


## A Bayesian hierarchical approach to estimate growth parameters from length data of narrow spread

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Estimating fish growth from length frequency data is challenging. There is often a lack of clearly separated modes and modal progression in the length samples due to a combination of factors, including gear selectivity, slowing growth with increasing age, and spatial segregation of different year classes. In this study, we present an innovative Bayesian hierarchical model (BHM) that enables growth to be estimated where there are few distinguishable length modes in the samples. We analyse and identify the modes in multiple length frequency strata using a multinormal mixture model and then integrate the modes and associated variances into the BHM to estimate von Bertalanffy growth parameters. The hierarchical approach allows the parameters to be estimated at regional levels, where they are assumed to represent subpopulations, as well as at species level for the whole stock. We carry out simulations to validate the method and then demonstrate its application to Indian Ocean longtail tuna (*Thunnus tonggol*). The results show that the estimates are generally consistent with the range of estimates reported in the literature, but with less uncertainty. The BHM can be useful for deriving growth parameters for other species even if the length data contain few age classes and do not exhibit modal progression.

**Keywords:** Bertalanffy, hierarchical model, migratory, neritic tuna, substocks

### Introduction

Modelling fish growth is often an important component of fish stock assessment and for fisheries management. In data-poor situations, growth is one of the most important life history traits for quantifying productivity and resilience (Patrick *et al.*, 2010; Zhou *et al.*, 2011, 2018). In modern age-structured, integrated models, the growth model has multiple applications, including translating numbers at age into biomass-based quantities, converting length-based selectivity to selectivity-at-age, and calculating expected length compositions (Maunder *et al.*, 2016). The classical method for estimating fish growth requires length and age measurements (Quinn and Deriso, 1999). Although fish length is relatively easy to measure, fish age is more difficult and expensive to obtain. Direct age estimation from hard body parts, such as scales or otoliths, is often uncertain due to irregular early growth patterns or structural resorption near the primordium (Campana, 2001; Kolody *et al.*, 2016). Methods for estimating growth parameters

using length data alone have also been developed (e.g. Fournier *et al.*, 1990; Roa-Ureta, 2010). A key challenge of this type of analysis is to identify a sufficient number of modes in the length frequency distribution that can be assumed to represent true ages. The decomposition of length frequency into appropriate age classes is often statistically difficult. Typically, length modes are easier to distinguish for the younger age classes (Gulland and Rosenberg, 1992) but are more difficult and sometimes impossible to separate for older age classes as fish growth slows or even ceases in later life (Maunder *et al.*, 2018).

In addition to these common problems, growth modelling using length data faces some other challenges for migratory species and species composed of multiple distinctive stocks such as tunas. Migratory species are often captured by various fishing gears at different life stages, so a disproportionate demographic subset of the population may be captured due to the characteristic selectivity of the fishing gear (Kolody *et al.*, 2016). For widely distributed

species, growth rates may vary among different regions due to diverse environmental conditions. Although length samples are available in many fisheries, they are often not representative of the population due to the lack of consistency in sampling protocols.

One example of widely distributed species is Indian Ocean neritic tunas distributed in coastal waters. These fish contribute significantly to the economic well-being and food security of many Indian Ocean coastal states and fall under the mandate of the Indian Ocean Tuna Commission (IOTC). However, compared with the more valuable commercially important species harvested in the region, life history parameters, including information on growth, and population dynamics are less well understood for neritic tunas.

A range of independent studies on the growth of neritic tuna species have been undertaken in various regions across the Indian Ocean in recent years, but the estimates are highly variable (IOTC Secretariat, 2015a, b, c, 2016a, b). This may be indicative of the presence of substocks with distinctive life history traits within the Indian Ocean, or could simply reflect sampling variability among studies (neritic tuna are harvested by a variety of fishing gears in the Indian Ocean which have distinctive selectivities). It is also worth noting that a wide range of analytical methods have been applied to derive growth parameters in these studies. The majority of these studies used ELEFAN (IOTC Secretariat, 2015b, c, 2016b, c), which was based on the modal progression method and designed mainly for application to closed populations (Pauly, 1987). While these isolated regional studies may characterize the growth of the subpopulations they represent, the results may not be representative of the growth characteristics of populations across wider areas, such as ocean basins, which are likely to consist of multiple subpopulations.

Given the concerns regarding the methodologies and assumptions adopted for regional studies, we develop an innovative approach that collates and combines available data to estimate growth parameters for the population at the basin scale using a hierarchical Bayesian framework. The method differs from a traditional meta-analysis that synthesizes the results from multiple studies. While both are dependent on the quality of the original data, one notable limitation of traditional meta-analysis is that the conclusion can only be as good as the original methodologies and assumptions and is, therefore, dependent on the validity of individual studies. We then carry out a simulation test to validate the approach. Finally, we apply the Bayesian hierarchical model (BHM) to Indian Ocean longtail tuna (*Thunnus tonggol*) as an example to demonstrate the utility of this method. The new meta-analysis developed under a robust modelling framework is expected to yield more consistent and credible estimates than a simple summary across individual studies.

## Material and methods

This section describes the Bayesian meta-analysis approach that simultaneously models the multiple length frequency datasets collected from a wide spatial and temporal range (e.g. different regions and years). We model the growth at stock and species levels using a hierarchical model structure. We assume that for a single species, fish within the same spatial-temporal stratum share similar life history traits, which can vary across wider spatial and temporal dimensions. Thus, fish from the same stratum are assumed to form a population unit whose length and age composition may differ from other strata (the difference might be caused

by a range of factors including multiple stocks and migration). This would allow spatial and temporal variations in growth to be incorporated and estimated.

## Growth model

Several alternative models have been used for fish growth. However, the von Bertalanffy growth function (VBGF) is the most widely adopted (Quinn and Deriso, 1999; Kolody *et al.*, 2016) and is used in this study:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}, \quad (1)$$

where  $L_\infty$  is the asymptotic length,  $L_t$  is the length at age  $t$ ,  $K$  is the parameter controlling the rate of growth (called the growth constant), and  $t_0$  is the theoretical age at zero length. Parameter estimation can be straightforward if both age and length measurements are known. When age data are not available, growth is often estimated from length by assuming that the modes in the length frequencies represent annual or seasonal cohorts (Pauly, 1987; Gulland and Rosenberg, 1992; Laslett *et al.*, 2004; Roa-Ureta, 2010). When length frequency data contain very few modes, estimating von Bertalanffy growth parameters becomes very difficult (e.g. it is impossible to estimate  $K$ ,  $L_\infty$ , and  $t_0$  from fewer than three data points). To overcome this challenge, we applied a meta-analysis approach that combines multiple length frequency samples under a hierarchical model structure. We assumed that the growth of a fish species is dictated by a common underlying pattern but may vary somewhat among regional subpopulations. Examining growth parameters at both species and subpopulation levels has important implications for stock assessments if alternative stock or spatial structures are to be considered. The analysis also accounted for random variations in length and age compositions arising from localized sampling, changes in sampling time, location, or gear selection (Sainsbury, 1980). Variations in the sampling process may lead to inconsistent growth estimates if they are not adequately accounted for (Francis, 1988a, b).

