Approaches for estimating natural mortality in tuna stock assessments: application to Indian Ocean yellowfin tuna

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Executive Summary

The values used for natural mortality (*M*) are very influential in stock assessment models, affecting model outcomes and management advice. There is often limited information about the true levels.

This paper summarises the evidence used to estimate natural mortality at age for the four main stocks of yellowfin tuna, identifying some problems and information gaps. It also describes the history of parameter values used in stock assessments by each tuna RFMO.

Through time, Indian Ocean yellowfin tuna (IO-YFT) stock assessments have assumed a variety of values for M. The values used in the most recent assessment were intermediate between the higher levels assumed in assessments for the Eastern Pacific and the Western and Central Pacific, and the lower levels assumed in the Atlantic.

In June 2021 an online meeting was held by the Center for the Advancement of Population Assessment Methodology (CAPAM), to provide advice and guidance on practices for modeling natural mortality in fishery assessments. Based on presentations and discussions at the meeting, this paper provides IO-YFT natural mortality options for prior distributions derived from maximum observed age and suggests approaches for using these priors in stock assessments. It also recommends future research needed to develop improved estimates of natural mortality.

Introduction

Natural mortality, an aspect of population dynamics and productivity, is very influential in stock assessment models and affects model outcomes and management advice (Punt *et al.* 2021).There is often limited information about the true levels of natural mortality, so analysts' decisions and assumptions about natural mortality can be difficult yet important. This working paper provides advice to analysts on approaches for estimating natural mortality to use in the Indian Ocean yellowfin stock assessment.

In addition to uncertainty in natural mortality (*M*), there is considerable variability. *M* varies at all scales – between sexes, ages, locations, seasons, and years, and potentially trending through time. *M* will be affected by the availability of food, by predators, by parasites and disease, as well as by environmental stressors.

Fisheries data are rarely directly informative about natural mortality, and even its average level is difficult to estimate. Analysts must often make choices about the values, or range of values, assumed in an assessment. This uncertainty is unavoidable, as is the resulting uncertainty in model outcomes and management advice. For stock assessment and management strategy evaluation, this uncertainty needs to be included and explored. It is therefore appropriate for analysts to consider a range of plausible approaches, rather than assuming just one estimate or approach. Their goal is not necessarily to obtain the correct estimate of *M*, but to choose the most appropriate estimates for their particular purpose.

In this working paper we focus mainly on the base or average value of natural mortality for yellowfin tuna. We also briefly consider age-dependence and variation between sexes. For an earlier discussion of natural mortality for yellowfin tuna, see Maunder & Aires-da-Silva (2012).

History of *M* in yellowfin tuna stock assessments

Past assessments for yellowfin tuna have assumed various levels of natural mortality. An early and influential estimate of natural mortality was derived in the eastern Pacific from fish caught mostly in the bait boat fishery and aged using cohort slicing to convert size to age. Total mortality (*Z*) of 1.72 was estimated from a catch curve on fish aged 2-4 years, and estimated fishing mortality (*F*) of 0.95 subtracted to give *M* of 0.77, usually rounded up to 0.8, or between 0.6 and 1.0 (Hennemuth 1961). This was later revised by Schaefer (1967) to between 0.55 and 1.05.

However, there is good reason to expect the estimate of *M*=0.8 to be biased high. Catch curve models assume constant selectivity with increasing age, since declining selectivity with age will bias the estimate high. Most fishing at the time was relatively close to shore, with approximately 90 percent of the yellowfin catch less than 100 cm FL, and sizes increased considerably when later fishing moved offshore (Wild 1986). Bait boats select the smallest fish of any fishery, with selectivity now estimated to rapidly decline with age (Minte-Vera *et al.* 2020). Therefore, the *Z* estimate of 1.72 for fish aged 2-4 years is likely to be positively biased, with the proviso that the *F* estimate of 0.95 also is likely to be unreliable given the methods available at the time.

This same estimate of *M*=0.8 per year has been used in many stock assessments since. Wild (1994) reviewed natural mortality estimates in the eastern Pacific Ocean (EPO) and noted that although Francis (1977) considered 0.8 to be too high based on a simulation study, 0.8 was used in IATTC stock assessments for the eastern Pacific until 1989. Due to the lack of females larger than 140 cm in the fishery, the assessment was changed in 1989 to apply higher natural mortality to females (IATTC 1991), while retaining 0.8 for males. The same value of natural mortality has consistently been applied for males since then in EPO yellowfin tuna assessments (e.g. Maunder & Harley 2004; Hoyle

& Maunder 2006; Maunder & Aires-da-Silva 2010; Minte-Vera *et al.* 2020), with some refinements to the approach for female *M* (Maunder & Watters 2001).

Analyses of tagging data have been used to estimate natural mortality for yellowfin tuna in the Western and Central Pacific and Indian Oceans (WCPO). In the WCPO, an analysis of tagging data estimated natural mortality to be 0.68, 0.44, and 0.69 per year for the 51-60, 61-70 and 71-80 size classes respectively, and much higher for smaller and larger fish (Hampton 2000). This analysis focused more on size-variation than on the levels of the estimates. It assumed constant fishing mortality through time, and uniform reporting rates across sizes. Results may have been affected by low reporting rates of the longline vessels that catch larger fish, slower than assumed mixing of tagged fish with the population, and other spatial and seasonal dynamics. These estimates have been used in WCPO stock assessments to support the shape of the ogive (Tremblay-Boyer *et al.* 2017), but not as fixed estimates. In the Indian Ocean, two implementations of Brownie-Petersen models were used to estimate natural mortality rates for tropical tunas based on tag attrition. Bousquet *et al.* (2012) estimated surprisingly low natural mortality rates for bigeye, yellowfin, and skipjack tunas, with median estimates for yellowfin aged 1-5 of approximately 0.5, 0.27, 0.22, 0.27, 0.28. However, they characterised their results as preliminary and requiring confirmation by simulation studies, and this work has not been carried out. Eveson *et al.* (2012) applied a different model to the same dataset and similarly estimated low natural mortality, with rates that were effectively 0 for yellowfin tuna aged 1.5 or more in most model configurations. They also characterised their analyses as preliminary, noting the lack of spatial structure in the model, sensitivity to assumptions about the growth curve, and lack of tag returns from the longline fisheries. Simulation has shown that mortality estimates from Brownie models can be very sensitive to model misspecification around issues such as the spatial and seasonal patterns (Lauretta & Goethel 2017), and these issues were certainly present in the IO and WCPO tagging experiments.

Time at liberty of tagged tunas has also been used to support assumptions about natural mortality. For recaptured yellowfin tuna, the longest periods at liberty in 2015 were lower than the maximum ages from otoliths, at 6.5 years in the WCPO, 7.5 years in the EPO, 9.1 years in the Atlantic, and 6.0 years in the Indian Ocean (Fonteneau & Hallier 2015) for fish mostly tagged at about age 1 year. However, these lower times at liberty are expected due to tag loss, effects of tags on fish survival, and low tag reporting rates in the longline fisheries that take the largest fish.

