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Estimating growth of tropical tunas in the Indian Ocean using tag-recapture data and otolith-based age estimates

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ABSTRACT

A growth model from which the expected age of a fish can be estimated based on its length is a key component to most stock assessments. For the three tropical tuna species in the Indian Ocean – yellowfin (YFT; *Thunnus albacares*), bigeye (BET; *T. obesus*) and skipjack (SKJ; *Katsuwonus pelamis*) – information about growth has been very limited until recently, when data from a large-scale Indian Ocean tuna tagging program became available. In this paper, parametric growth models were fit to tag-recapture data for all three species using a maximum likelihood method that models the joint density of release and recapture lengths as a function of age by treating age at tagging as a random variable. The method allows for individual variability in growth by modelling the asymptotic length parameter as a random effect. Direct age and length data from otolith readings were also included in the analysis for YFT and BET. The results support two-stanza growth models for all three species; however, the growth patterns for YFT and BET differ from SKJ. YFT and BET exhibit a transition in growth between age 2 and 3, with faster growth in the second stanza than the first, whereas SKJ exhibit a transition in growth around age 1, with much faster growth in the first stanza than the second. Most likely, YFT and BET also experience a phase of rapid growth directly following hatching, but lack of data for fish less than 50 cm for these species precludes its estimation. Differences in growth between sexes were found for YFT and BET, with males growing to a larger size; information on sex was not available for SKJ.

1. Introduction

Understanding how fish grow is a fundamental component of fisheries research. Growth models are used either directly or indirectly in stock assessments to estimate the age composition of the catch. Moreover, changes in growth can have important implications about stock status; for example, changes in the mean and variance of length-at-age can have a substantial impact on fishing mortality and biomass estimates and on derived reference points for management (e.g., Aires-da-Silva et al., this volume). For yellowfin (YFT), bigeye (BET) and skipjack (SKJ) tuna in the Indian Ocean, growth remains a key area of uncertainty in stock assessments (IOTC, 2011). In order to address uncertainties in growth, as well as other key inputs to the Indian Ocean tuna stock assessments, a large-scale tagging programme was started in 2005, known as the Regional Tuna Tagging Project of the Indian Ocean (RTTP-IO). As part of this project, large numbers of YFT, BET and SKJ were tagged in the western Indian Ocean during 2005–2007 and subsequently recaptured in commercial fishing operations.

Tag-recapture data – specifically the change in length of a tagged animal between the time it was released and the time it was recaptured – are one of the primary sources of information used for estimating fish growth. Because the age of a fish at release is unknown, the traditional approach has been to model the incremental change in length of the fish over the time it was at liberty (Fabens, 1965; Francis, 1988; James, 1991). This approach can lead to biased parameter estimates when individual variability in growth exists (Sainsbury, 1980). More recently, maximum likelihood approaches have been developed that model the joint density of the release and recapture lengths as opposed to modelling the length increment (Palmer et al., 1991; Wang et al., 1995; Laslett et al., 2002). In these cases, the age at release is modelled as a random variable.

Here we apply the method of Laslett et al. (2002), which we will refer to as the LEP (Laslett, Eveson and Polacheck) method, to the RTTP-IO tag-recapture data for YFT, BET and SKJ. It is important to characterize not only the mean growth of a population, but also variability among individuals. The LEP method allows for

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individual variability in growth by modelling asymptotic length as a random variable. The method can be applied to any growth curve that can be expressed as an asymptotic length parameter multiplied by a monotonically increasing growth function; this includes the commonly known von Bertalanffy (VB), generalized VB, Richards, Gompertz and logistic growth curves, as well as the two-phase growth models presented in Hearn and Polacheck (2003) and Laslett et al. (2002). Several recent studies of tuna growth in the Indian Ocean suggest that a two-stanza growth curve is more appropriate than a simple VB curve for YFT and BET (Fonteneau and Gascuel, 2008; Eveson and Million, 2008a,b; Hillary et al., 2008; Morize et al., 2008; Dortel et al., 2013) and possibly for SKJ as well (Fonteneau and Gascuel, 2008; Eveson, 2011; Hillary et al., 2008). We used exploratory data analyses to investigate the hypothesis of two-stanza growth and guide our choice of an appropriate growth curve for each species.

A drawback of using tag-recapture data to model growth is that the data do not provide information about absolute age, only relative age. Auxiliary data, such as age readings from otoliths or other hard parts, are required to anchor the estimated growth curve to an absolute age axis. Previous studies have verified that daily increments are formed in the otoliths of YFT in the eastern Pacific (Wild and Foreman, 1980) and BET in the central and eastern Pacific (Schaefer and Fuller, 2006) and in the Atlantic (Hallier et al., 2005), but this had not yet been verified for tunas in the Indian Ocean. As part of the RTTP-IO, a validation study was carried out which concluded that Indian Ocean YFT and BET deposit daily increments in their otoliths, but that the deposition rate for SKJ is variable (Sardenne et al., this volume). However, the study also found that age readings for YFT and BET were inconsistent between different reader teams and led to significantly different growth curves (Sardenne et al., this volume). Consequently, we integrated the otolith age data from each reader team separately into our growth models for YFT and BET. By doing so, we could assess the effect of the different data sets on the parameter estimates and also evaluate their consistency with the tag-recapture data.