## Identifying length modes

Growth models based on length frequency data typically require knowledge of the total number of age groups in the length distribution (Schnute and Fournier, 1980; Fournier *et al.*, 1990). Narrow spread of the length distribution makes it difficult to identify older age classes. In the case of IOTC neritic tuna species, there were typically fewer than three or four length modes for most samples. As such, we applied a multinomial mixture model (MNMM) to determine the number of age classes in each sampling stratum (Macdonald and Pitcher, 1979). The following assumptions were made: (i) fish from the same cohort inhabit or migrate together and fish in the same sampling stratum represent one or more cohorts spawned in the same seasons, but different years; (ii) the length frequency of each age class followed a normal distribution; and (iii) the length increment from one age to the next was greater than a threshold determined by the VBGF (see below).

In our case study below, Indian Ocean longtail tuna are considered to have regionally confined distributions and protracted spawning patterns (Pillai and Satheshkumar, 2012), with one or two annual spawning peaks (Griffiths *et al.*, 2010b; Abdussamad *et al.*, 2012). Assumption (i) ensures identification of modes

within each sampling stratum, and violation of this assumption, e.g. fish from more than one cohort within 1 year are captured in the same stratum, may lead to underestimating growth rate. Assumption (ii) is a common practice in length frequency analysis (Macdonald and Pitcher, 1979; Fournier *et al.*, 1990, 1998; Pons *et al.*, 2019), and alternative distributions, such as skew- $t$  and log-skew- $t$ , have been proposed (Contreras-Reyes *et al.*, 2014, 2018; López Quintero *et al.*, 2017) to reduce the potential bias, because fishing selectivity can disproportionately remove faster-growing individuals from each age class. The majority of Indian Ocean longtail tunas are harvested by gillnets, which typically feature a dome-shaped selectivity pattern. This means that gillnets may not be selective for fast-growing individuals as fish tend to become less vulnerable at an older age. Nonetheless, our method can be easily modified to accommodate alternative length-at-age distributions.

The MNMM estimates the optimal number of age classes in each sampling stratum as well as the mean length and variance at each mode. For fish  $i$  captured in fleet (or region)  $f$ , year  $y$ , month  $m$ , and  $5^\circ \times 5^\circ$  latitude and longitude grid  $g$ , the probability distribution of the length measurement is

$$p(L_{f,y,m,g,i}) = \sum_{t=\min}^A \phi_{f,y,m,g,t} N(L_{f,y,m,g,i} | L_{f,y,m,g,t}^{MN}, \sigma_{f,y,m,g,t}^{MN}), \quad (2)$$

where  $t$  iterates from the smallest to the largest identifiable year class in the stratum,  $L_{f,y,m,g,t}^{MN}$  is the MNMM estimate of the mean length of age class  $t$  (mode in the length frequency), and  $\sigma_{f,y,m,g,t}^{MN}$  is the standard deviation (SD) associated with the mean length for that year class. The mixture component weights are defined as  $\phi_{f,y,m,g,t}$  for year class  $t$ , with the constraint that  $\sum_t \phi_{f,y,m,g,t} = 1$  so that the total probability normalizes to 1. For each age class in (2):

$$N(L_{f,y,m,g,i} | L_{f,y,m,g,t}^{MN}, \sigma_{f,y,m,g,t}^{MN}) = \frac{1}{\sigma_{f,y,m,g,t}^{MN} \sqrt{2\pi}} \exp \left[ -\frac{(L_{f,y,m,g,i} - L_{f,y,m,g,t}^{MN})^2}{2\sigma_{f,y,m,g,t}^{MN 2}} \right]. \quad (3)$$

For model-fitting purposes, it is usually preferable to identify as many modes as possible. However, there is a potential to introduce false modes, as the length increment between modes declines with age while the variance increases. Therefore, we opted to use the minimum number of modes that can be clearly identified in each sampling stratum. The resulting lower number of data points in each sampling stratum was, however, compensated for through the inclusion of a large number of sampling strata. The impact of the assumed minimum number of modes is evaluated in the simulation exercise (see below).

### Bayesian hierarchical model

The outputs from MNMM, i.e.  $L_{f,y,m,g,t}^{MN}$  and  $\sigma_{f,y,m,g,t}^{MN}$  for each age class  $t$ , are used as inputs (data) into the BHM. The variability of size at age is captured by introducing a latent length  $l$ :

$$L_{f,y,m,g,t}^{MN} \sim N(l_{f,y,m,g,t}, \sigma_{f,y,m,g,t}^{MN}), \quad (4)$$

where  $L_{f,y,m,g,t}^{MN}$  and  $\sigma_{f,y,m,g,t}^{MN}$  are outputs from the MNMM and  $l_{f,y,m,g,t}$  is the latent length. The introduction of the latent variable

allows uncertainty in the MNMM component to be propagated onto the VBGF model (9).

One of the primary difficulties with using length data is that the actual age associated with each mode is unknown. In particular, the first mode may not be exactly age 1 (e.g. it may be 0.7 or 1.3 years old) or it might be much older than age 1 (e.g. 3.1 or 4.2 years old). Since age  $t$  in VBGF (1) is the true age, but the age of the first mode from mode identification is unknown, we derived the true age ( $tt$ , which includes uncertainty) of fish belonging to the first mode from VBGF as:

$$tt_{f,y,m,g,1} = t_{0,f} - \frac{1}{K_f} \log \left( 1 - \frac{L_{f,y,m,g,1}^{tt}}{L_{\infty,f}} \right), \quad (5)$$

where  $L_{f,y,m,g,1}^{tt}$  is the true mean length of the age class belonging to the first mode and

$$L_{f,y,m,g,1}^{tt} \sim N(L_{f,y,m,g,1}^{MN}, \sigma_{f,y,m,g,1}^{tt}). \quad (6)$$

For age classes other than the first mode, the estimated age is

$$tt_{f,y,m,g,t} = tt_{f,y,m,g,1} + t - 1. \quad (7)$$

The modified VBGF becomes:

$$L_{f,y,m,g,t}^{VB} = L_{\infty,f} \{1 - \exp[-K_f(tt_{f,y,m,g,t} - t_{0,f})]\}, t = 1, 2, \dots, A. \quad (8)$$

Equation (8) implies that fish captured by the same fleet (i.e. in the same region) followed the same region-specific growth parameters ( $L_{\infty,f}$ ,  $K_f$  and  $t_{0,f}$ ), estimation of which are thus facilitated by combining lengths across multiple sampling strata, albeit there may only be a few data points in each stratum. With the hierarchical model formulation, age for the first mode is estimated at stratum level, whereas the growth parameters are estimated at regional (fleet) level and species level (the latter results from hyperparameters; see Figure 1).

