Natural mortality ogives for the Indian Ocean bigeye tuna stock assessment

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Introduction

Natural mortality (M) is a very influential parameter in fish stock assessments but is also difficult to estimate. Various sources of information have been used to support M estimates in different species, including the age structure of the population, the maximum observed age, tagging data, and inferences from related species. Two of the main components to estimate are the mean value of M, and its possible variation among population subgroups (e.g., sexes and age classes). In 2021, an analysis of potential approaches for modelling natural mortality was initiated for yellowfin tuna (Hoyle, 2021a). After comments by the IOTC Working Party on Tropical Tunas, additional analysis has been requested. The aim of this work is to compare approaches for defining appropriate levels of M for inclusion in stock assessments of Indian Ocean bigeye and yellowfin tuna, including:

1. Investigate the influence of alternative M assumptions on management advice, by running IO YFT and BET assessments with different M ogives and mean values.
2. Recommend default assumptions for use in IOTC stock assessments.
3. Recommend research to improve estimates of the most influential aspects of M.

Initially, the data, methods, and natural mortality ogives used for bigeye stock assessments by all tuna RFMOs are explored via a literature review.

Many aspects of the determination of natural mortality at age are considered, including

- methods for estimating the target level of M,
- methods for determining relative M at age,
- methods for combining the target M with M at age,
- whether or not M should vary by sex; and
- whether or not M should vary between oceans.

Data and approaches by tuna RFMO

Oldest fish (otoliths)

IOTC

14.7 years from ageing of 108 otoliths (Farley et al., 2021).

WCPFC

The oldest fish aged using otoliths in the WCPO is approximately 15 years (Ducharme-Barth et al., 2020) from 1172 otoliths (Farley et al., 2020).

IATTC

NA (daily ageing only).

ICCAT

The oldest fish aged was 17 years old (Andrews et al., 2020), although this was considered low since the number of fish aged was just over 200, and samples came from an already heavily-depleted stock (ICCAT, 2021b).

Time at liberty

WCPFC

The longest period at liberty for a recaptured bigeye tuna tagged in the WCPO is approximately 14 years, for a fish 1-2 years old at release (SPC unpublished data) (Ducharme-Barth et al., 2020; Langley et al., 2008), indicating an age of 15-16 years.

IOTC

The longest time at liberty was eight to nine years, corresponding to an age of eleven to twelve years (Langley, 2016).

IATTC

The longest time at liberty was eight years (Aires-da-Silva et al., 2015).

ICCAT

Longest time at liberty in 2019 was five to six years (ICCAT, 2019).

Natural mortality

IOTC

In 2006, Hillary and Mosqueira (2006) develop a bigeye tuna assessment with the integrated assessment package CASAL (Bull et al., 2003), using natural mortality at ages 0 to 6+ of 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.4. They ran two sensitivity trials, the first with M at age 0 increased to 1.2, and the second with juvenile natural mortality of 0.6 for ages 0 and 1. They noted that changing M at age 0 affected B0, but had little effect on depletion, selectivity, or fits to the data. Also in 2006, Shono et al. (2006) developed a preliminary assessment of bigeye tuna using Stock Synthesis 2 (Methot, 2005). Natural mortality at ages 0 to 6+ was 0.8, 0.8, 0.4, 0.4, 0.4, 0.4, 0.4. They ran sensitivity analyses with a different trend for juveniles:1, 0.8, 0.6, 0.4, 0.4, 0.4, 0.4; with the same ogive as the CASAL model: 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.4; and adding senescence: 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.6. However, it is unclear from the report how these changes affected results.

In 2009 Shono et al. (2009) updated this assessment using the original M at age ogive. Nishida and Rademeyer (2009) ran an ASPM assessment using M of 0.8 for ages 0 and 1, and 0.4 for ages 2 to 9+.

In 2010, Kolody et al. (2010) introduced Stock Synthesis 3 (Methot and Wetzel, 2013), with the baseline M vector derived from Shono et al. (2009). They trialed two additional ogives with M for all ages raised or lowered by 20%. Higher M led to estimates that the stock was in better condition. Attempts to estimate M were not considered credible, since the model consistently referred lower M for younger ages, and also because the analysts considered that, given the structure of the model, the data are unlikely to be informative about M. Nishida and Rademeyer (2010) updated their model from 2009 but did not change the M at age.

In 2011 Zhu et al. (2011) ran a tuned VPA assessment with the same M ogive as Shono et al. (2009).

In 2013, bigeye assessments were run using ASAP (Zhu et al., 2013), ASPM (Nishida and Iwasaki, 2013), and SS3 Langley (Langley et al., 2013). All 3 used the same Shono et al. (2009) M ogives as in previous versions, but Langley et al. (2013) introduced a curve with a lower natural mortality for adult age classes (0.0625 per quarter).

The 2016 bigeye stock assessment using SS3 Langley (2016) explored the implications of these two alternatives natural mortality ogives, particularly with reference to adult M, and considered the lower level more plausible since it allowed the model to fit better to the tag data. There were a considerable number of tag recaptures after 7–8 years at liberty, indicating that proportion of these fish reach an age of 8–10 years; 8 tags were recovered after 10 years at liberty and a few tags were recovered in 2015, corresponding to an age at recovery of 11–12 years.

The 2019 stock assessment for Indian Ocean bigeye tuna (Fu, 2019) used two alternative levels of natural mortality, following Langley (2016). The higher level of natural mortality was considered comparable with IATTC and WCPFC approaches, with relatively high M for the younger age classes and M of about 0.1 per quarter for adults. The lower level of natural mortality was proposed based on a Lorenzen curve analysis, along with lower natural mortality for the adult age classes (0.0625 per quarter). This was seen as comparable to the level of natural mortality assumed for Atlantic bigeye tuna in the 2015 ICCAT stock assessment (ICCAT, 2016). An inverse relationship between M and age/size (high M for juveniles and low M for adults) is well established (Lorenzen, 1996; Lorenzen, 2000; Lorenzen, 2005; Lorenzen et al., 2022) and corresponds well with some of the biological factors contributing to the variability of natural mortality of tuna (Fonteneau and Pallares, 2004).

Natural mortality in the 2019 assessment is provided in Figure 1, along with ogives currently used by each of the other 3 tuna RFMOs that assess stocks of bigeye tuna.

