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## *Approaches for estimating natural mortality in tuna stock assessments: application to global yellowfin tuna stocks*

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### Abstract

The values used for natural mortality ( $M$ ) are very influential in stock assessment models, affecting model outcomes and management advice. Natural mortality is one of the most difficult demographic parameters to estimate, and there is often limited information about the true levels. Here, we summarise the evidence used to estimate natural mortality at age for the four main stocks of yellowfin tuna (Indian, Western and Central Pacific, Eastern Pacific, and Atlantic Oceans), and identify important issues and information gaps. We describe the history of natural mortality values used in stock assessments by the tuna Regional Fisheries Management Organisations responsible for managing each stock and assess the evidence supporting these values. 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 modelling natural mortality in fishery assessments. Based on approaches presented and discussed at the meeting, we develop a range of yellowfin tuna natural mortality prior distributions for each stock. We also recommend future research to improve these estimates of natural mortality.

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## Introduction

The natural mortality of a species, 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 poorly informed. In addition to estimation uncertainty for natural mortality ( $M$ ), there is considerable process variability.  $M$  will be affected by the availability of food, predators, parasites and disease, as well as by environmental stressors.  $M$  can also vary between sexes, ages, locations, seasons, and years, and potentially trending through time (Gislason et al., 2010; Lorenzen, 1996).

Fisheries data are rarely directly informative about natural mortality, and even its average level can be difficult to estimate (Lee et al., 2011). 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 for  $M$ . It is typically not possible to obtain a 'correct' estimate of  $M$ , but the analyst must choose the most appropriate estimates and uncertainty distributions for their particular purpose.

Yellowfin tuna (*Thunnus albacares*) are broadly distributed across tropical and subtropical regions of all oceans. Global annual catches of yellowfin tuna have exceeded 1.4 million tons in recent years, making it the second most harvested tuna species globally (ISSF 2021). Yellowfin tuna support significant industrial-scale fisheries as well as important artisanal and subsistence fisheries of coastal states and small island developing states. Four stocks of yellowfin tuna are assessed and managed by four tuna Regional Fisheries Management Organisations (RFMOs): Indian Ocean Tuna Commission (IOTC), Western and Central Pacific Fisheries Commission (WCPFC), Inter-American Tropical Tuna Commission (IATTC) and the International Commission for the Conservation of Atlantic Tunas (ICCAT).

Here, we provide advice to analysts working in these RFMOs on approaches for estimating natural mortality to use in stock assessments for yellowfin tuna. We focus mainly on the base or average value of natural mortality for yellowfin tuna for the Indian Ocean, but the same approach can be used for other yellowfin tuna stocks. We also briefly consider age-dependence and variation between sexes. For an earlier discussion of natural mortality for yellowfin tuna, see Maunder and Aires-da-Silva (2012) and for broader discussion of natural mortality see Vetter (1988), Brodziak et al. (2011) and Maunder et al. (submitted).

### History of estimating $M$ for yellowfin tuna stock assessments

Past assessments for yellowfin tuna have assumed various levels of natural mortality (Table 1). An early and influential estimate of natural mortality (Hennemuth, 1961) 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 year<sup>-1</sup> was estimated from a catch curve on fish aged 2-4 years, and estimated fishing mortality ( $F$ ) of 0.95 year<sup>-1</sup> subtracted to give  $M$  of 0.77 year<sup>-1</sup>, usually rounded up to 0.8 year<sup>-1</sup>, or between 0.6 and 1.0 year<sup>-1</sup>. This was later revised by Schaefer (1967) to between 0.55 year<sup>-1</sup> and 1.05 year<sup>-1</sup>.

However, there is good reason to expect these  $M$  estimates of approximately 0.8 year<sup>-1</sup> to be biased high. Catch curve models assume constant selectivity with increasing age, so 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  $1.72 \text{ year}^{-1}$  for fish aged 2-4 years is likely to be positively biased, with the proviso that the  $F$  estimate of  $0.95 \text{ year}^{-1}$  also is likely to be unreliable given the methods available at the time.

This same estimate of  $M=0.8 \text{ year}^{-1}$  has been used in many stock assessments since 1961. Wild (1994) reviewed natural mortality estimates in the eastern Pacific Ocean (EPO) and noted that although Francis (1977) considered  $0.8 \text{ year}^{-1}$  to be too high based on a simulation study,  $0.8 \text{ year}^{-1}$  was used in stock assessments for the EPO 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  $0.8 \text{ year}^{-1}$  for males (Figure 1). The same value of natural mortality has consistently been applied for adult males since then in EPO yellowfin tuna assessments (e.g. Hoyle and Maunder, 2006; Maunder and Aires-da-Silva, 2010; Maunder and Harley, 2004; Minte-Vera et al., 2020), with some refinements to the approach that increased the natural mortality for mature females (Maunder and Watters, 2001).