The latent length-at-age class  $t$  for each stratum is modelled as a normal distribution along the mean of the VBGF:

$$l_{f,y,m,g,t} \sim N(L_{f,y,m,g,t}^{VB}, \sigma_{f,y,m,g,t}^{VB}). \quad (9)$$

The SD (process error)  $\sigma_{f,y,m,g,t}^{VB}$  is estimated at fleet level, which generally resulted in lower deviance information criteria than SD estimated at stratum level.

The following prior distributions are assumed for the parameters at the fleet level:

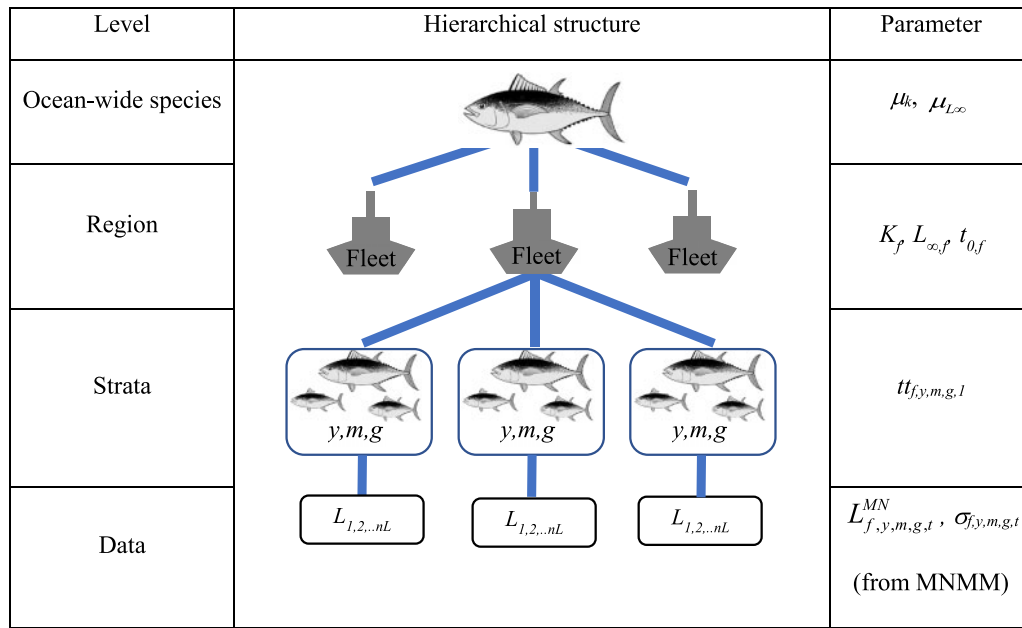
$$K_f \sim N(\mu_K, \sigma_K),$$

$$L_{\infty,f} \sim N(\mu_{L_{\infty}}, \sigma_{L_{\infty}}),$$

$$t_{0,f} \sim N(0, 0.001),$$

$$\tau_f^{VB} \sim \text{Gamma}(0.01, 0.01) \text{ and } \sigma_f^{VB} = 1/\sqrt{\tau_f^{VB}}.$$

Parameter  $t_0$  could also be modelled within the hierarchical structure, but as it is known to be around zero, a prior is given instead



**Figure 1.** Schematic design of the BHM structure and model parameters. Parameters ( $L_{f,y,m,g,t}^{MN}$  and  $\sigma_{f,y,m,g,t}$ ) produced by MNMM at data level are inputs into BHM.

to reduce the number of parameters estimated. Weak priors are used for hyperparameters:

$$\begin{aligned} \mu_K &\sim N(0, 0.01), \\ \tau_K &\sim \text{Gamma}(0.01, 0.01) \text{ and } \sigma_K = 1/\sqrt{\tau_K}, \\ \mu_{L_\infty} &\sim N(L_{\max}, 10^{-8}), \\ \text{where } L_{\max} &\text{ is the observed maximum length,} \\ \tau_{L_\infty} &\sim \text{Gamma}(0.01, 0.01) \text{ and } \sigma_{L_\infty} = 1/\sqrt{\tau_{L_\infty}}. \end{aligned}$$

### Simulation test

We carried out a simulation test to evaluate the performance of the model. We simulated 100 strata consisting of a combination of 5 fleets (regions), 4 years, 5 months, and one spatial grid in each region. Initial abundance at age 0 was set to be 10 000 fish for each cohort. The number at age declined at a total mortality rate of  $0.3 \text{ year}^{-1}$ . We assumed  $\mu_{L_\infty} = 100 \text{ cm}$ ,  $\mu_K = 0.5$ , and  $\mu_{t_0} = -0.2$ , and these were allowed to differ among fleets with  $C.V. = 0.1$ . The mean length-at-age was generated from the fleet-specific VBGF, assuming a multiplicative error structure with  $\sigma = 0.05$  for each stratum. The length-at-age distribution was generated assuming  $C.V. = 0.07$  (the mean value from the IOTC database). Hence, variability was introduced at all levels of the hierarchical model. Two different year classes were generated in each stratum, mimicking the migration effect, and the length distribution was further moderated by a dome-shaped selectivity (following a Gamma distribution).

The MNMM was fitted to the simulated datasets, assuming 1–6 age classes in each stratum. The maximum age classes (modes) were determined using model selection criteria based on Akaike information criterion (AIC) and a minimum length increment threshold:

- (1) The model with the lowest AIC among the models that have smaller AICs than that of the model for one age class, i.e.  $\min(\Delta\text{AIC}_t | \Delta\text{AIC}_t < 0)$ , where  $\Delta\text{AIC}_t = (\text{AIC}_t - \text{AIC}_1)$ .
- (2) Minimum length increment from mode  $t$  to  $t+1$ . The threshold depends on the assumed values of  $K$  and  $L_\infty$ . For example, with  $K = 0.8$ , the length increment for age  $< 2$  fish must be  $L_2^{MN}/L_1^{MN} \geq 1.45$  and the length increment for fish age  $< 3$  must be  $L_3^{MN}/L_2^{MN} \geq 1.14$ . We tested the sensitivity of posterior parameters to these restraining variables by varying assumed  $K$  from 0.1 to 1.0 by a step of 0.1 (a total of 10 levels) and varying assumed  $L_\infty$  from 60 to 150 cm (also 10 levels).