IATTC
Text from Xu et al. (2020). "Age-specific vectors of natural mortality (M) are assumed for bigeye in the EPO. This assessment uses sex-specific models and natural mortality schedules are provided for each sex (Figure 3.2 in Aires-da-Silva and Maunder, 2010). M at age 0 is assumed to be 0.25 for both sexes, and M is assumed to decrease to 0.1 at 5 quarters of age. As in previous assessments, it is assumed that female M increases after the fish mature. These age-specific vectors of M are based on fitting to the estimates of age-specific proportions of females, maturity at age, and M of Hampton (2000)." In fact, most of the decrease to 0.1 occurs by 4 quarters, when M is equal to 0.101087.

Effects of alternate juvenile M have been evaluated (SARM-9-INF-B)

WCPFC
M-at-age was calculated using an approach applied to other tunas in the WCPO and EPO (Harley and Maunder, 2003; Hoyle, 2008; Hoyle and Nicol, 2008). The generally increasing proportion of males observed in the catch with increasing size was assumed to be due to an increase in the natural mortality of females, associated with sexual maturity and the onset of reproduction. Values of M-at-age were initially calculated at-length, back-transformed to age using the growth curve, and input to the MFCL assessment model as fixed values.

Meta-analysis using different life-history based M estimators was also conducted (Vincent et al., 2020) to provide a range of plausible natural mortality values for the assessment (Ducharme-Barth et al., 2020). These included the lower 95% confidence interval (0.109; M-low), the mean (0.127; M-mid) and the upper 95% confidence interval (0.146; M-hi). As a sensitivity analysis these values were applied to the age-specific deviates used in the diagnostic case.

ICCAT
In the 2021 ICCAT bigeye assessment, natural mortality ogives were calculated by applying the Then et al. (2015) estimator to a maximum observed age of 17 years (Andrews et al., 2020), and scaling the ogive so that natural mortality was a Lorenzen function of weight at age (Lorenzen, 1996) (ICCAT,

2021a). Additional ogives were based on alternative maximum ages of 20 and 25, because the aged fish were sampled from a heavily fished stock (ICCAT, 2021b).

The method for combining the estimate of *M* based on *Amax* with the Lorenzen curve was not fully described in any of the ICCAT documents, and to date I have not been able to derive similar numbers. They can be roughly approximated by applying the Then et al (2015) estimate at age 4 years, with *M* at other ages determined by the mean length at age, i.e., $M(L_a) = M(L_4).L_4/L_a$.

Further considerations
Methods for estimating the target level of *M*
The oldest fish observed in a population (*Amax*) can be used to infer a target level of natural mortality, based on meta-analyses of databases of *Amax* and *M* estimates (Hoenig, 1983; Then et al., 2015; Hamel and Cope, in review). Then et al (2015) updated the Hoenig (1983) estimator by greatly increasing the size of the database. Hamel and Cope (see currently in peer review) used the Then et al (2015) database but identified an improvement to the statistical methods that materially changed the resulting predictions. We anticipate recommending that the Hamel and Cope (in review) (HC) approach should be used once it has completed peer review. In the interim we recommend applying both the HC and Then et al (2015) methods.

Methods for determining relative *M* at age
It is increasingly well established that natural mortality is inversely proportional to length (Lorenzen et al., 2022). There is also little evidence for a step change in natural mortality between juveniles and adults (Lorenzen et al., 2022). We therefore recommend using this approach in preference to the more complicated method discussed at WPTT 2021 and implemented in Stock Synthesis (Hoyle, 2021b; Maunder and Aires-da-Silva, 2012; Methot et al., 2021).

Methods for combining the target *M* with *M* at age
Lorenzen et al. (2022) found that predictions of constant *M* based on Then et al. (2015)'s growth-based empirical predictor (which is distinct from the predictor based on *Amax*) were approximately equal to size-dependent *M* values at around the center of the adult size range. They argued that "this supports the established practice of scaling the 'Lorenzen *M*' so that its average over the adult size or age groups equals empirical estimates of constant *M* (SEDAR (Southeast Data, Assessment and Reviews), 2018)." However, the evidence for applying the growth-based empirical predictor to adult age classes does not necessarily transfer to other empirical predictors. The approach for applying them will depend on the information that was used to estimate them.

Applications of Lorenzen *M* at age for Atlantic bigeye (e.g., ICCAT, 2021a; ICCAT, 2021b; Schirripa, 2016) have combined the two components (target M and Lorenzen curve), largely using the approach adopted by the Southeast Data, Assessment and Review (SEDAR) process, as documented by Porch (2011). It should be noted that this approach differs somewhat from the recommendation of Lorenzen et al. (2022) in that the average is applied across fully exploited age classes rather than across adult age classes.

Porch (2011) describes the approach to rescale the Lorenzen curve so that the average mortality rate matches a target value over the relevant life history period. "This is typically accomplished in three steps: 1) the Lorenzen curve is converted to a function of age by use of a growth equation, 2) the target value of *M* is determined external to the assessment model, and 3) the Lorenzen curve is rescaled such that $M_t = M_{target} \frac{n\lambda_t}{\sum_{t=t_c}^{t_{max}} \lambda_t}$, where *t* is age, λ_t is the age-converted Lorenzen curve, t_c is the first fully exploited age class, t_{max} is the oldest age class, and *n* is the number of exploited age

classes. [In other words, M_{target} is multiplied by λ_t / mean(λ), across the range of fully exploited age classes.] The results of this rescaling approach are sensitive to the value of t_c when it falls within the age range where growth is rapid."

The Atlantic bigeye approach is a little more complicated. First, length at age t_c is calculated, based on a von Bertalanffy growth curve, as $len_{t_c} = L_\infty\left(1 - e^{-K(t_c - t0)}\right)$. Next, an adjusted mortality at unit length, M_1, is calculated as:

$$M_1 = \frac{(t_{max} - t_c)L_\infty K M_{target}}{log\left(len_{t_c} \middle/ \left(len_{t_c} + L_\infty\left(e^{(K(t_{max} - t_c))} - 1\right)\right)\right)} \tag{1}$$

Lengths at age are calculated based on the midpoint of the age class, using the equation:

$$len_{t+0.5} = L_\infty\left(1 - e^{-K(t - t0 + 0.5)}\right) \tag{2}$$

M is then estimated at each age class t as $M_t = M_1/len_{t+0.5}$, based on the assumption that M is inversely proportional to length (Lorenzen et al., 2022). A slightly more accurate formulation of M at age integrates across the growth curve for the period inc between ages t and $t+1$, given the units of K.

$$M_t = -log\left(\frac{len_t}{len_t + L_\infty.(e^{K.inc} - 1)}\right) \cdot \frac{M_1}{L_\infty K} \tag{3}$$

Should M vary by sex?
As previously discussed (Hoyle, 2021b), M has been assumed in the past to vary by sex due to the predominance of males at large sizes, as seen in all species of *Thunnus*. However, ageing using annuli has provided considerable evidence that males grow to larger sizes than females in all *Thunnus* species. This contributes some of the difference in sex ratio at length and may be the only reason for the difference. Although such a difference remains possible, it is unlikely to be large. Lacking reliable estimates of length at age by sex for bigeye tuna in the Indian Ocean, we do not have a basis for estimating the difference in M.