In general, WCPO assessments have used the same approach to modelling natural mortality as IATTC, combining (for a model that does not distinguish between sexes) the Hennemuth (1961) estimate of 0.8 per year for males, along with a higher estimate for females that is sufficient to account for the reduced proportion of females observed at larger sizes (see further discussion below). These WCPO assessments have used either the IATTC combined-sex natural mortality ogive or a version calculated for the WCPO (Hoyle *et al.* 2009). These approaches are still being used (e.g. Hampton *et al.* 2005; Langley *et al.* 2011; Davies *et al.* 2014; Tremblay-Boyer *et al.* 2017; Vincent *et al.* 2020b), with the shape of the WCPO ogive recalculated in 2020 to allow for changes in the growth curve (Vincent *et al.* 2020a). The 2020 assessment (Vincent *et al.* 2020b) continued this approach in the diagnostic model but explored alternatives based on a meta-analysis of life-history and empirical relationships (Vincent *et al.* 2020a), with lower annual rates of 0.44-0.6.

In the Atlantic, natural mortality in the 2016 yellowfin assessment (Walter & Sharma 2017) was determined according to Lorenzen-scaled *M*-at age functions for the Gascuel *et al.* (1992) growth curve for ages 0-10, with average *M* of 0.54 based on maximum age of 11 years. The subsequent update of the maximum age to 18 years resulted in lower *M* of 0.35 at age 5 in the 2019 assessment (Walter *et al.* 2020).

In the Indian Ocean, a range of values has been used. In 2005 an ad hoc working group recommended M=2 at length 35 cm, declining linearly to 0.6 at 70cm and remaining constant thereafter (IOTC 2005, Appendix IV). In 2007, ASPM and SS2 assessments (Nishida & Shono 2007; Shono et $al.$ 2007) assumed M=0.8 at age 0, declining to 0.6 for ages 1+, as did the 2008 SS2 assessment (Shono et $al.$ 2008).

In 2008, preliminary runs of the first Indian Ocean yellowfin assessment using MULTIFAN-CL (Langley et $al.$ 2008) assumed the same natural mortality ogive used in WCPO yellowfin assessments, with base adult M of 0.8 and with increased M for a period representing higher natural mortality for mature females (for the combined-sex model). However, IOTC-WPTT 2008 recommended lower levels of natural mortality based on the preliminary results of tagging analyses using Brownie models (later provided as Bousquet et $al.$ 2012; Eveson et $al.$ 2012), and the lower base rate of approximately 0.36 was used in final runs for management advice, with average M across all ages of 0.4. The 2010 MFCL assessment (Langley et $al.$ 2010) applied 3 alternatives, with high (base M=0.8), low (0.36) and estimated (approximately 0.54) levels of natural mortality; the low M option was selected for management advice by the WPTT. Shono et $al.$ (2010) similarly assumed the lower base natural mortality of about 0.36. The 2015 Stock Synthesis assessment (Langley 2015) used the base M estimated in 2012 of about 0.54 from age 1.5 (with higher M for younger ages, and a period of higher M for mature females), with a sensitivity analysis at the lower level of about 0.36. The 2018 assessment (Fu et $al.$ 2018) retained these options as base case and sensitivity, and introduced an ogive based on the shape of the Lorenzen (1996) model as a sensitivity analysis.

M for mature females

Many natural mortality ogives used in stock assessments for yellowfin, bigeye and albacore tuna assume higher natural mortality for mature females. This assumption is driven by the observation that the sex ratio is close to 1:1 until at least the size when females become sexually mature but becomes increasingly male-dominated at larger sizes (Everett & Punsly 1990; Itano 2000). This trend in sex ratio at length may be caused by natural mortality of females increasing after maturity. It should be noted that the change in sex ratio occurs above the size of sexual maturity, and this was estimated by assuming that M for females increased 1.5 years after maturation for EPO yellowfin (Harley & Maunder 2003), and with a similar lag in the WCPO (Hoyle et $al.$ 2009).

However, alternative explanations may contribute to observed changes in sex ratio at length: female growth rates may become slower than males after maturity, and/or mature females may become less catchable than males due to changes in their behaviour or spatial distribution. In the Atlantic, females have been shown to grow to smaller sizes than males (Pacicco et $al.$ 2021), to a greater extent than the small differences observed in the EPO (Wild 1986), but differences between sexes have not been found in the WCPO (Farley et $al.$ 2020). Large sex differences in growth were observed in the Indian Ocean, though based on limited data (Shih et $al.$ 2014). Reduced vulnerability of large females due to behaviour change appear unlikely because sex ratios change with age in both longline and purse seine fisheries (Everett & Punsly 1990; Maunder & Aires-da-Silva 2012). In the WCPO there is considerable spatial variation in the size at which sex ratio at length changes (Hoyle et $al.$ 2009), and also spatial variation in the EPO (Everett & Punsly 1990), so there is some evidence that spatial distribution may affect availability by sex. There are also large spatial differences in size at maturity and growth curves between the EPO and WCPO, and within the WPCO. These complicate our attempts to understand the issue, as do the limited spatial and temporal coverage of ageing, sex ratio and maturity data. Understanding these spatial patterns and their causes will require more widespread sampling.

The assumption of higher natural mortality for mature females was supported by yellowfin tuna ageing observations that showed only small differences in growth rate by sex, and large declines in the sex ratio at age (Wild 1986; Schaefer 1998). Farley *et al.* (2020) similarly observed low proportions of females older than 5 years in the WCPO. However, females appear to live longer than expected given their assumed natural mortality. In the Atlantic the oldest male and female were 18 and 17 years respectively (Pacicco *et al.* 2021), in the WCPO 15 and 13 years (Farley *et al.* 2020), while in the Indian Ocean the differences (based on limited sampling) were larger at 9.5 and 6.5 years (the sex of the oldest fish at 10.5 was unknown) (Shih *et al.* 2014). These Indian Ocean estimates have now been updated to 10.9 and 10.0 for males and females (Farley *et al.* 2021). There is not uniform consensus about the reliability of these maximum ages, which although consistent with the results of bomb radiocarbon analyses (Andrews *et al.* 2020), and consistent with the weights of the otoliths (Farley *et al.* 2021), have not yet been validated with oxytetracycline marking (Farley *et al.* 2019; IATTC 2019).