The minimum length increment threshold aims to attain a plausible model with a biologically meaning interpretation of length modes.

### Application to longtail tuna

We applied the model to the length samples of Indian Ocean longtail tuna obtained between 1983 and 2014 from seven commercial fishing fleets: India, Islamic Republic of Iran, Sri Lanka, Malaysia, Oman, Pakistan, and Thailand (the data were extracted from the length frequency databases maintained by the IOTC Secretariat). These national fleets operated predominantly within their own EEZs, hence the term “fleets” is synonymous with “regions”. The fishing areas covered by these fleets do not overlap. Length measurements were recorded by fleet, year, gear, month, and  $5^\circ \times 5^\circ$  latitude/longitude area (referred to as a “stratum”). There were a total of 2636 strata (we excluded strata with  $< 50$  length measurements), and the sample size ranged from 1 to a maximum of 13 116 fish per stratum. Gillnets were the predominant gear in 58% of the strata, and  $> 80\%$  of the fish in the length database were captured by gillnets. The range of fish sizes was usually very narrow with very few identifiable modes, and there was also a lack of clear modal progression in these length



distributions. The narrow size range was possibly a result of a number of factors including migration, fishing selectivity, and possibly the snagging processes (Jude *et al.*, 2002; Hosseini *et al.*, 2017).

## Model implementation

The hierarchical Bayesian growth model was implemented in R (R Core Team, 2017) and OpenBUGS/JAGS (Lunn *et al.*, 2000; Plummer, 2003). We ran three MCMC chains, with the first 100 000 iterations discarded and an additional 100 000 iterations used for parameter inference. Chain convergence was verified through visual inspection of the MCMC trace as well as the use of the Gelman–Robin diagnostic.

## Results

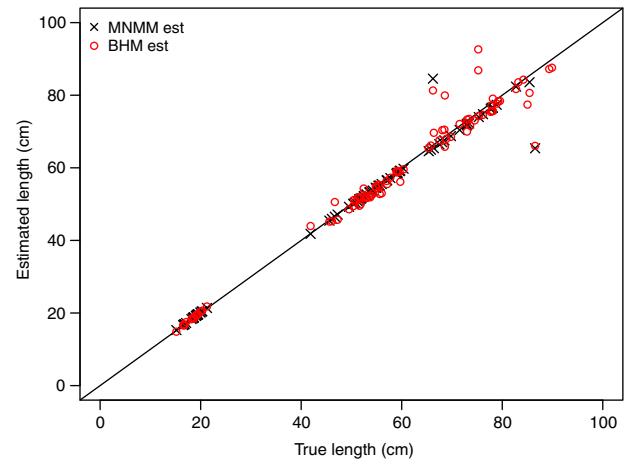
### Simulations

The MNMM was able to accurately identify the length frequency modes when the simulated fish were relatively young where the modes were clearly separated from each other. However, the larger the fish grew, the more difficult it became for the MNMM to correctly identify the mode, and so some estimates were clear false modes (Figure 2). Applying the screening criteria to the simulated length in 100 strata, we obtained a total of 48 strata where two (47 strata) or three (one stratum) age classes were identified, that is the MNMM failed to identify modes in about one half of the strata. For these retained strata, the MNMM was accurate, except for large fish (>80 cm) (Figure 3). The relative error  $\left[ \left( L_{f,y,m,g,t}^{MN} - L_{f,y,m,g,t}^{True} \right) / L_{f,y,m,g,t}^{True} \right]$  for the first mode ranged from  $-2.0$  to  $1.0\%$  with a mean of  $-0.2\%$ ; the relative error for the second mode ranged from  $-2.8$  to  $-0.16\%$  with a mean of  $-1.2\%$ , so the estimated first mode tends to be more accurate than the second mode. The absolute relative error for all modes ranged from  $0.05$  to  $2\%$  with a mean of  $0.9\%$ .

We then applied the BHM to the strata that passed the screening criteria. If we treated each stratum separately, it would be impossible to estimate growth parameters as they contained only two or three modes, and if we combined all strata, the modes were masked by each other, often resulting in a single mode. However, through the Bayesian meta-analysis approach, we were able to obtain accurate length modes (Figure 3). The relative error  $\left[ \left( L_{f,y,m,g,t}^{BHM} - L_{f,y,m,g,t}^{True} \right) / L_{f,y,m,g,t}^{True} \right]$  for all modes ranged from  $-6.0$  to  $8.9\%$  with a mean of  $-0.5\%$ ; the absolute relative error for all modes ranged from  $0.04$  to  $8.9\%$  with a mean of  $2\%$ .

The slightly reduced accuracy in BHM estimates includes errors resulting from the MNMM step.

The posterior VBGF parameters were quite accurate for most fleets and particularly for the hyperparameters, even though length modes in only about a half of the strata are identified (Table 1). At the fleet level, relative error (measured as the relative difference between the estimated and true values) varied between  $-12$  and  $4\%$