Should M vary between oceans?
Rates of natural mortality can vary considerably between locations, including between oceans (e.g., Strøm et al., 2019), so it may not be appropriate to apply M from one stock to another. However, estimates of natural mortality in individual stocks, based on *Amax*, may be affected by the history of fishing mortality experienced by the stock. They can also be affected by the amount and quality of age sampling. Inferences from the Then et al (2015) database should ideally be applied to relatively unfished stocks. Estimates of *Amax* from a heavily fished stock may therefore be biased low (and M biased high). In such cases inferring M from the A_{max} of a conspecific in another location that is less heavily exploited may be a more reliable approach for determining M.

What if all stocks are heavily exploited?
Tunas are believed to be currently heavily exploited in all oceans, and ageing using annuli is a recent development. Maximum ages are likely to reflect the effects on age structure of total mortality rather than natural mortality alone. However, maximum ages will be increased by spatial heterogeneity in fishing pressure on the stock, so it is not appropriate to estimate M by assuming that the empirical method estimates Z, and simply subtracting F. Ideally, maximum age should be

obtained by sampling longline catches as broadly as possible, and potentially by longline surveys in areas with little history of fishing effort.

Uncertainty

There are various sources of uncertainty:

- The symmetrical error distribution in the relationship between *Amax* and *M*. This can be characterized.
- Uncertainty about which age classes to include in the reference period. Negative bias from too many young age classes, or positive bias from old age classes.
- Positive bias due to low sample sizes and limited sampling distribution (IO: n=108, AO: n=~200).
- Positive bias due to exploitation of the stocks.

Analysis

The input files for the 2019 stock assessment were modified to run with the four alternative versions of natural mortality. No other parameters were modified.

Results

Proposed values of *M* for IOTC

Alternative values of target *M* (i.e., the natural mortality predicted by the empirical method) were calculated based on maximum observed ages of 14.7 years in the Indian Ocean and 17 years in the Atlantic Ocean.

Maximum age	Then et al 2015	Hamel and Cope in review
IO=14.7	0.410	0.360
AO=17	0.365	0.317

The target *M* was distributed across age classes using the Lorenzen curve and the Farley et al. (2021) von Bertalanffy growth curve, with the target *M* equal to the average *M* of age classes 1 to 15 (Figure 2 and Table 1). The ogive Then17 differs slightly from the corresponding ICCAT ogive due to the differences between the growth curves and because the ICCAT ogive uses a slightly different approach that increases size at age by 6 months growth, by replacing len_t with $len_{t+0.5}$ in equation (3).

The inverse relationship of natural mortality with length had a particularly large impact on *M* for young fish. All resulting estimates of natural mortality were considerably higher than even the high 2019 ogive for fish up to about 1 years of age.

The stock assessment models run with the four alternative versions of natural mortality fitted the data about as well as the 2019 model (Figure 3), with a slight improvement in likelihood for the model with the lowest natural mortality (HC 17) and slightly worse likelihood for the model with the highest natural mortality (Then 14.7).

All models with Lorenzen *M* tended to have lower spawning biomass time series estimates than the base model (Figure 4), but the spawning biomass ratio *SSB / SSB0* trends were almost identical (Figure 5). The time series of total biomass started lower for the Lorenzen *M* models, but all models ended up at similar levels (Figure 6). The *F* ratio time series indicated slightly lower *F / Fmsy*, particularly at the end of the time series, for the Lorenzen *M* models compared to the 2019

assessment (Figure 7). Impacts on recruitment were much larger, with highest average recruitment estimated for model Then 14.7 which has the highest natural mortality (Figure 8).

Discussion

It is reasonable to apply an empirically based estimator to the same range of age classes as were used to develop the estimator. Then et al. (2015) state that "Most of the M estimates were derived from age-based catch curve analyses (79%), 5% from length-based catch curves, 8% from tagging, and 2% from the regression of total mortality rate vs. effort (or variants)." We can therefore infer that the 215 M estimates in the Then et al. (2015) database were based on fully exploited age classes.

However, it is unclear if all the exploited age classes contribute equally to the mostly age-invariant M estimates included in the database. For example, tagging-based estimators generally include fewer of the older, rarer age classes, if fish are tagged in proportion to abundance. In some cases, such as tuna tagging on pole and line vessels, tagged fish are almost exclusively young and small (Fonteneau and Hallier, 2015; Leroy et al., 2013). Tagging-based estimators may therefore estimate M to be higher, since younger fish are expected to have higher M. Catch curve analyses, on the other hand, potentially include all ages up to t_{max}, usually assuming asymptotic selectivity at age of the fishery providing the samples. They will omit some younger age classes that are not fully selected, with full selection judged by the catch curve's linearity on the log scale. They may also give equal statistical weight to each age class, rather than weighting in proportion to numbers. Catch curves may therefore tend to estimate lower M than tag-based estimators.

Changing to Lorenzen M and reducing mean natural mortality have less impact on the assessment outcomes than might be expected, given the large differences apparent in Figure 2. However, the largest differences in natural mortality occur for very small fish before or in the early stages of recruitment to the fishery, which mostly serves to scale recruitment. The low level of variation between model runs may reflect the impact of the tags in the assessment model, since they tend to constrain the estimates of fishing mortality in the fisheries that capture the tags. Since catch in those fisheries is assumed known, this also constrains the biomass vulnerable to those fisheries. The fisheries taking the most tags are fisheries 5 (R1 free school purse seine - south), 9 (R1 associated purse seine -south), and 15 (R1 associated purse seine - north). Hence, the biomass of all models tends to be similar in the period of tag recovery (pseudo-years 315-355), particularly for purse-seine vulnerable biomass in R1.

