Fisheries Research 163 (2015) 69–84

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

An integrated Bayesian modeling approach for the growth of Indian Ocean yellowfin tuna

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ARTICLE INFO

Article history:
Received 10 October 2013
Received in revised form 1 July 2014
Accepted 5 July 2014
Available online 7 September 2014

Keywords:
Indian Ocean yellowfin
Hierarchical Bayesian model
Tagging
Fisheries

ABSTRACT

The Indian Ocean Tuna Tagging Program provided a unique opportunity to collect demographic data on the key commercially targeted tropical tuna species in the Indian Ocean. In this paper, we focused on estimating growth rates for one of these species, yellowfin (*Thunnus albacares*). Whilst most growth studies only draw on one data source, in this study we use a range of data sources: individual growth rates derived from yellowfin that were tagged and recaptured, direct age estimates obtained through otolith readings, and length-frequency data collected from the purse seine fishery between 2000 and 2010. To combine these data sources, we used an integrated Bayesian model that allowed us to account for the process and measurement errors associated with each data set. Our results indicate that the gradual addition of each data type improved the model's parameter estimations. The Bayesian framework was useful, as it allowed us to account for uncertainties associated with age estimates and to provide additional information on some parameters (e.g., asymptotic length). Our results support the existence of a complex growth pattern for Indian Ocean yellowfin, with two distinct growth phases between the immature and mature life stages. Such complex growth patterns, however, require additional information on absolute age of fish and transition rates between growth stanzas. This type of information is not available from the data. We suggest that bioenergetic models may address this current data gap. This modeling approach explicitly considers the allocation of metabolic energy in tuna and may offer a way to understand the underlying mechanisms that drive the observed growth patterns.

1. Introduction

The knowledge of growth variability between individuals is essential to understanding the biology of fish populations, their productivity, and their response to environmental changes and fishing pressure. Indeed, growth rates are an integral part of stock assessments, a process which aims to supply scientific advice on the health of a fishery (Cotter et al., 2004). Consequently, biased growth estimates can affect our understanding of a stock's status and lead to poor fisheries management decisions (Fournier and Archibald, 1982; Kell and Bromley, 2004).

There are three principal data sources available for studying wild fish growth rates: (i) direct aging of a fish of a known size from periodic deposits in hard tissues, (ii) modal progression in length-frequency distributions obtained from commercial fisheries catches or scientific monitoring, and (iii) the increase in fish length over time-at-liberty from mark-recapture experiments. Direct aging data have been widely used to study growth in fish species that consistently deposit growth increments in calcified tissues, such as otoliths (Campana, 2001; Panfili et al., 2002). For example, counting the microstructural features deposited daily in otoliths has been shown to be a useful aging technique for many species of tropical fishes (Pannella, 1971; Green et al., 2009). However, the preparation and analysis of otoliths is time consuming,

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http://dx.doi.org/10.1016/j.fishres.2014.07.006
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requires considerable care, and can involve some biases and uncertainties (e.g., miscounting increments can lead to errors in age estimations) (Sardenne et al., 2014). Although considered less accurate than direct aging methods, the analysis of length-frequency data obtained from fisheries catches can provide indirect age estimates for species that exhibit well defined spawning periods (Pauly and Morgan, 1987). In this method, modes (assumed to represent fish cohorts) are identified in the length-frequency distributions of catches and their length progression is tracked over time. Finally, mark-recapture data have been widely used since the first tagging experiments were conducted in the early 1950s on tropical tunas in the Pacific Ocean. With this method, the change in fish length during the time between release and recovery provides valuable information on how each individual grows over time (Amstrup et al., 2005). However, tagging data do not provide information on the age of a fish and complementary data or expert knowledge are required to anchor the growth curve.

It can be difficult to obtain an overall growth pattern from a single data source, and using all three data sources provides complementary information on the different growth phases experienced over the lifespan of a fish. Although considerable research effort is invested in determining age and growth patterns of fish, to our knowledge, with the notable exception of Eveson et al. (2004), only a few studies have previously attempted to combine the three different data sources into an integrated growth model. Assimilating different growth data sets within a statistical framework is challenging because to do so effectively, we must address: (i) the multiple observation errors in the data, (ii) potential contradictions between data sets, and (iii) the variability in growth among individuals, which is typically modeled by a process error term. The hierarchical Bayesian approach appears particularly well suited for modeling growth because it can integrate several different data sources and allows for stochasticity at multiple levels (Clark, 2005). Bayesian models can draw inferences from large numbers of parameters and latent variables that describe complex relationships. In addition, the Bayesian framework allows for the inclusion of expert judgment and supplementary information.