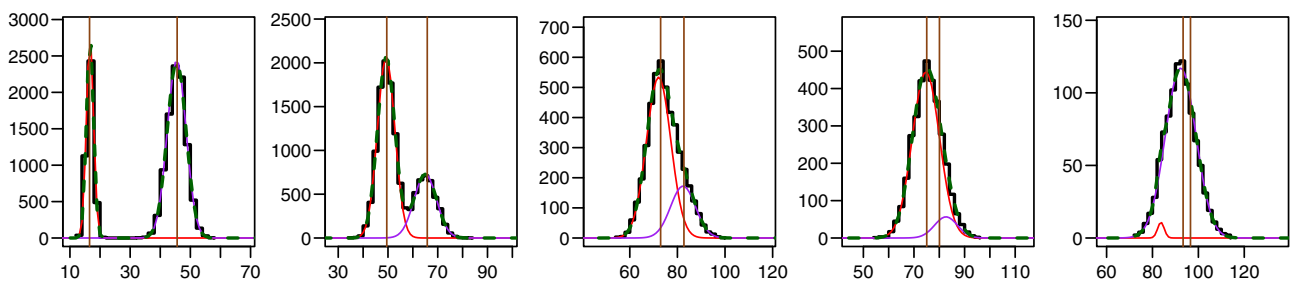


**Figure 3.** Comparison of the estimated length modes by MNMM and BHM with the true length for the simulated data.

**Table 1.** Posterior key VBGF parameters from BHM applied to simulated length data in five fleets (regions).

Parameter	Mean	SD	2.50%	Median	97.50%	True	RE
$K_1$	0.42	0.06	0.32	0.42	0.55	0.47	-0.12
$K_2$	0.51	0.07	0.38	0.50	0.65	0.51	0.00
$K_3$	0.44	0.07	0.31	0.44	0.59	0.50	-0.12
$K_4$	0.57	0.08	0.41	0.57	0.74	0.54	0.04
$K_5$	0.53	0.07	0.40	0.53	0.66	0.51	0.04
$\mu_K$	0.49	0.09	0.33	0.49	0.66	0.50	-0.01
$L_{\infty,1}$	100.82	7.13	89.11	100.00	118.40	94.98	0.05
$L_{\infty,2}$	101.03	7.04	90.02	100.20	117.90	101.32	-0.01
$L_{\infty,3}$	101.39	6.60	90.82	100.50	116.90	99.21	0.01
$L_{\infty,4}$	101.96	7.07	91.23	100.70	119.60	108.87	-0.08
$L_{\infty,5}$	101.35	6.86	90.48	100.40	118.60	101.17	-0.01
$\mu_{L\infty}$	101.33	6.66	90.94	100.40	117.20	100.00	0.00

RE = (posterior median length – true length)/true length.

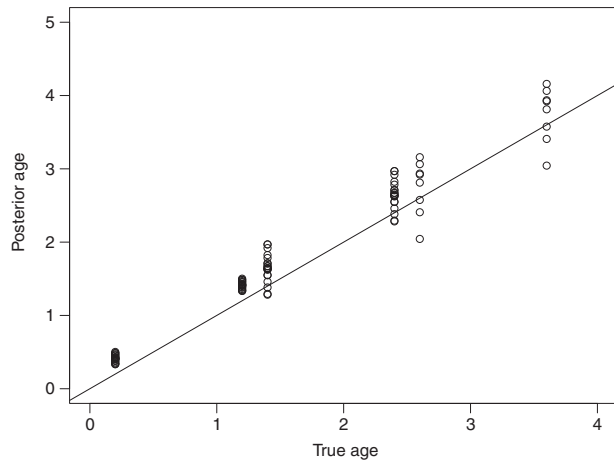


**Figure 2.** Example of mode identification by fitting an MNMM to simulated length data for five strata with two true age classes and 1–6 assumed modes. Fish grow larger (and older) from left to right. The histogram is the input length frequency, the red line is the first normal distribution, the purple line is the second normal distribution, and the dashed green line is the mixture distribution represented as a weighted sum of the two normals. The two vertical lines are the true length modes.

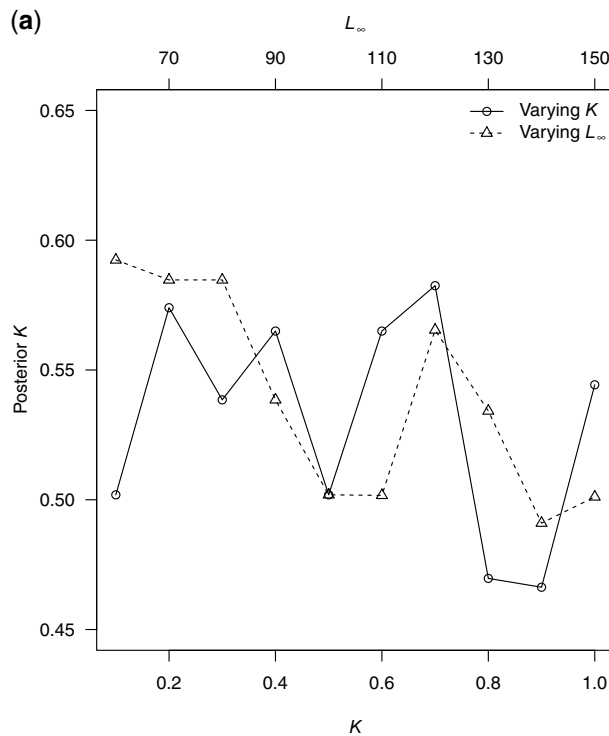
for  $K_f$  and between  $-8$  and  $5\%$  for  $L_{\infty,f}$  but was very small for the hyperparameters, e.g.  $-1\%$  for  $\mu_K$  and  $<1\%$  for  $\mu_{L_{\infty}}$ .

Estimating true age from length data was more challenging. The BHM tended to overestimate age when the true age was relatively young ( $<2.5$  years), and although the bias improved for older fish, the uncertainty increased (Figure 4). Nevertheless, although estimated age was less accurate than the estimated length and VBGF parameters, the posterior ages and true ages were highly correlated.

Sensitivity tests to the  $K$  and  $L_{\infty}$  values used to screen the datasets showed that when the assumed  $K$  varied from  $0.1$  to  $1.0$ , the



**Figure 4.** Comparison between BHM posterior median age and true age in the simulated length data.

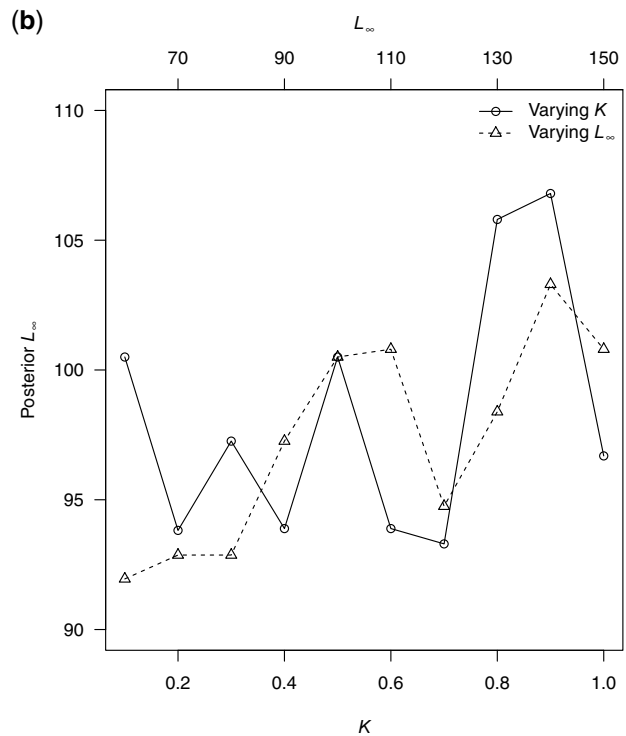


median posterior  $\mu_K$  fluctuated between  $0.47$  and  $0.57$ , i.e. a relative error between  $-7$  and  $17\%$ , with a mean of  $6\%$  (Figure 5a). Varying the assumed  $K$  caused the median posterior  $\mu_{L_{\infty}}$  to vary between  $93$  and  $107$  cm, i.e. a relative error between  $-7$  and  $7\%$ , with a mean of  $-2\%$  (Figure 5b). Changing the assumed  $L_{\infty}$  from  $60$  to  $150$  cm resulted in similar variabilities in  $\mu_K$  and  $\mu_{L_{\infty}}$  (Figure 5). There was no clear pattern between the assumed restraining variables and the resulting posterior VBFG parameters, as the assumed restraining variables were merely used to screen datasets to ensure biologically realistic length increments.