Acknowledgements

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Tables

Table 1: Four alterative ogives of quarterly natural mortality for bigeye tuna.

| Age	Length	Then15	Then17	Hamel15	Hamel17
0	24	0.480	0.420	0.422	0.365
0.25	35	0.354	0.310	0.312	0.270
0.5	45	0.286	0.250	0.251	0.217
0.75	54	0.242	0.212	0.213	0.184
1	62	0.212	0.186	0.187	0.162
1.25	70	0.191	0.167	0.168	0.145
1.5	77	0.174	0.152	0.153	0.132
1.75	84	0.161	0.141	0.142	0.123
2	90	0.151	0.132	0.133	0.115
2.25	96	0.143	0.125	0.125	0.108
2.5	101	0.136	0.119	0.119	0.103
2.75	106	0.130	0.113	0.114	0.099
3	110	0.125	0.109	0.110	0.095
3.25	115	0.120	0.105	0.106	0.091
3.5	118	0.117	0.102	0.102	0.089
3.75	122	0.113	0.099	0.100	0.086
4	125	0.110	0.097	0.097	0.084
4.25	128	0.108	0.094	0.095	0.082
4.5	131	0.106	0.093	0.093	0.080
4.75	134	0.104	0.091	0.091	0.079
5	136	0.102	0.089	0.090	0.078
5.25	139	0.100	0.088	0.088	0.076
5.5	141	0.099	0.087	0.087	0.075
5.75	143	0.098	0.085	0.086	0.074
6	144	0.096	0.084	0.085	0.073
6.25	146	0.095	0.084	0.084	0.073
6.5	148	0.094	0.083	0.083	0.072
6.75	149	0.094	0.082	0.082	0.071
7	150	0.093	0.081	0.082	0.071
7.25	152	0.092	0.081	0.081	0.070
7.5	153	0.091	0.080	0.080	0.070
7.75	154	0.091	0.080	0.080	0.069
8	155	0.090	0.079	0.079	0.069
8.25	156	0.090	0.079	0.079	0.068
8.5	156	0.089	0.078	0.079	0.068
8.75	157	0.089	0.078	0.078	0.068
9	158	0.089	0.078	0.078	0.067
9.25	159	0.088	0.077	0.078	0.067
9.5	159	0.088	0.077	0.077	0.067
9.75	160	0.088	0.077	0.077	0.067
10	160	0.087	0.076	0.077	0.066