2. Data

2.1. Tag-recapture data

As part of the RTTP-IO, large numbers of YFT, BET and SKJ were tagged in the western Indian Ocean, primarily off Tanzania (Fig. 1), between May 2005 and August 2007. Additional tagging also occurred in the eastern Indian Ocean as part of small-scale tagging operations, including extensive tagging of SKJ and YFT off the Maldives in 2004 and 2007–2009. In total, over 63 000 YFT, 35 000 BET, and 100 000 SKJ were tagged as part of the RTTP-IO and small-scale tagging operations, collectively known as the Indian Ocean Tuna Tagging Programme (IOTTP). Recaptures occurred subsequently in commercial fisheries operating in the Indian Ocean (Fig. 1). To date, the percent of tag returns has been approximately 16% for each of the three species. More details of the tagging and recovery operations can be found in Hallier (2008) and Hallier and Fonteneau (this volume).

Not all tag-recapture data are appropriate for growth analysis since some of the necessary information may be missing or unreliable. Thus, a set of screening criteria (Appendix A) was determined by the Secretariat of Indian Ocean Tuna Commission (IOTC) and only the data that met all the screening criteria were included in our analysis. The last of the criteria is not definitive, but rather cautions about using data from recaptures prior to tag recovery teams being put aboard vessels (April 2007). Since the number of recaptures after this date is more than adequate (Table 1), we chose to be conservative and omit these data. Histograms of release length, recapture length and days at liberty summarize the data included in the growth model for each species (Fig. 1).

The majority of recaptures for all species came from the purse seine fishery (Table 1). This is likely due to very low tag reporting rates for all other fisheries (estimates ranging from 0 to 26%; Carruthers et al., this volume). As long as fish caught in the different fisheries have the same underlying growth dynamics, then variable reporting rates amongst fisheries should not bias our growth estimates. However, the size range of fish available for growth estimation is affected; for example, information on large individuals for YFT and BET is lacking because large fish are generally caught by the longline fishery. If growth dynamics do in fact differ between fishery components, then the estimated growth models may be biased.

2.2. Otolith data

The otolith age and length data used in our analyses were the same data used in the growth models for YFT and BET in Sardenne et al. (this volume). The otolith samples were collected from fish caught in the Indian Ocean during 2006–2011 and read by (up to) three different teams of readers (see Sardenne et al., this volume). An age estimate for each fish and reader team was derived from the otolith counts using the method described in Dortel et al. (2013). The age estimates differed significantly between reader teams (Sardenne et al., this volume), so we included the data from each team separately in our growth models. Samples sizes by species and reader team are given in Table 1.

3. Methods

Before fitting growth models to the data, an exploratory analysis was undertaken to determine an appropriate functional form for the growth curve for each species. This included calculating an average growth rate (cm/day) for each fish by dividing the difference between its recapture length and release length by the number of days it was at liberty and plotting against the average of its release and recapture length. If fish grow according to a standard VB curve, then the relationship between growth rate and length will be linear with a negative slope, where the values of the slope and intercept depend on the length of time at liberty.

Based on the exploratory analyses (see Section 4), a two-stanza growth model was deemed most appropriate for all three species. We chose to fit the VB $\log k$ growth function (von Bertalanffy with a logistic growth rate parameter) developed by Laslett et al. (2002). This function allows for a smooth transition between growth phases, which seems more likely from a biological point of view than the instantaneous transition assumed by the two-phase VB growth model of Hearn and Polacheck (2003).

The VB $\log k$ growth function can be expressed as

$$l(a) = L_\infty f(a - a_0; \theta)$$

where L_∞ is asymptotic length, $\theta = \{k_1, k_2, \alpha, \beta\}$ and

$$f\left(a - a_0; \theta\right) = 1 - \exp\left(-k_2\left(a - a_0\right)\right) \times \left\{ \frac{1 + \exp\left(-\beta\left(a - a_0 - \alpha\right)\right)}{1 + \exp\left(\alpha\beta\right)} \right\}^{-(k_2 - k_1)/\beta}$$

The equation for the VB $\log k$ function represents a change in growth from a VB curve with growth rate parameter k_1 to a VB curve with growth rate parameter k_2, with a smooth transition between the two stages governed by a logistic function. The parameter α governs the age at which the midpoint of the transition occurs, and β governs the rate of the transition (being sharper for larger values).