and (2), a nonlinear mixed-effects estimation model was developed to quantify individual and temporal variation in otolith growth increments. This model was implemented using Template Model Builder (TMB; Kristensen et al., 2016). β_{K} and β_{w_∞} were freely-estimated, to allow estimation of a positive or negative correlation with the year effects. ε_t was estimated independently (i.e., without an autoregressive component) within this model, under the assumption that ε_t is normal with mean 0 and standard deviation 1. This was to allow for analyses of the year effects to be conducted external to this model procedure, such as fitting AR-1 models to them.

2.3. Fits to data

Several versions of the estimation method were applied to the actual otolith increment data for 66 splitnose rockfish (Black, pers. comm., as