Figures
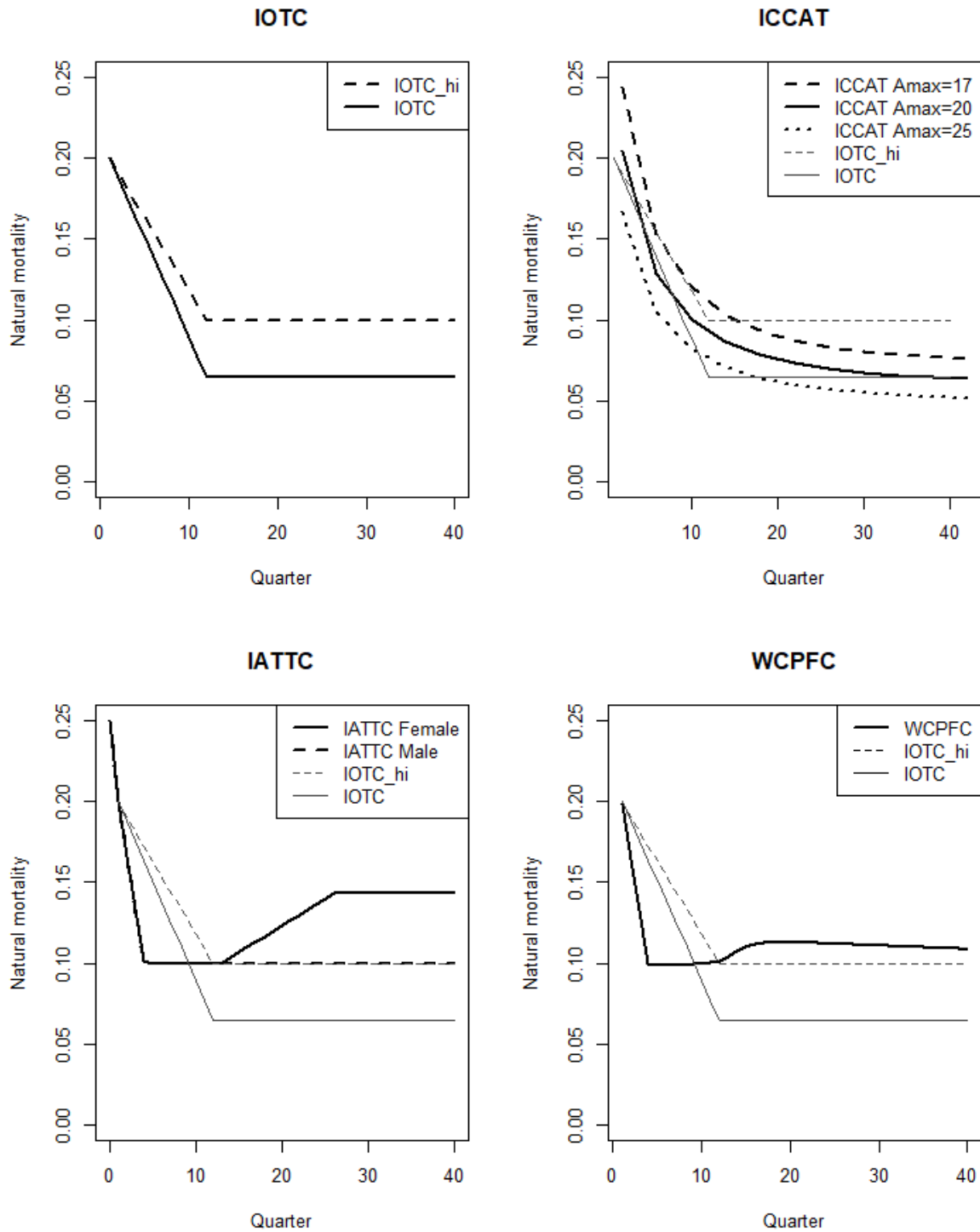
Figure 1: Quarterly natural mortality at age ogives for bigeye tuna used by each of the four tRFMOs that conduct bigeye stock assessments. The IOTC ogives are included in all subplots for comparison with the ogives used by the other tRFMOs.
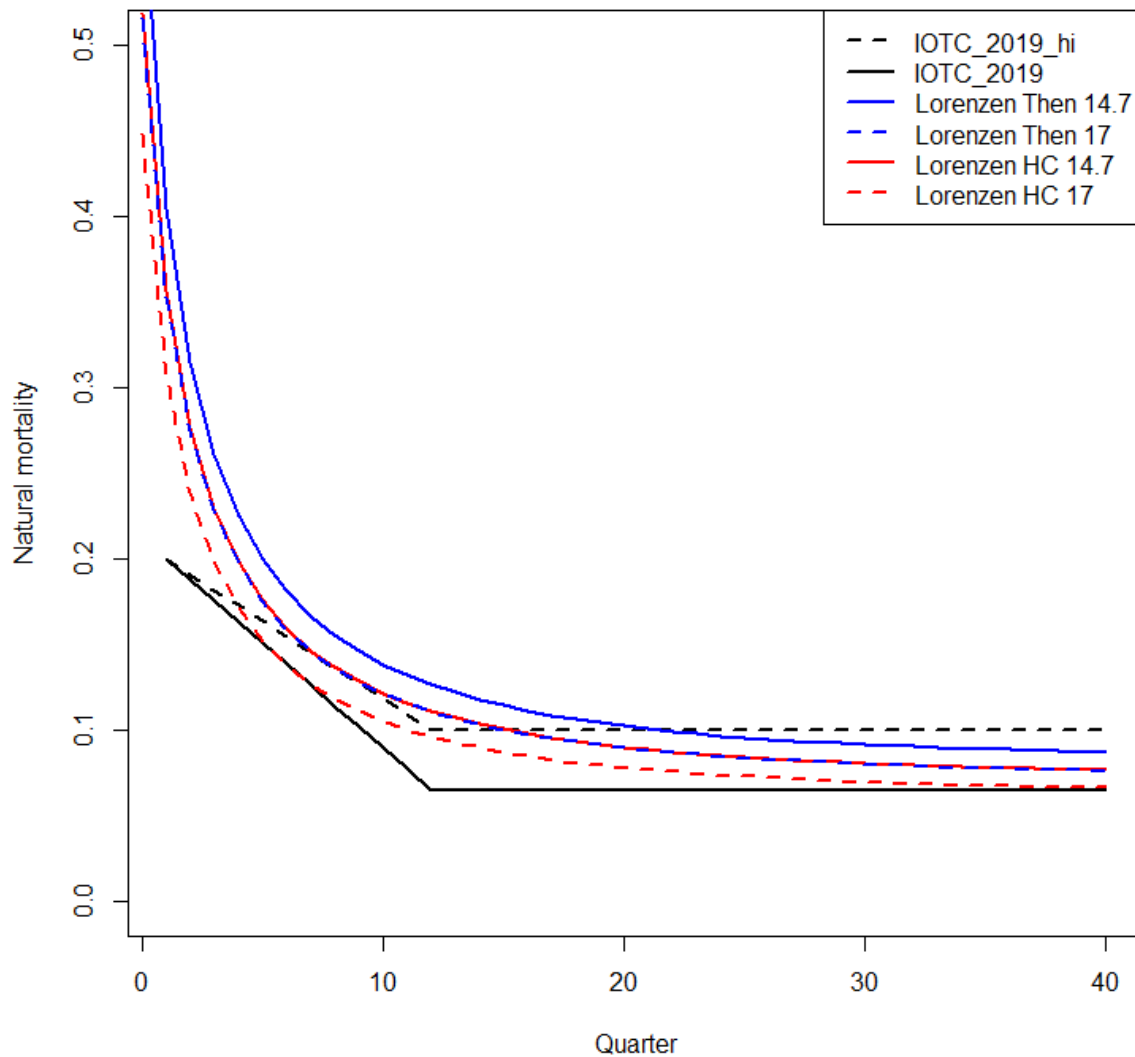
Figure 2: Natural mortality ogives used in the 2019 Indian Ocean bigeye tuna assessment, and the Lorenzen ogives proposed for the 2022 assessment.
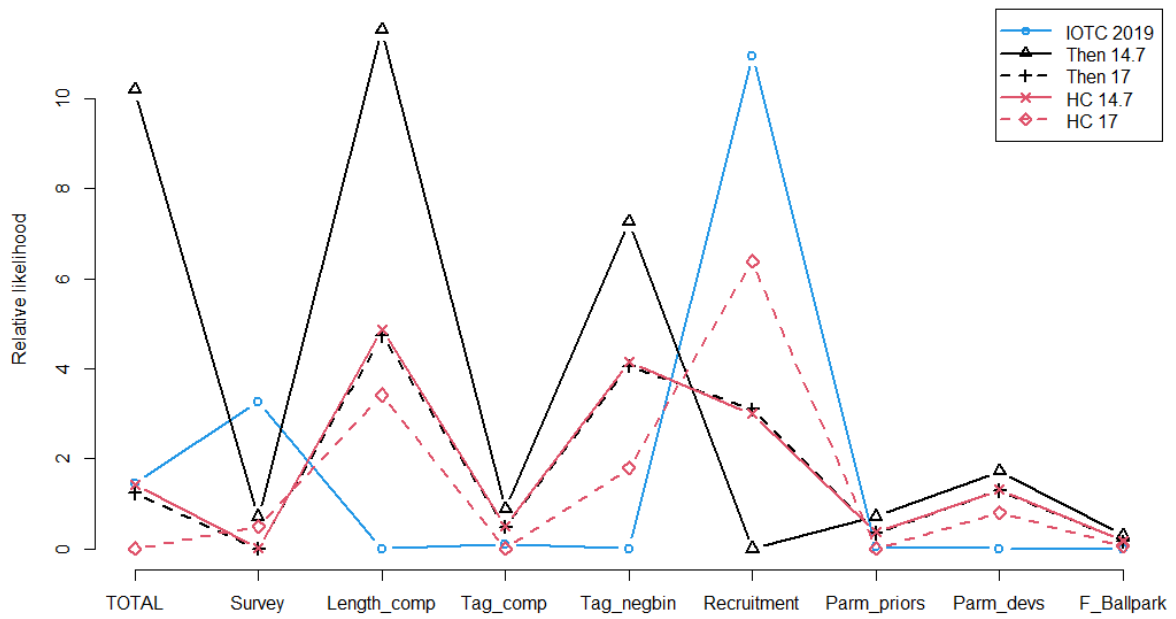
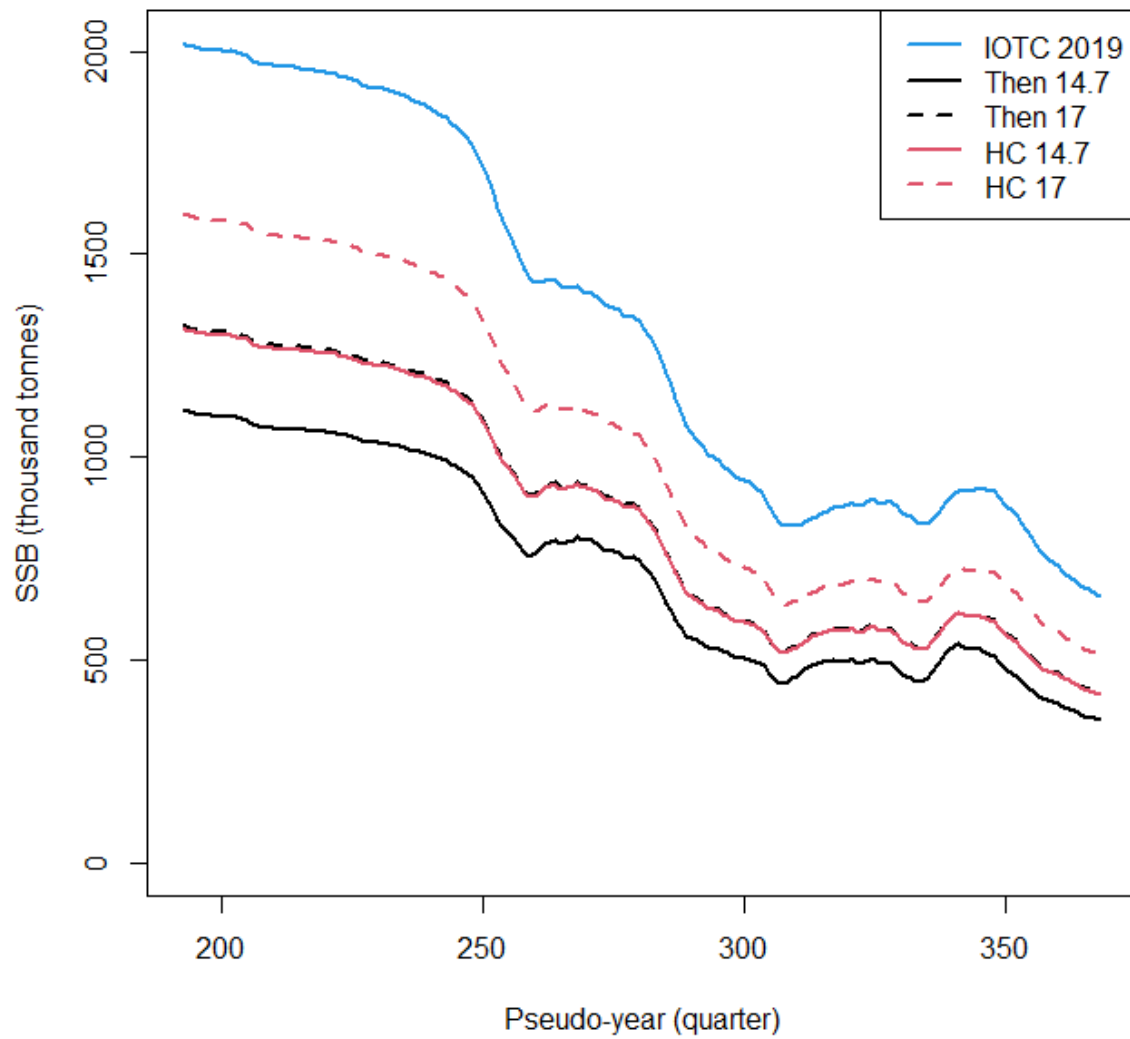*Figure 3: Relative total log likelihoods and the main likelihood components for each of the 5 models.*