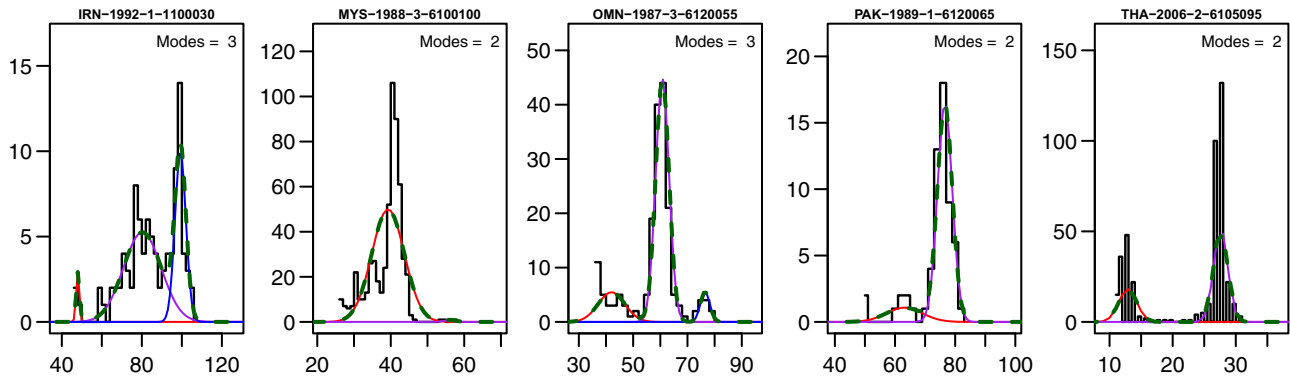
### Application to longtail tuna

The length frequency database contained a total of  $416$  strata (i.e. fleet, year, month, and grid) for longtail tuna. We assumed that there were possibly  $1-6$  age classes in each stratum. One normal distribution model and five MNMMs were fitted to each of the strata. For many strata, fitting MNMMs did not result in a significantly lower AIC than fitting the normal distribution model, indicating that there was possibly only one dominant age class in the single stratum or the fish were relatively old so it was difficult to statistically distinguish between age classes. For some strata, MNMMs significantly reduced the AIC, but the length increment between modes was too small to be biologically plausible. This was often the case when more than three age classes were assumed. To avoid creating spurious age classes, we applied similar criteria to those used in the simulation:

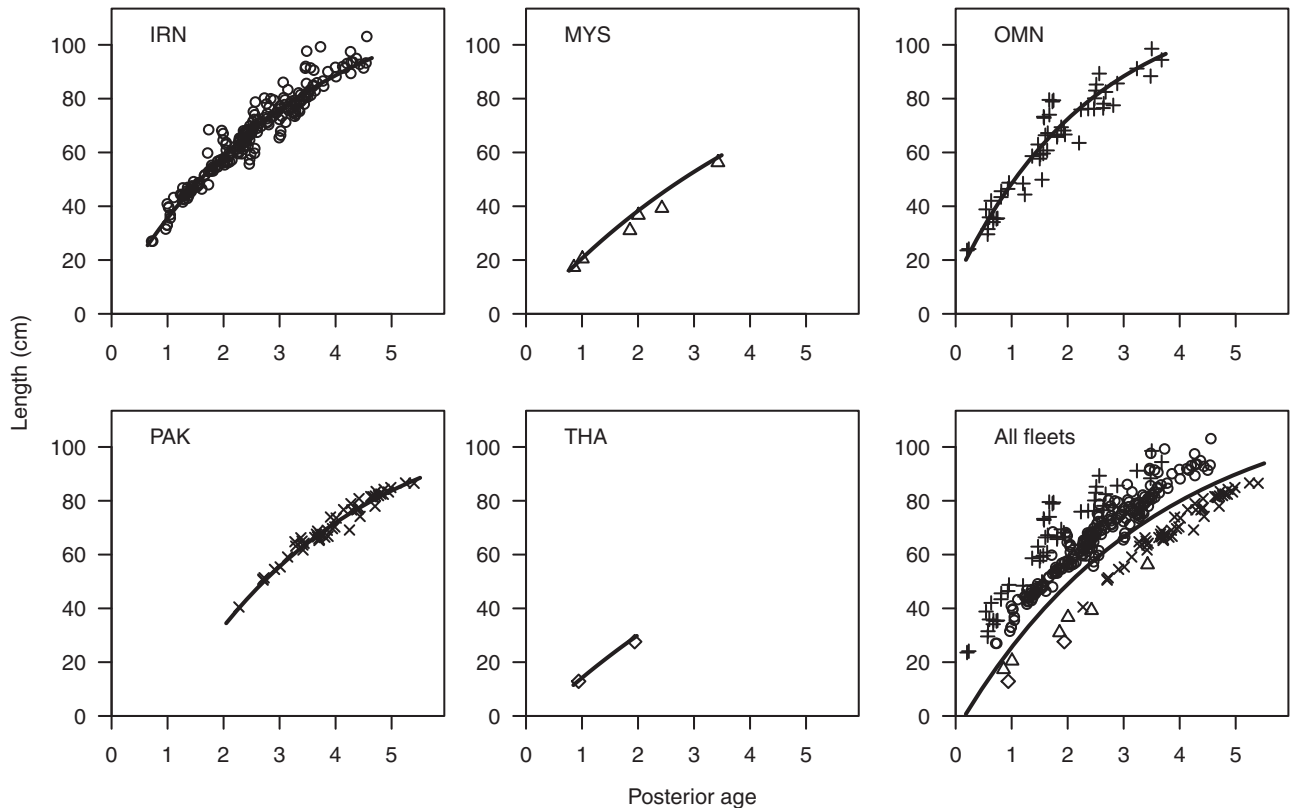
- (i) number of age class:  $1 < A \leq 3$ ,
- (ii)  $\min(\Delta AIC_t | \Delta AIC_t < 0)$ , and



**Figure 5.** Sensitivity of posterior (a)  $\mu_K$  and (b)  $\mu_{L_{\infty}}$  to varying input  $K$  and  $L_{\infty}$  used to screen the MNMM estimate length modes in each stratum to ensure that the modes are biologically valid.