Maunder & Watters (2001) estimated female and total natural mortality as follows: they assumed the same growth rate for both sexes and estimated the increase in female natural mortality at age that would account for the observed differences in sex ratio at length, given constant natural mortality at age for males. Similar approaches were followed in the EPO for bigeye tuna (Watters & Maunder 2001; Harley & Maunder 2003), and in the WCPO for yellowfin (Hoyle *et al.* 2009), bigeye (Hoyle & Nicol 2008) and albacore tunas (Hoyle 2008). For details of the calculations see Maunder & Aires-da-Silva (2012) and Hoyle *et al.* (2009).

These models did not account for potential/likely growth differences between males and females. Allowing for growth differences by sex in the models would reduce the estimates of female natural mortality, because growth differences would account for some of the change in sex ratio at length. Such growth differences are now becoming apparent for many *Thunnus* species and stocks (e.g., Farley *et al.* 2006; Shimose *et al.* 2009; Chen *et al.* 2012; Williams *et al.* 2012; Farley *et al.* 2014; Pacicco *et al.* 2021), with development of ageing methods that count annual increments in otoliths.

Approaches for estimating *M*

In June 2021, an online meeting on the estimation of natural mortality (http://capamresearch.org/Natural-Mortality-Workshop) was hosted by the Center for the Advancement of Population Assessment Methodology (CAPAM). The primary goal of the workshop was to provide advice and guidance on practices for modeling natural mortality in fishery assessments. The focus was on model specification, parameter estimation, and management consequences.

In this working paper we use the presentations and conclusions of the workshop to develop some advice on approaches for implementing natural mortality in stock assessments for Indian Ocean tropical tunas.

Punt *et al.* (2021) (see also https://www.youtube.com/watch?v=Br_IbN1Krqo) found in a series of simulations that estimating *M* performed better than pre-specifying *M*. They recommended estimating *M* in the model, with a prior distribution that reflects information on *M* from sources not included in the model likelihood. This combined approach uses all available information about *M*, and also allows uncertainty in *M* to be propagated into model advice. Punt *et al.* (2021) also recommended using diagnostics to check for model misspecification and contradictory data (residual analysis, retrospective analysis, ASPM method, R0 profiles). They recommended examining the final estimates of *M* output from the model to see if they are plausible, acknowledging that this final step is inherently subjective. It may nevertheless be argued that a final estimate that is very far from the

prior indicates inconsistency between the prior and the information in the model. If they are inconsistent then both cannot be true at the same time, so it is reasonable to reject the estimate that includes both. Punt *et al*. (2021) also noted that estimating steepness may help to alleviate problems with mis-specifying M, since the two parameters appear to be correlated.

We should note that Punt *et al.* (2021) used simulations to show that M was estimable, but conducted these simulations using informative simulated data, including age compositions, that were quite dissimilar to those available for tuna. Indian Ocean tuna data are likely to be considerably less informative and more conflicted, with lower likelihood of successfully estimating M inside the model. Punt *et al.* (2021) recommend using simulation to explore the potential to estimate natural mortality in the context of each stock assessment.

Various approaches are available for developing priors, including those based on life history theory, derived from empirical analyses, estimated from tagging data, and estimated from catch at age data. There was general agreement at the CAPAM workshop that of the empirical analysis methods, empirical meta-analyses of maximum age (A_{max}) had the lowest residual variance and were considered to have the best predictive power.

Hamel and Cope (in press) presented a method that used a large database of fish species (Then *et al.* 2015) and argued that their approach improved on the Then *et al.* (2015) analysis by fitting the regression of observed M versus maximum age on the log scale. Hamel and Cope (in press) justified this theoretically, based on the fact that mortality is a multiplicative process (Hamel 2014), so the log scale is appropriate.

The resulting model was $\log_e(M) \sim N(\log(5.4/A_{max}), 0.438^2)$, so $M = 5.4/A_{max}$. A simple explanation of this is that in an unfished population with natural mortality M, the proportion of fish remaining at age t is $\frac{N_t}{N_0} = e^{-tM}$. This transforms to $-\log\left(\frac{N_t}{N_0}\right)/t = M$, or $-\log\left(\frac{N_t}{N_0}\right)/M = t$. As t increases, there are fewer and fewer fish. For example, if M was constant then the age at which the numbers was 1% of N_0 would be $-\log(0.01)/M$, or $4.605/M$ and, similarly for 0.1% of N_0 is, $-\log(0.001) = 6.91$. The relationship $M=5.4/A_{max}$ implies that the expected proportion remaining in the oldest observed age class is 0.45%. In practice, the oldest observed age class will depend upon the proportions of fish remaining alive, the age selectivity of the fisheries, the age selectivity of the process used to select fish for ageing, and the number of fish aged.

Hamel and Cope (in press) argued that standard deviation of 0.438 included two components: individual stock variance around the relationship between maximum age and M, and observation error in both the maximum age and M estimates. They estimated the first component as 0.31 and proposed that this should be used as the standard deviation of the prior. Maunder et al (personal communication) argued that we cannot separate these components so should use a standard deviation of 0.438 for the prior distribution.

A new approach for modelling natural mortality has been implemented in Stock Synthesis 3.30.17 (Methot *et al.* 2021), based on proposals by Maunder et al (personal communication), a development of Maunder *et al.* (2010) and Maunder (2011). It is described by Rick Methot in the CAPAM workshop (https://www.youtube.com/watch?v=pY77VQ9i5QM), and in the updated SS user manual. It was also applied in the 2021 South Pacific albacore stock assessment (Castillo-Jordan *et al.* 2021).

The new model starts with high natural mortality for younger fish which declines with age, since mortality is assumed to be caused mainly by processes that are functions of size (e.g.,

predation). Mortality increases after individuals become reproductively mature, and this increase is linked to the proportion mature which follows a logistic curve. Senescence is assumed to be either small or to occur at an age when too few fish alive to affect dynamics. The new model is specified as follows:

$$M_{s,a} = M_{juv}\left(\frac{L_{s,a}}{L_{mat*}}\right)^{\lambda} + \frac{M_{mat,s} - M_{juv}\left(\frac{L_{s,a}}{L_{mat*}}\right)^{\lambda}}{1 + exp[\beta_s(L_{s,a} - L_{50,s})]}$$ (1)

The maturity parameters β_s and $L50_s$ can be obtained from the logistic maturity curve.

The following values are proposed by Methot $et\ al.$ (2021) as defaults: The rate of decline in natural mortality with size λ =-1.5 (Gulland 1987). Natural mortality for mature adults is based on the analysis by Hamel and Cope (in press): $M_{mat,s}$ = 5.4/$t_{max.s}$ if t_{max} is available, otherwise $M_{mat,s}$ = 4.118 $K_s^{0.73}$ $Linf_s^{-0.33}$ (Then $et\ al.$ 2015). M_{juv} = 3$W_{mat}^{-0.288}$ (Lorenzen 1996). The parameters L_{mat*} and W_{mat*} are the length and weight of a fish when they first become mature for either sex, and could be set to the minimum length at which 5% of fish (both sexes) are mature, but this is flexible.