Figure 4: Estimated spawning biomass time series for the five models.
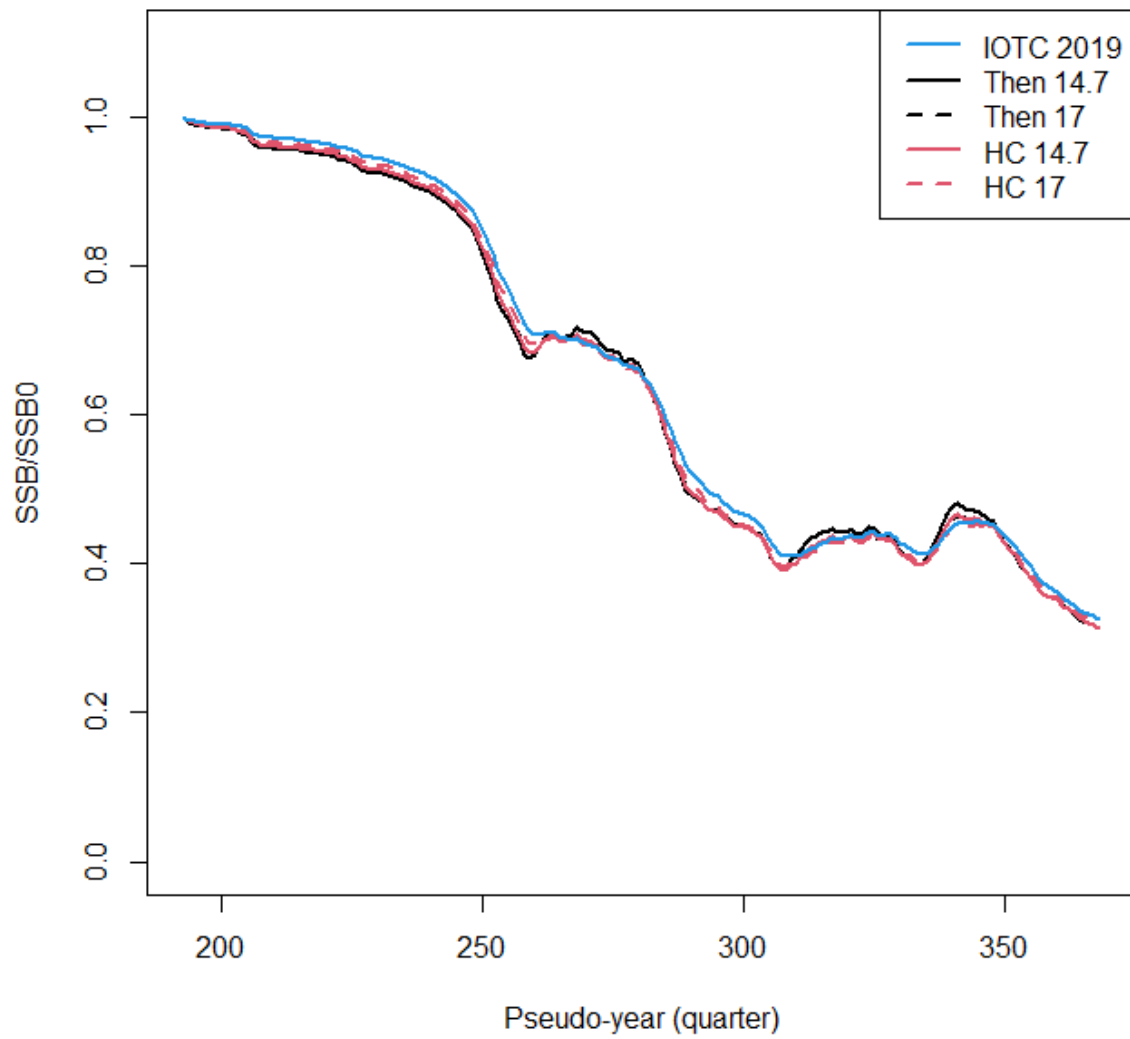
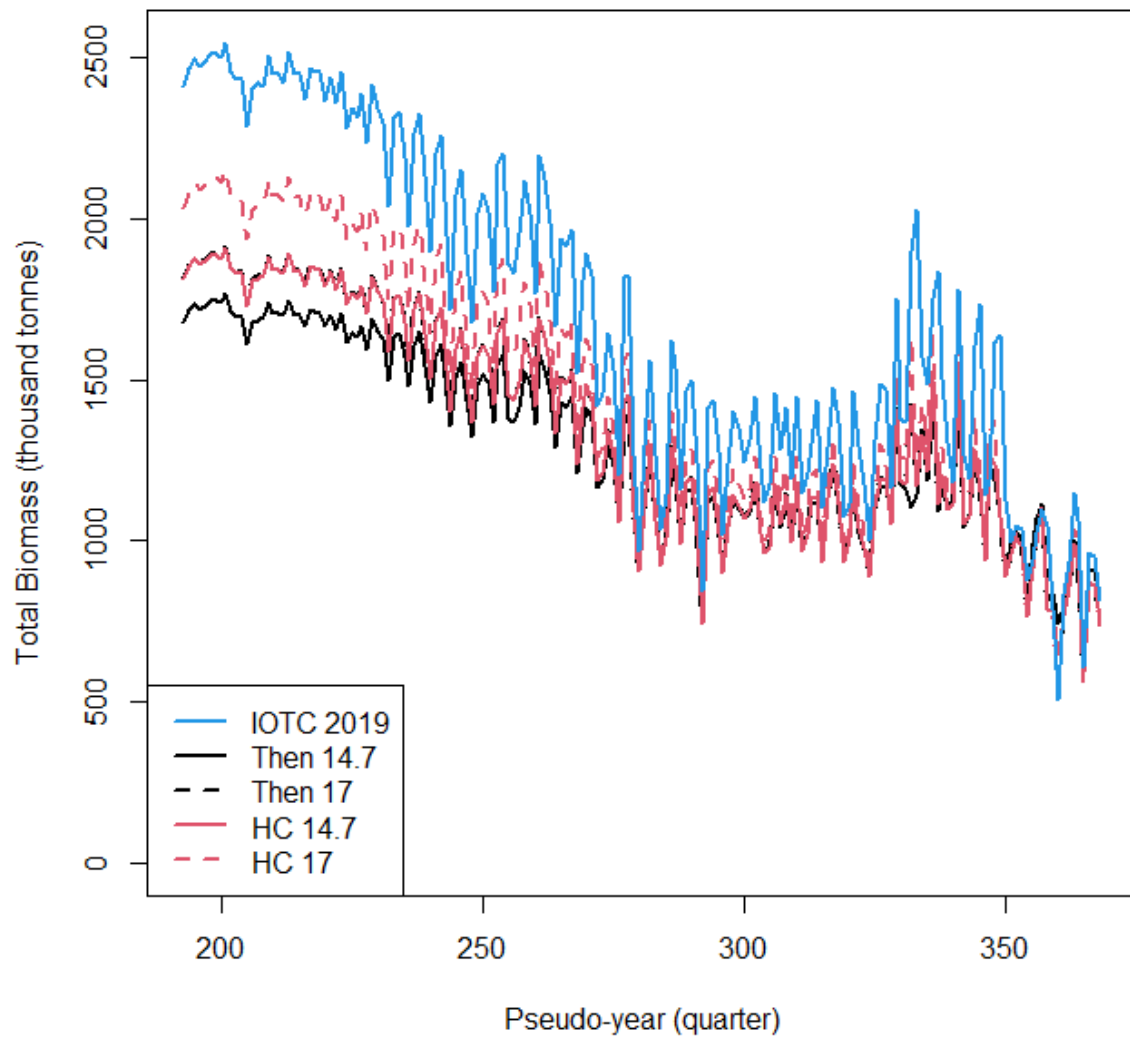*Figure 5: Estimated time series of the ratio SSB / SSBmsy for each model.*