**Figure 6.** Example of fitting an MNMM to length frequency (black histogram) for longtail tuna (one for each fleet in its first year) assuming 1–6 modes. The red line is the first normal distribution, the purple line is the second normal distribution, and the blue line is the third normal distribution. The dashed green lines are the weighted sums of the identified normal distributions.



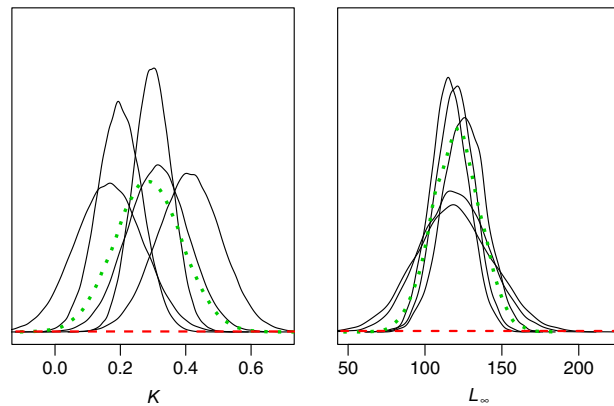
**Figure 7.** Posterior length and age for longtail tuna in five regions and overlaying together.

(iii) values of the restraining variables  $K$  and  $L_{\infty}$  were taken from literature. The mean  $K$  was 0.37 and the mean  $L_{\infty}$  was 118.2 cm from 12 independent studies (IOTC Secretariat, 2015c).

Note that the assumed restraining variables  $K=0.37$  and  $L_{\infty}=118.2$  cm were not priors, as in the Bayesian model, but were used to screen datasets to ensure biologically realistic length increments. Simulation results above indicated no clear pattern between the values of these variables and the resulting posterior growth parameters. Applying these screening criteria to all 416

strata resulted in a total of 152 that satisfied the conditions (see example in Figure 6 and all strata in the Supplementary Material). Among the retained strata, 122 had two age classes and 30 had three age classes. Because the location of modes varied among strata even when the number of age classes was only two or three, the 152 strata comprised many age classes at finer time steps than 1 year. Meta-analysis of these strata together allowed true ages to be estimated (Figure 7; note the fine scale of the posterior age on the x-axis).

Compared with the hyperpriors, the posteriors exhibit a fairly narrow distribution (Figure 8). The posterior mean  $K_f$  varied



**Figure 8.** Density of hyperpriors and posteriors for longtail tuna. The thin black lines are for five fleets. The red dashed lines are the hyperprior, and the green dotted lines are posteriors of the hyperparameters.

**Table 2.** Posterior key VBGF parameters for longtail tuna.

Parameter	Mean	SD	2.5%	Median	97.5%	C.V.	N strata
$K_{\text{IRN}}$	0.29	0.06	0.18	0.30	0.41	0.20	98
$K_{\text{MYS}}$	0.21	0.07	0.10	0.20	0.39	0.33	3
$K_{\text{OMN}}$	0.42	0.10	0.26	0.41	0.67	0.23	25
$K_{\text{PAK}}$	0.33	0.09	0.19	0.31	0.58	0.28	25
$K_{\text{THA}}$	0.19	0.10	0.07	0.17	0.46	0.53	1
$\mu_K$	0.29	0.10	0.11	0.29	0.51	0.35	152
$L_{\infty, \text{IRN}}$	129.0	14.3	109.9	125.4	166.9	0.11	98
$L_{\infty, \text{MYS}}$	118.8	21.9	79.0	119.0	167.8	0.18	3
$L_{\infty, \text{OMN}}$	120.2	12.5	98.4	119.7	150.6	0.10	25
$L_{\infty, \text{PAK}}$	116.4	12.5	93.5	116.1	145.3	0.11	25
$L_{\infty, \text{THA}}$	115.7	25.0	58.9	118.4	158.6	0.22	1
$\mu_{L_{\infty}}$	120.0	15.7	90.7	120.0	154.8	0.13	152
$t_{0, \text{IRN}}$	-0.11	31.19	-61.09	-0.12	60.95	-	98
$t_{0, \text{MYS}}$	-0.09	31.39	-62.28	0.04	61.76	-	3
$t_{0, \text{OMN}}$	-0.30	31.57	-62.51	-0.26	61.79	-	25
$t_{0, \text{PAK}}$	1.21	31.58	-59.55	0.92	63.32	-	25
$t_{0, \text{THA}}$	0.34	31.48	-60.88	0.23	61.86	-	1

IRN, Iran; MYS, Malaysia; OMN, Oman; PAK, Pakistan; THA, Thailand.

from 0.19 for the Thai fleet (THA) to 0.42 for the Oman fleet (OMN; Table 2). The ocean-wide hyperparameter  $\mu_K$  was 0.29 (95% CI between 0.11 and 0.51). The median  $L_{\infty, f}$  ranged from 115.7 cm for the THA to 129 cm for the Iranian fleet (IRN). The ocean-wide mean hyperparameter  $\mu_{L_{\infty}}$  was 120 cm (95% CI between 90.7 and 154.8). The number of strata used for the BHM had a direct effect on the uncertainty. For example, the Malaysian fleet (MYS) had only three strata and the THA had one stratum, leading to their large C.V.s for  $K_f$  and  $L_{\infty, f}$ . However, there was no clear relationship between the parameter uncertainty and the number of strata when the number of strata was relatively large (i.e.  $>20$ ), as other contributing factors also affected the uncertainty (e.g. the estimated length by MNMM). The median  $t_0$  varied between -0.26 (IRN) and 0.92 (THA), but their credible intervals were very wide.

The meta-analysis suggests that fish tend to grow more slowly in the east (Thailand and Malaysia) than the west (Iran and Oman; Table 2). Overlaying estimated length  $\sim$  age relationships for the five regions revealed two possible growth curves

(Figure 7): fish caught in Iran and Oman were above the average curve from the hyperparameters, and fish caught in Thailand, Malaysia, and Pakistan were under the average curve.

The Bayesian model also produced estimated ages in each stratum. The mean minimum age was 0.17 years from the OMN, and the mean maximum age was 5.70 years from the Pakistani fleet. However, age estimation had a very large variance, e.g. C.V. = 554% for the maximum mean age.

Parameters  $K_f$  and  $L_{\infty, f}$  are often highly correlated. This proved to be true for longtail tuna, with an average correlation coefficient  $r = -0.86$ ; however, the correlation between  $\mu_K$  and  $\mu_{L_{\infty}}$  was low, merely  $-0.19$ .