Yellowfin tuna are large fish and the expected value of natural mortality implied by the Lorenzen (1996) equation $M=3W_{mat}^{-0.288}$ for fish of such a size at maturity is lower than the estimates derived from current observations of A_{max}. This results in higher natural mortality for mature than for immature fish, which may or may not be realistic. It also results in natural mortality for juveniles that is unaffected by the observed value of A_{max}.

An alternative approach to estimating M preserves the shape of the Lorenzen curve across the life span, and adjusts the entire curve based on the observed value of A_{max}. The parameter a in the relationship M=$a.W^{-0.288}$ is adjusted so that the average natural mortality for mature fish is equal to the value implied by A_{max}.

Application to yellowfin tuna

Implementing these approaches for Indian Ocean yellowfin tuna requires estimates of maximum age. Ageing of yellowfin tuna has been relatively limited, and mostly restricted to daily age estimates of younger individuals. A maximum age of 10.5 years has been observed for Indian Ocean yellowfin tuna (Shih $et\ al.$ 2014), based on relatively limited ageing. This has now been updated to 10.9 years (Farley $et\ al.$ 2021). A maximum age of 18 years has been obtained in the Atlantic Ocean (Andrews $et\ al.$ 2020; Pacicco $et\ al.$ 2021), and 15 years in the WCPO (Farley $et\ al.$ 2020). We calculated natural mortality for mature fish based on two alternatives: the maximum age observed in the Indian Ocean (10.9 years), and the maximum age observed for yellowfin tuna in all oceans (18 years).

Natural mortality for mature fish was calculated as M_{mature}=5.4/A_{max}. Uncertainty in the prediction was assigned using a SD of 0.31 on the log scale (Hamel and Cope, in press).

Following the advice in the SS manual to calculate the juvenile component of natural mortality, the Lorenzen (1996) equation was used, assuming that $M_{juv} = aW^b$, with weight (W) measured in grams. Uncertainty was assigned as follows. Lorenzen gives median and 90% CI for parameter a (3.00, 2.70, 3.30), or 3 +- 0.3. Assuming a normal distribution gives SD of 0.182. Similarly, for parameter b (-0.288, -0.315, -0.261), assuming a normal distribution gives SD of 0.0164. Residual variance was not reported so we assumed the same residual SD as the mature component of M, or 0.31 on the log scale.

Equation 1 requires a maturity ogive using the logistic equation, but maturity in the yellowfin tuna SS assessment (Fu *et al.* 2018) is assigned as maturity at age (Table 1, maturity ogive 1). A maturity at length ogive (Table 1, maturity ogive 2) was calculated for this purpose using the equation $mat_{length} = 1/\exp{(\beta(L_a - L_{50}))}$ that gave similar maturity at age to ogive 1 (Figure 1). Parameters were β = -0.1, and L_{50}=74.721 (length at age 9 quarters). Sex differences are known to occur in both maturity-at-length and length-at-age but were not considered in this case.

To develop 80% confidence intervals, 100,000 values were sampled at random from the uncertainty distributions of parameters *a*, *b*, and M_{mature}. The rate of decline in natural mortality with length, λ = -1.5 (Gulland 1987) was also sampled from a distribution with mean -1.5 and SD of 0.31. Each set of samples was used to calculate a natural mortality ogive using equation 1. The 80% prediction interval was calculated by taking the 10th and 90th percentiles of the distribution for each age class.

Estimates of natural mortality are provided in Table 1 for both values of maximum age (10.9 and 18 years). For each value of A_{max}, natural mortality estimates for maturity ogives 1 and 2 were almost identical. The base estimates and 80% confidence intervals for the natural mortality curves are provided in Table 3 and Figure 2.

An alternative approach was applied based on scaling the entire natural mortality ogive according to the Lorenzen equation $M=aW^b$, with b set to -0.288. Weights at age *W* were calculated based on the Richards growth curve provided by Farley *et al.* (2021) and the length-weight relationship from Fu *et al.* (2021). The scaling parameter *a* was adjusted so that the mean natural mortality for mature fish was equal to M^{Amax}, the value of M implied by Amax, as follows.

$$M_a^{Lor} = 3. W_a^{-0.288}$$

$$meanM^{Lor} = \sum_a (M_a^{Lor}.mat_a) \Big/ \sum_a mat_a$$

$$M_a^{A_{max}} = M_a^{Lor}. \left(\frac{M^{Amax}}{meanM^{Lor}} \right)$$

Maximum ages for males and females in the Atlantic are similar (18 and 17 respectively), suggesting mature male and female natural mortality of 0.3 and 0.32 year^{-1} respectively. The WCPO A_{max} observations of 15 for males and 13 for females suggest 0.36 and 0.42 year^{-1}.

Discussion and recommendations

This paper has developed a proposal for several alternative natural mortality ogives to consider as prior distributions and fixed values in the yellowfin tuna stock assessment. The proposal is mostly based on an empirical meta-analysis of the relationship between the maximum observed age and natural mortality estimates from a database of over 200 stocks. The proposed mean level of natural mortality is lower than that of the base ogive used in the 2018 assessment (Fu *et al.* 2018), and even somewhat lower than the lower natural mortality ogive used as a sensitivity analysis in that assessment.

That lower natural mortality ogive, based primarily on preliminary results from Brownie models of tag attrition, was considered by assessment scientists to be inconsistent with other data in the model. They preferred instead to use the level of natural mortality estimated in a previous assessment (Langley 2015).

However, given the additional support provided by the present analysis for lower levels of natural mortality, it is recommended that assessment scientists reconsider this lower rate of natural mortality. There may be alternative explanations for the inconsistency of low M with other model assumptions. Changing other aspects of the model structure may allow the model to include both the lower M and the existing data. There are many uncertainties in the SS model of Indian Ocean yellowfin tuna, given the large spatial domain, the difficulty of estimating movement rates between regions, uncertainty about the stock structure, the strong assumptions required when fitting to tagging data, the possibility that growth varies between locations, years and sexes, and uncertainties about reliability of catch, size and CPUE data.

It should be noted that the relationship $M=5.4/A_{max}$ was determined by fitting to data from populations that were mostly unfished or lightly fished, with heavily exploited populations excluded (Then *et al.* 2015). The Indian Ocean yellowfin tuna population was assessed in 2018 as overfished and experiencing overfishing, which would considerably reduce the expected value of A_{max}. The WCPO and AO populations have also been fished more heavily than the stocks in the Then *et al.* (2015) database. This suggests that applying the $M=5.4/A_{max}$ method to Indian Ocean yellowfin tuna would tend to upwardly bias the estimate of M.