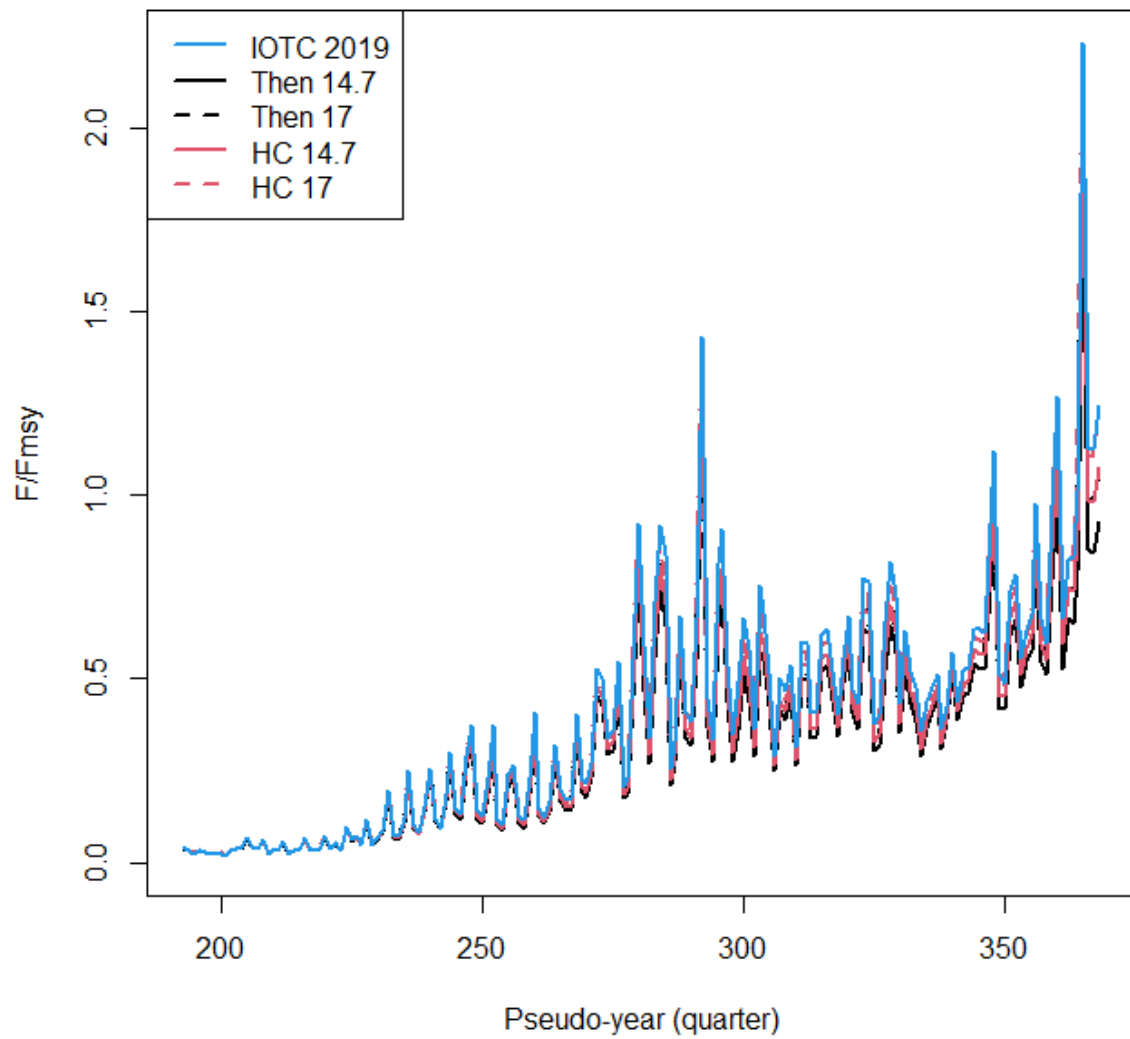*Figure 6: Time series of total biomass estimated for the five models.*