## Discussion

Estimating growth from length data is challenging as lengths sampled from catches often exhibit a narrow spread due to gear selectivity, slow growth in old fish, and spatial segregation of different age classes. We demonstrate that a Bayesian meta-analysis approach that integrates fishery data across a wider spatial and temporal dimension can yield estimates of growth parameters that are representative of a larger population as well as subpopulations at regional levels. Even though the method is designed for length data with few identifiable modes, it can be easily adopted for length data with more than three modes in each stratum.

Generally, there are two types of meta-analysis: (i) quantitatively summarizing published results and (ii) analysing data pooled from multiple sources. Summarizing published papers has several limitations (Blettner *et al.*, 1999). Studies may differ considerably in their methodologies including the experimental design, data collection methods, and analytical approaches used. A meta-analysis cannot correct for poor design or bias in the original studies. Another potential pitfall is the reliance on the availability of published studies, i.e. publication bias, as studies that show negative, conflicting, or insignificant results are less likely to be published. In the case of growth studies for neritic tuna, bias may be caused by the fact that available results are limited to certain regions. In addition, assumptions adopted in the published studies may not be appropriate, for example, assuming migratory neritic tunas are part of a closed subregional population.

The second type of meta-analysis can avoid some of the aforementioned problems by reanalysing the pooled data through a coherent statistical modelling framework. With a larger sample size, the effect of rare exposures can also be examined, which is often not possible in a single study (Blettner *et al.*, 1999). Our analysis included fish from multiple spatial and temporal strata of the same species, so it is important to apply a coherent method. However, one caveat of this approach is that it is computationally expensive and time-consuming.

While several length-based methods have been developed for fish growth (Schnute and Fournier, 1980; Pauly, 1987; Fournier *et al.*, 1990, 1998; Gulland and Rosenberg, 1992; Laslett *et al.*, 2004; Spence and Turtle, 2017), these methods do not work well when the data contain only a few modes and/or lack modal progression over time. In addition, these methods typically require an assumption about the age of the first mode (Leigh and Hearn, 2000). Bayesian hierarchy models have been used when the age is known (Helser and Lai, 2004; He and Bence, 2007; Chang *et al.*, 2013), but their application is more difficult when only length data are available.



One challenge in length frequency analysis is to reliably identify length modes. Individual datasets used for regional growth studies of neritic tuna comprise up to five age classes (Abdussamad *et al.*, 2012). However, some aging studies have found that longtail tuna can live up to 18 years (Griffiths *et al.*, 2010a). It should be recognized that fish aging studies almost inevitably involve some form of subjective decision-making (e.g. differentiating annual rings in the otoliths) and are thus subject to error (Francis, 2016). Determining the number of age classes in a length frequency dataset is challenging in many length-based methods (ELEFAN, Shepherd's length composition analysis, projection matrix, and MULTIFAN; Bjørndal and Bolten, 1995). We applied three criteria to determine the optimal number of age classes: (i) the number of age classes in any stratum is limited to three, which eliminates potentially identifying false age classes; (ii) the use of AIC for model selection, which aims to produce a more parsimonious parameterization (Fournier *et al.*, 1990, Roa-Ureta, 2010); and (iii) the requirement of a minimum length increment, which serves to prevent the identification of false modes. It is likely that some valid data may have been excluded by applying these criteria, but we expect that the impact is small given the large amount of data available within each region. Additional constraints can be applied, such as placing bounds on the mean lengths at some ages (Fournier *et al.*, 1990; Laslett *et al.*, 2004), or thresholds on the proportion and SD for each mode (Quinn and Deriso, 1999). However, these constraints require more information on the biology of the species, which is difficult to obtain for data-poor species.

The narrow spread of the length distribution in each sampling stratum and the resulting low number of age classes may be due to a number of reasons: (i) movement or migration, i.e. only fish of a certain life-stage are present in the stratum at the time of fishing; (ii) high mortality rate resulting in few old fish in the population; (iii) gear selectivity; and (iv) indistinguishable age classes, particularly for the last mode. The meta-analysis method is not expected to be influenced by (i) and (ii). Regarding gear selectivity, combining samples from a number of gear types (which have different selectivity patterns) would allow a wide range of fish sizes to be incorporated into the analysis. Nevertheless, larger fish may have been disproportionately underrepresented in the data as the selectivity of gillnets (the predominant gear for neritic tuna) is dome-shaped.

The screening criteria are designed to minimize the possibility of erroneously identifying a false age class. Retrospectively, the estimates of the MNMM are not sensitive to additional modes added (the model with  $n + 1$  modes yields similar estimates for the first  $n$  modes). This is because older fish are weighted less in the mixture component. Although erroneously excluding the last mode generally has a minor effect on the estimates of length increment for previous modes, it may lead to some bias in the estimate of the asymptotic length. However, the simulation exercise indicates that excluding large fish whose length modes cannot be identified has little impact on the parameter estimates. The aging study of longtail tuna by Griffiths *et al.* (2010a) using sectioned sagittal otoliths yielded estimates that are broadly consistent with the results from this study despite the growth model from the aging study being fitted to a much larger number of age classes.

Detailed comparison with the results of previous regional studies is difficult due to differences in sampling locations, time, and methods. Yesaki (1994) reviewed the growth of longtail tuna in the Indo-Pacific region. The estimated growth parameters varied

markedly from study to study:  $K$  ranged from 0.23 to 1.44 and  $L_{\infty}$  ranged from 58.2 to 133.6. The IOTC Secretariat (2015c) compiled estimated growth parameters from 13 studies: the mean  $L_{\infty}$  was 113.3 cm (ranging from 55.0 to 135.4 cm with an SD of 24.1) and the mean  $K$  was 0.47 (ranging from 0.18 to 1.70 with an SD of 0.39). Overall estimates from the current study are within the range reported in the literature (Abdussamad *et al.*, 2012; IOTC Secretariat, 2015c). The current analysis also yielded narrower credible boundaries for the estimates than previous studies.

The indication of possible two distinct growth patterns deserves some thoughts. Fish captured in Thailand and Malaysia have a similar growth pattern, whereas fish harvested in Iran and Oman are distinct from this group. Fish captured in Pakistan appear to be between the two groups. The "parallel" growth curves may indicate possible stock separation among the five regions examined. Further research is needed to validate this hypothesis. If the hypothesis turns out to be true, multiple stocks and spatial assessment should be considered in stock assessments.

The potential weakness in the two-step approach is that uncertainty around the estimates (modal values and their variances) from the MNMM and BHM are not estimated together. Ideally, the two steps should be combined into an integrated BHM. We have tested this approach but encountered two major challenges. First, running the integrated model was very slow and required substantial computer power (we used a high-performance computer). Second, model convergence proved difficult when using the real data even after many days. We recommend further research on developing integrated models in the future.

## Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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