Estimates are provided for both the Hamel and Cope (submitted) method and the Then et al (2015) method. Although the Hamel and Cope method claims to have identified a statistical error in the approach used by Then et al (2015), peer review of this claim is not yet complete (to my knowledge) and the paper is currently unpublished.

The models used to estimate higher natural mortality for mature females based on sex ratio at length should be updated to account for the reduced female growth rate after sexual maturity, for stocks where the difference is supported by data. This would estimate female natural mortality to be more like male natural mortality than currently assumed. Offsets for female natural mortality in the IO ogives could not be developed in the available time, but this should be done in future. Data on sex ratio at length is needed to support this analysis. In the interim it may be reasonable to assume the same ogive for both sexes.

The natural mortality ogives developed here should be applied in the yellowfin stock assessment, both as fixed values, and as priors with M estimated in the model. As recommended by Punt et al (2021), a range of diagnostics should be used to check models in which M is estimated, and the balance of evidence carefully considered.

The natural mortality proposed for immature fish of 1.5-2.5 years is lower than the proposal for adult fish and does not vary for different values of A_{max}. The method applied for this stage may need more work, (for example) given the uncertainty about the sizes at which the Lorenzen (1996) M prediction should be applied. Natural mortality for the youngest fish can often simply scale recruitment and have little or no effect on assessment outcomes, but fish aged 1.5-2.5 are caught in large numbers and their natural mortality rate can be influential.

A simulation study is recommended to test the feasibility of reliably estimating M in the Indian Ocean YFT assessment, and to explore what kinds of datasets and model configurations might work best. A suitable simulation model has been developed (Dunn *et al.* 2020) and could be adapted for this purpose. This simulation approach could be used to explore the potential to obtain further value from the RTTP tagging dataset, such as by completing the Brownie-Petersen analyses (Bousquet *et al.* 2012; Eveson *et al.* 2012).

Reliable estimates of *Amax* are important for developing natural mortality prior distributions. Natural mortality is such an important parameter for determining stock status that it warrants giving a high priority to age sampling across the population. Better data could also give us insights into issues such as spatial patterns in growth, sex ratio, and maturity, and their causes.

This new approach for developing priors for natural mortality is applicable to all Indian Ocean tuna and billfish species for which reliable ageing is available, either in the Indian Ocean or other populations. Further work is recommended to develop suitable priors for all species assessed by IOTC, and to aim to age at least 200 length-stratified and spatially distributed samples of all such species for which ageing is reliable. Ageing samples should come primarily from fisheries that catch the largest fish, which are usually the longline fisheries. The recommended number of samples comes from the Hoenig's (1983) advice that maximum age tends to increase slowly above a sample size of about 200. Nevertheless, fish sampling and ageing require efficient resourcing, and multiple objectives must be considered when developing such programmes.

Finally, in the medium to long term the development of close-kin mark-recapture for yellowfin tuna is recommended (Bravington *et al.* 2016; Kolody & Bravington 2019). This technique offers the prospect of estimating natural mortality more effectively than other methods. Telomere shortening rate can be a general predictor of species life span (Whittemore *et al.* 2019) and could be used to provide information about senescence, which is potentially related to natural mortality rates.

Acknowledgments

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Tables

Table 1a:Table of two alternative natural mortality ogives, based on the new natural mortality function in Stock Synthesis. The two alternatives assume A_{max} is either 10.9 or 18 years. Two versions of each alternative are provided, using either the age-based maturity implemented in the 2018 assessment, or a similar maturity curve fitted as a logistic function of length.

Age		Natural Mortality with A_{max} = 18		Natural Mortality with A_{max} = 10.9		Maturity ogive 1	Maturity ogive 2	*M* juvenile component
Qtr	Yr	Mat 1	Mat 2	Mat 1	Mat 2			
1	0.25	0.911	0.915	0.912	0.915	0	0.005	0.915
2	0.5	0.447	0.450	0.451	0.450	0	0.019	0.450
3	0.75	0.353	0.354	0.359	0.354	0	0.034	0.354
4	1	0.305	0.305	0.315	0.305	0	0.052	0.305
5	1.25	0.270	0.271	0.285	0.290	0.1	0.077	0.268
6	1.5	0.245	0.248	0.267	0.277	0.15	0.111	0.238
7	1.75	0.228	0.232	0.258	0.271	0.2	0.155	0.215
8	2	0.214	0.218	0.264	0.277	0.3	0.259	0.183
9	2.25	0.223	0.223	0.321	0.321	0.5	0.500	0.146
10	2.5	0.254	0.246	0.400	0.383	0.7	0.747	0.119
11	2.75	0.279	0.280	0.455	0.456	0.9	0.897	0.100
12	3	0.290	0.300	0.477	0.495	1	0.955	0.087
13	3.25	0.295	0.300	0.486	0.495	1	0.978	0.079
14	3.5	0.297	0.300	0.490	0.495	1	0.988	0.073
15	3.75	0.298	0.300	0.492	0.495	1	0.992	0.069
16	4	0.299	0.300	0.493	0.495	1	0.995	0.066
17	4.25	0.299	0.300	0.494	0.495	1	0.996	0.063
18	4.5	0.299	0.300	0.494	0.495	1	0.997	0.061
19	4.75	0.299	0.300	0.494	0.495	1	0.998	0.060
20	5	0.300	0.300	0.495	0.495	1	0.998	0.059
21	5.25	0.300	0.300	0.495	0.495	1	0.998	0.058
22	5.5	0.300	0.300	0.495	0.495	1	0.999	0.057
23	5.75	0.300	0.300	0.495	0.495	1	0.999	0.056
24	6	0.300	0.300	0.495	0.495	1	0.999	0.056
25	6.25	0.300	0.300	0.495	0.495	1	0.999	0.055
26	6.5	0.300	0.300	0.495	0.495	1	0.999	0.055
27	6.75	0.300	0.300	0.495	0.495	1	0.999	0.055
28	7	0.300	0.300	0.495	0.495	1	0.999	0.055

Table 2

Age		Natural Mortality with $M=5.4/Amax$		Natural Mortality with *Then et al 2015*	
Qtr	Yr	Amax=10.9	Amax=18	Amax=10.9	Amax=18
1	0.25	1.738	1.053	1.928	1.217
2	0.5	1.353	0.820	1.501	0.948
3	0.75	1.119	0.677	1.240	0.783
4	1	0.963	0.583	1.068	0.674
5	1.25	0.853	0.516	0.946	0.597
6	1.5	0.772	0.468	0.856	0.541
7	1.75	0.711	0.430	0.788	0.498
8	2	0.663	0.401	0.735	0.464
9	2.25	0.625	0.378	0.693	0.438
10	2.5	0.594	0.360	0.659	0.416
11	2.75	0.569	0.345	0.631	0.398
12	3	0.548	0.332	0.608	0.384
13	3.25	0.531	0.321	0.588	0.372
14	3.5	0.516	0.312	0.572	0.361
15	3.75	0.504	0.305	0.558	0.353
16	4	0.493	0.298	0.547	0.345
17	4.25	0.484	0.293	0.536	0.339
18	4.5	0.476	0.288	0.528	0.333
19	4.75	0.469	0.284	0.520	0.329
20	5	0.463	0.281	0.514	0.324
21	5.25	0.458	0.277	0.508	0.321
22	5.5	0.454	0.275	0.503	0.318
23	5.75	0.450	0.272	0.499	0.315
24	6	0.446	0.270	0.495	0.313
25	6.25	0.443	0.269	0.492	0.311
26	6.5	0.441	0.267	0.489	0.309
27	6.75	0.439	0.266	0.486	0.307
28	7	0.437	0.264	0.484	0.306