Yellowfin tuna (*Thunnus albacares*, Bonnaterre 1788) is an epipelagic species that is widely distributed in the tropical and subtropical waters of the world's major oceans (Fonteneau, 2010). In the Indian Ocean (IO), yellowfin has been commercially exploited since the early 1950s and over the last decade, annual catches have exceeded 350,000 t (Herrera and Pierre, 2010). There is considerable diversity in the fleets that target this species; whilst industrial purse seiners and longliners dominate, small-scale fishing fleets were responsible for more than 35% of total catch estimates in the last decade (Herrera and Pierre, 2010). The management of the IO yellowfin is under the jurisdiction of the Indian Ocean Tuna Commission (IOTC, www.iotc.org). Currently, their management approach relies on temporal trends in fish abundance and fishing mortality-at-age data derived from a spatially-explicit population model (Langley et al., 2012). The most recent stock assessment from 2011 determined that current fishing pressure on the yellowfin stock was at a safe level (IOTC, 2012). Nevertheless, there are uncertainties associated with the current approach to the IO yellowfin stock assessment, including the growth curve that is used (IOTC, 2012).

This study describes a hierarchical growth model for IO yellowfin that combines aging data derived from otolith readings, length-frequency data sampled from the European purse seine fishery over the last decade, and mark-recapture data collected through the Indian Ocean Tuna Tagging Program of the Indian Ocean (IOTTP). The influence of each data source on growth estimates was assessed by gradually increasing the model's complexity. Developed in a hierarchical Bayesian framework, our model explicitly accounts for the uncertainties associated with age estimates and length measurements. In addition, the model reflects expert opinion on two key areas: otolith reading and historical length and growth observations for yellowfin. In this study, we provide a flexible statistical framework that accounts for uncertainty in growth modeling and addresses a current concern of the IOTC.

2. Materials and methods

We first describe the three datasets and the modeling approach used to estimate absolute age from multiple counts of otoliths. We then introduce the somatic growth model used for fitting the different datasets and we give technical details on the estimation procedure based on Bayesian inference. The parameters and variables used and the prior probability distributions are given in Tables 1 and 2, respectively. The subscripts c, d, i, j, k, and r used in the equations indicate cohort, month, fish, capture event, otolith reading, and reader team, respectively. The symbol $\cdot$ indicates a multiplication term and the symbol * used as exponent represents the observation of a variable.

2.1. Mark-recapture data

Mark-recapture data were collected during the Regional Tuna Tagging Program (RTTP-IO) that was the major component of the IOTTP (Hallier, 2008). The tagging operations were carried out in the western Indian Ocean from 2005 to 2007. During this time, a total of 64,323 yellowfin were tagged with dart tags. 2741 of these fishes were also tagged with oxytetracycline (OTC), a chemical that leaves a permanent fluorescent mark in the calcified tissues. Tag recovery operations took place across the entire Indian Ocean basin. As at September 2012, 10,395 tagged yellowfin had been recovered, including 256 OTC-tagged fish (Sardenne et al., 2014). Most of the recoveries were reported for fish caught by the European purse-seine fleet (88%). The pole and hand lines, gillnetters, longliners and troll lines were associated with low recovery rates (Carruthers et al., 2014). The range of dates associated with each recapture was derived from purse seiner logbook data and plans of brine-freezing tanks used for storing the tuna catch, and it was determined through close collaboration between the IOTC and purse seine fishing industry. The fork length (F_L), i.e. fish length from the tip of the snout to the fork of the tail, was recorded to the nearest 0.5 cm. At tagging, measurements were taken with a measuring board, while calipers were mostly used for recoveries.

Preliminary model runs including the >4000 recaptures available from the RTTP-IO that were considered to be good following the screening criteria of the IOTC resulted in some convergence problems, likely due to the imbalance between the likelihoods components of the model and the large variability observed in growth increments over time. To circumvent this issue, the mark-recapture component of the growth model was mainly used to compensate for the lack of large fish in the other model components (see below). Thus, only fishes characterized by accurate date of recovery (i.e. no uncertainty in time-at-liberty) and size-at-recapture measured with great precision (i.e. at the Seychelles Fishing Authority lab facility) and ≥120 cm FL, were used. The 373 yellowfin selected in the present study covered a large size range at tagging, i.e. between 44 and 113 cm F_L, with distinct modes at about 50, 60, and 90 cm (Fig. 1a). These tunas ranged in size between 120 and 159 cm F_L at recapture, having spent between 8 months and 5 years at sea (Fig. 1b).

2.2. Aging data from otolith readings

A total of 174 saggital otoliths were prepared and analyzed for aging purposes, comprised of (i) 128 fish, of which 124 were OTC-tagged, collected through the RTTP-IO program measuring between