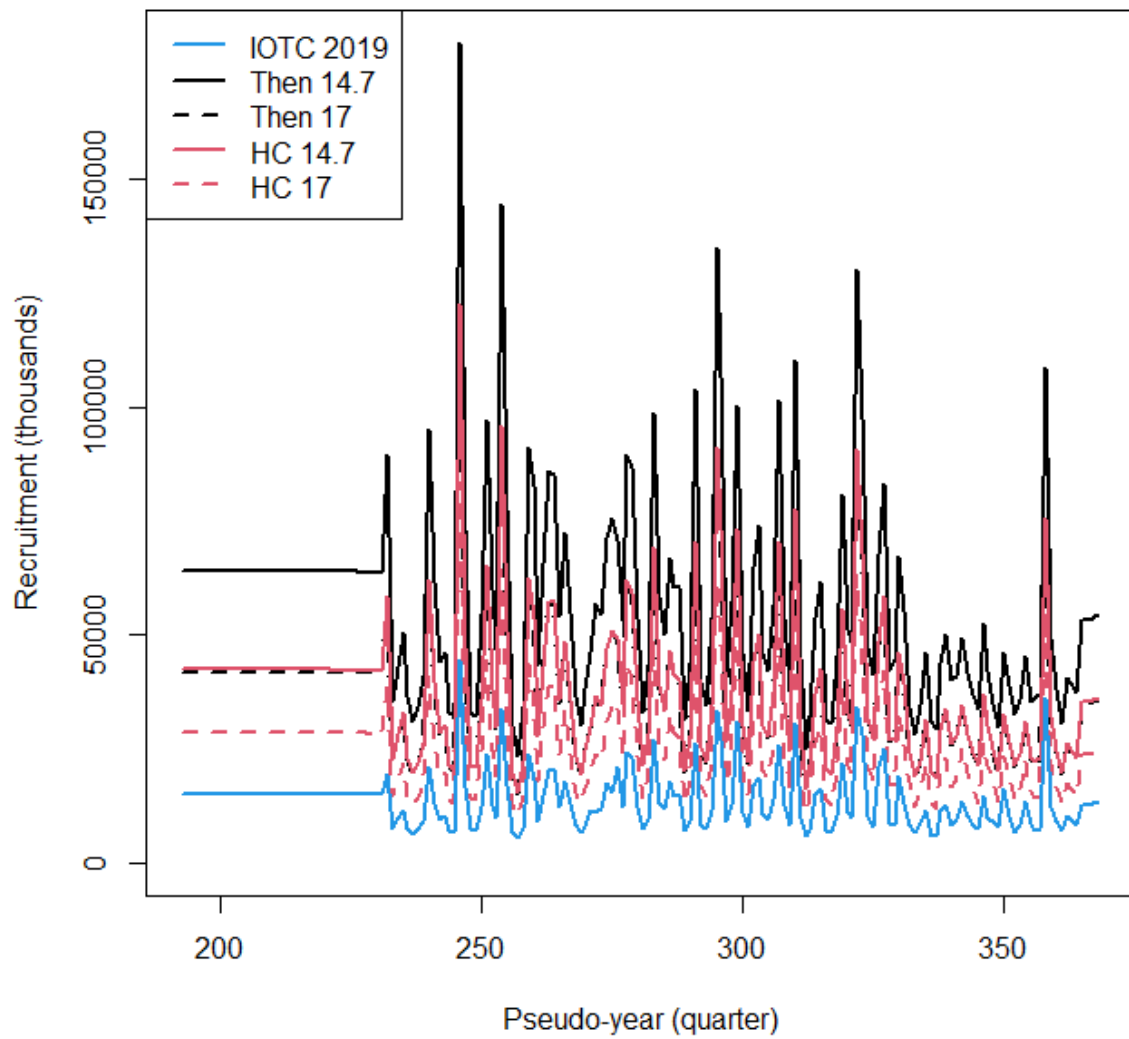*Figure 7: Estimated time series of the ratio F / Fmsy for each model.*

Figure 8: Estimated time series of quarterly recruitments for each model.