Table 3: Table of two alternative natural mortality ogives, based on the new natural mortality function in Stock Synthesis, with 80% confidence intervals for each curve.

| Age	Natural Mortality with A_{max} = 10.9			Natural Mortality with A_{max} = 18		
	Estimate	10%	90%	Estimate	10%	80%
0.25	0.915	0.558	1.496	0.915	0.558	1.496
0.5	0.450	0.290	0.695	0.450	0.290	0.695
0.75	0.354	0.229	0.545	0.354	0.229	0.545
1	0.305	0.197	0.471	0.305	0.197	0.471
1.25	0.290	0.204	0.428	0.271	0.185	0.406
1.5	0.277	0.201	0.400	0.248	0.174	0.366
1.75	0.271	0.201	0.385	0.232	0.167	0.338
2	0.277	0.209	0.387	0.218	0.162	0.311
2.25	0.321	0.236	0.455	0.223	0.167	0.314
2.5	0.383	0.270	0.556	0.246	0.177	0.353
2.75	0.456	0.311	0.674	0.280	0.192	0.412
3	0.495	0.333	0.736	0.300	0.202	0.446
3.25	0.495	0.333	0.736	0.300	0.202	0.446
3.5	0.495	0.333	0.736	0.300	0.202	0.446
3.75	0.495	0.333	0.736	0.300	0.202	0.446
4	0.495	0.333	0.736	0.300	0.202	0.446
4.25	0.495	0.333	0.736	0.300	0.202	0.446
4.5	0.495	0.333	0.736	0.300	0.202	0.446
4.75	0.495	0.333	0.736	0.300	0.202	0.446
5	0.495	0.333	0.736	0.300	0.202	0.446
5.25	0.495	0.333	0.736	0.300	0.202	0.446
5.5	0.495	0.333	0.736	0.300	0.202	0.446
5.75	0.495	0.333	0.736	0.300	0.202	0.446
6	0.495	0.333	0.736	0.300	0.202	0.446
6.25	0.495	0.333	0.736	0.300	0.202	0.446
6.5	0.495	0.333	0.736	0.300	0.202	0.446
6.75	0.495	0.333	0.736	0.300	0.202	0.446
7	0.495	0.333	0.736	0.300	0.202	0.446

Figures
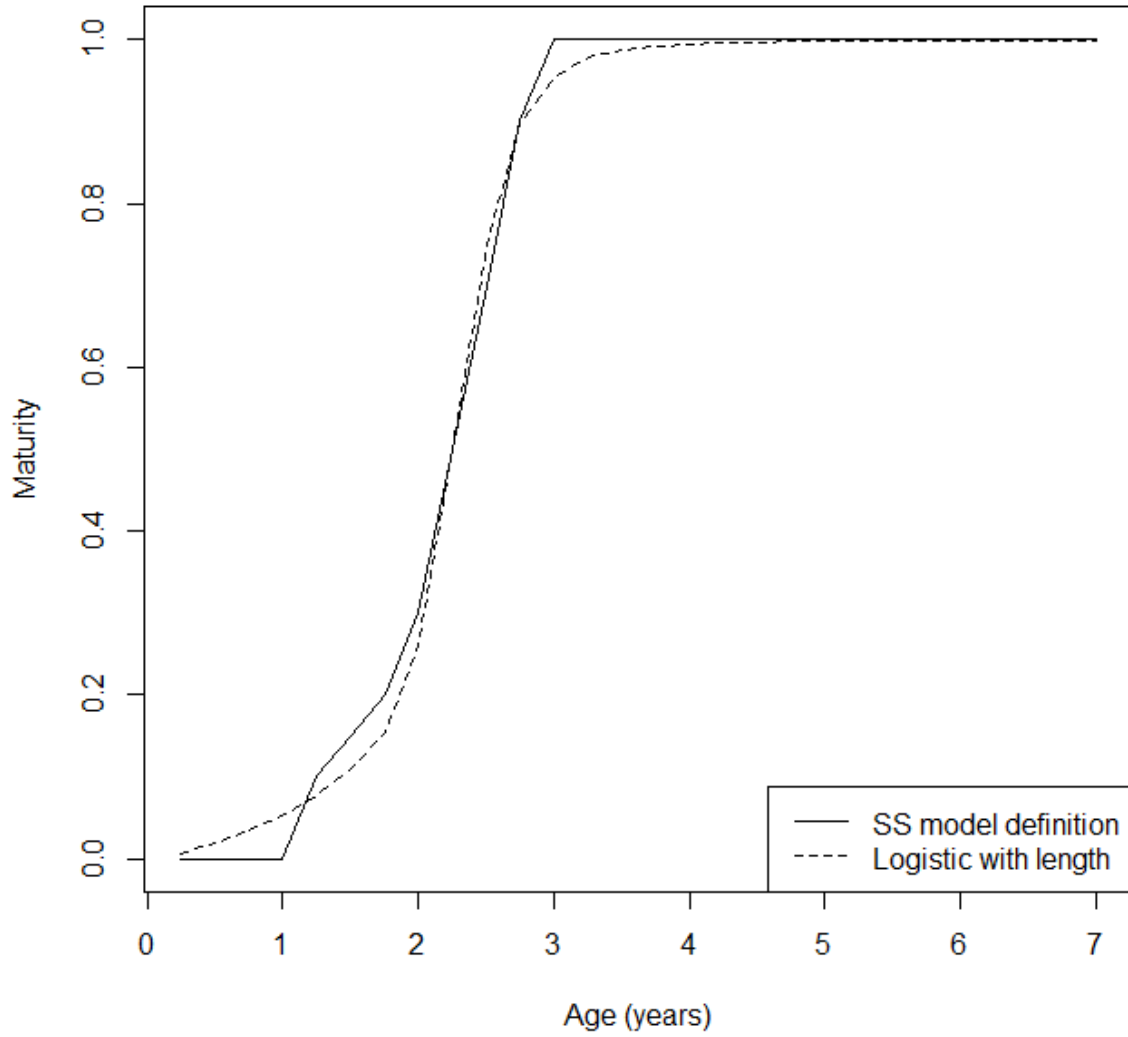
Figure 1: Maturity at age as implemented int eh 2018 yellowfin stock assessment, and a similar maturity ogive fitted as a logistic function of length.
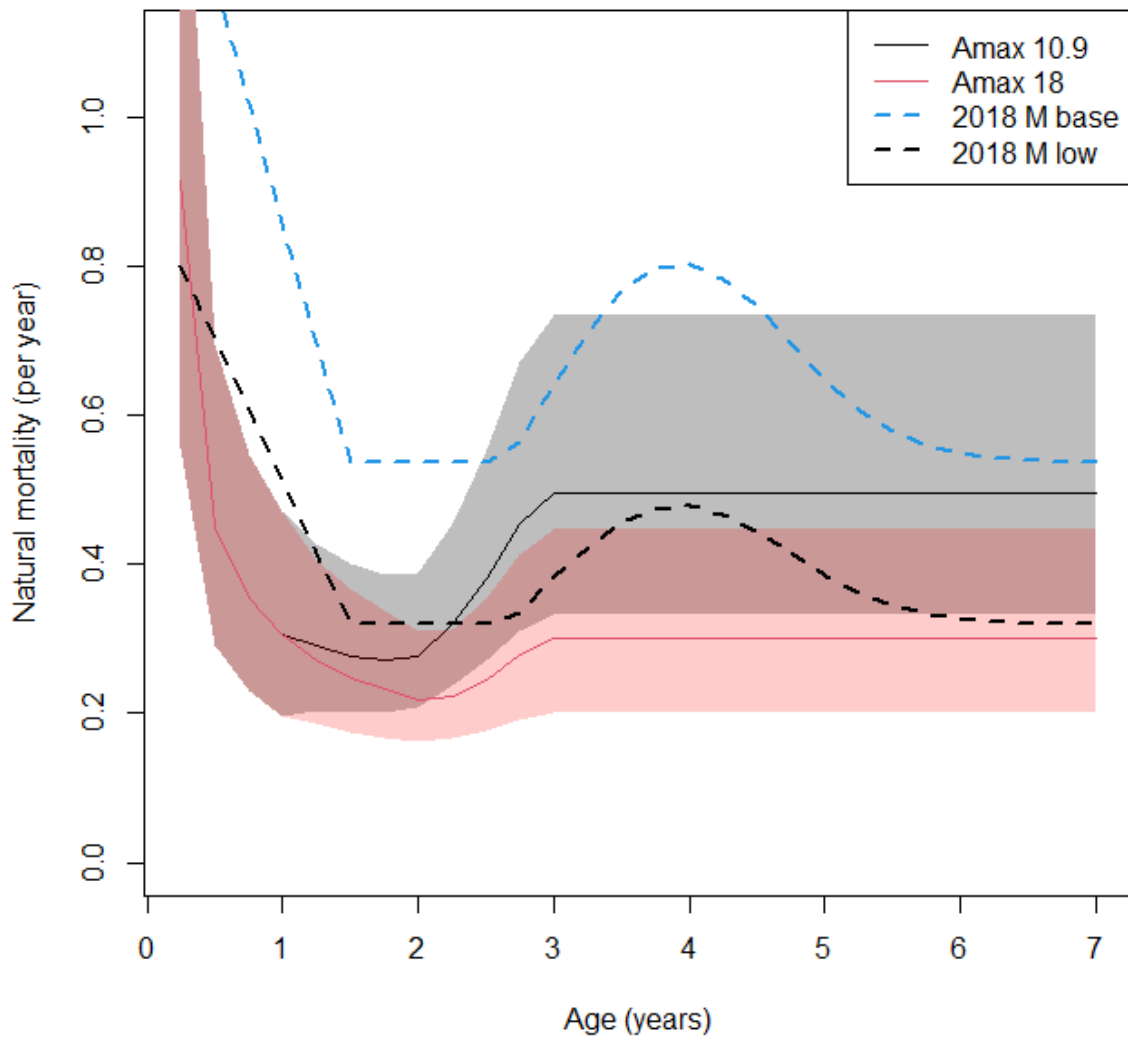
Figure 2: Two alternative ogives for yellowfin natural mortality at age, calculated from maximum observed age A$_{max}$, and the two ogives applied in the 2018 IO yellowfin assessment. The ogives using A$_{max}$ are based on a new natural mortality function in Stock Synthesis, and assume A$_{max}$ is either 10.9 or 18 years. The shaded areas represent the 80% confidence interval for each natural mortality curve.
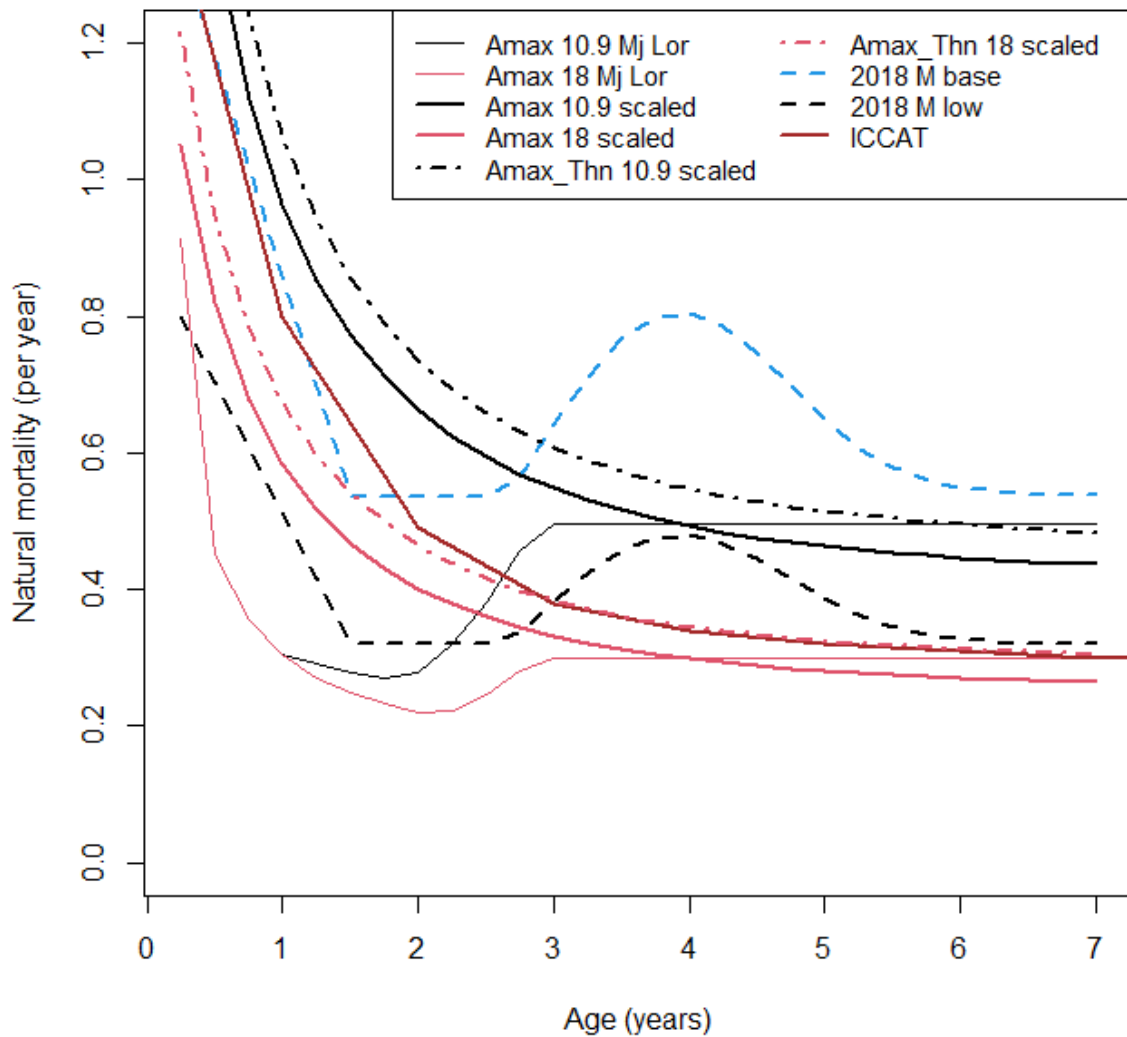
Figure 3: Six alternative ogives for yellowfin natural mortality at age, calculated from maximum observed age A_{max}, and the two ogives applied in the 2018 IO yellowfin assessment. The ogives assume that A_{max} is either 10.9 or 18 years. The ogives labelled 'Mj Lor' are based on a new natural mortality function in Stock Synthesis and use the Lorenzen equation to define juvenile natural mortality. The ogives labelled 'scaled' use the Lorenzen equation $M=a.W^b$ to define the entire ogive, with b=-0.288 and a adjusted so that the mean M for mature fish is equal to the value implied by Amax, according to either $M=5.4/Amax$, or the Then et al (2015) equation $M=4.899.Amax^{-0.916}$.
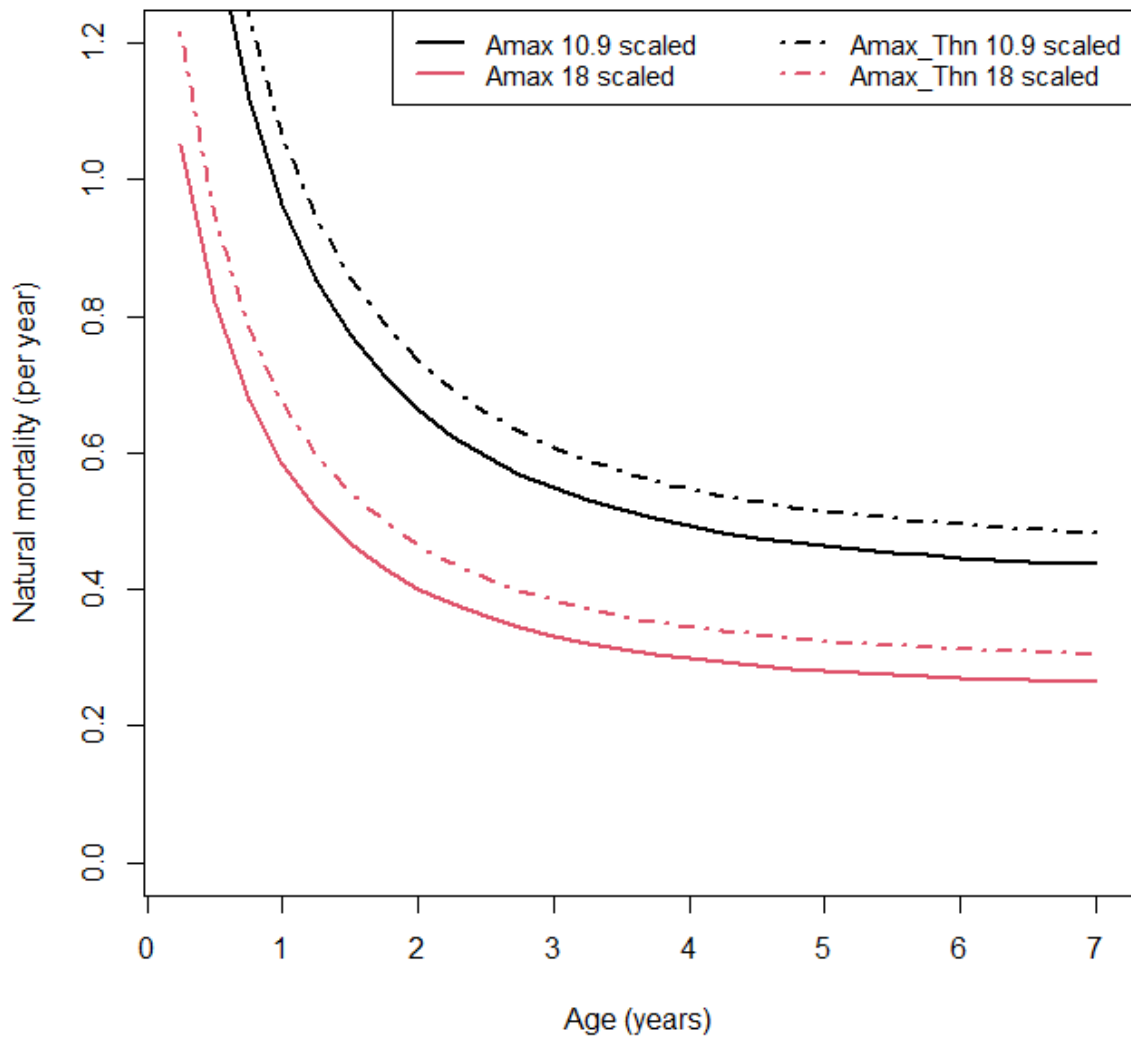
Figure 4: Four alternative ogives for yellowfin natural mortality at age, calculated from maximum observed age A$_{max}$. The ogives assume that A$_{max}$ is either 10.9 or 18 years. The ogives use the Lorenzen equation M=a.W^b to define the entire ogive, with b=-0.288 and a adjusted so that the mean M for mature fish is equal to the value implied by Amax, according to either M=5.4/Amax, or the Then et al (2015) equation M=4.899.Amax$^{-0.916}$.