Analyses of tagging data have been used to estimate natural mortality for yellowfin tuna in the Western and Central Pacific Ocean (WCPO) and Indian Ocean (IO). In the WCPO, an analysis of tagging data estimated natural mortality to be  $0.68$ ,  $0.44$ , and  $0.69 \text{ year}^{-1}$  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 absolute value of the estimates. It included various simplifying assumptions to make the analysis tractable, including constant fishing mortality through time, complete mixing of tagged and untagged fish after a pre-mixing period of 2 quarters, and uniform tag reporting rates across sizes and through time. However, the resulting size-dependent estimates may have been affected by breaches of each of these assumptions. Fishing mortality was relatively uniform across years but varied seasonally and spatially. The longline vessels that select larger fish tended to have very low reporting rates compared to the purse seine fisheries that select more small fish. This would tend to bias upward the natural mortality estimates of larger fish. Reporting rates are also likely to have varied substantially between fleets and through time (Peatman, 2020; Vincent et al., 2020b), which would also lead to spatial variability. Yellowfin tag mixing within the area of this analysis (but for a later tagging programme) was estimated to be incomplete even after 5 quarters (Kolody and Hoyle, 2013). These likely assumption breaches make the reliability of the  $M$  size variation estimates uncertain, in particular the increase for larger fish. Nevertheless, 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. The results from Hampton (2000) were also used to support the natural mortality changes by age assumed in the EPO stock assessments (Maunder and Aires-da-Silva, 2012). In the IO, 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  $0.5$ ,  $0.27$ ,  $0.22$ ,  $0.27$ , and  $0.28 \text{ year}^{-1}$ . 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 estimated unreasonably 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 and Goethel, 2017), and these issues were certainly present in the IO and WCPO tagging experiments.

Times at liberty of tagged tunas, in combination with approximate ages at release, can also provide information about mortality, and maximum time at liberty is in some ways analogous to maximum observed age. For recaptured yellowfin tuna, the longest periods at liberty are lower than the maximum observed ages from otoliths, at 6.5 years in the WCPO (Eveson et al., 2020), 5 years in the EPO (Schaefer and Fuller, 2022a), 9.1 years in the Atlantic (Fonteneau and Hallier, 2015), and 6.0 years in the Indian Ocean (Fonteneau and Hallier, 2015; Gaertner and Hallier, 2014) for fish mostly tagged at about age 1 year, although some tuna were tagged at older ages. The rankings by stock of maximum time at liberty match those of maximum observed age for the stocks aged using annuli (i.e. all except the EPO). Compared with maximum ages from otoliths, maximum times at liberty may be more directly related to total mortality than to natural mortality, as they are obtained without the size stratification usually applied when sampling otoliths. However, sample sizes of tagged fish are very small and estimates of fishing mortality would be needed to estimate natural mortality. Times at liberty are also reduced by tag loss, the effects of tags on fish survival, and low tag reporting rates in the longline fisheries that take the largest and oldest fish. An analysis of the whole tagging data set is an appropriate way to infer natural mortality (e.g. Maunder et al., 2010). Analysts should be cautious about applying equations based on meta-analyses of ageing studies (e.g., Hamel and Cope in review; (Then et al., 2015) to time-at-liberty data, because  $M$  is likely to have a different relationship with maximum time at liberty than it does with maximum observed age.

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  $0.8 \text{ year}^{-1}$  for males 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). 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. Davies et al., 2014; Hampton et al., 2005; Langley et al., 2011; 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 also explored alternatives based on a meta-analysis of life-history and empirical relationships (Vincent et al., 2020a), with lower annual rates of  $0.44\text{-}0.6 \text{ year}^{-1}$  (Figure 1).

In the Atlantic Ocean (ATL), natural mortality was also assumed to vary by age in the 2008 assessment (ICCAT, 2009), with the Hennemuth (1961) estimate of  $0.8 \text{ year}^{-1}$  for ages 0 and 1, and  $0.6 \text{ year}^{-1}$  for ages 2+ , without distinction by sex (Figure 1). In the 2016 assessment (ICCAT, 2016; Walter and Sharma, 2017), however,  $M$  was assigned an average across ages 1 to 11 of  $0.545 \text{ year}^{-1}$ , based on the Then et al. (2015) estimator and maximum observed age of 11 years. The maximum age was determined from a tagged fish at liberty for 9 years originally tagged at a size corresponding to an age around 2. The  $M$ -at-age was adjusted according to Lorenzen (1996), based on the Gascuel et al. (1992) growth curve for ages 0-11+. For the 2019 assessment (Walter et al., 2020) maximum age was updated to 18 years (Pacicco et al 2021), which implied lower  $M$  of  $0.35 \text{ year}^{-1}$ . The same functional form of the Lorenzen curve was used, but the estimate of  $0.35 \text{ year}^{-1}$  was applied to age 5, resulting in an average of  $0.39 \text{ year}^{-1}$  across ages 1-11.

In the IO, a range of values has been used. In 2005 an *ad hoc* working group recommended  $M=2 \text{ year}^{-1}$  at length 35 cm, declining linearly to  $0.6 \text{ year}^{-1}$  at 70cm and remaining constant thereafter (IOTC, 2005, Appendix IV). In 2007, age-structure production model (ASPM) and Stock Synthesis

(SS2) assessments (Nishida and Shono, 2007; Shono et al., 2007) assumed  $M=0.8 \text{ year}^{-1}$  at age 0, declining to  $0.6 \text{ year}^{-1}$  for ages  $>1$  year, as did the 2008 SS2 assessment (Shono et al., 2008) (Figure 1). 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  $0.8 \text{ year}^{-1}$  and with increased  $M$  for a period representing higher natural mortality for mature females (for the combined-sex model). However, the IOTC Working party on Tropical Tunas (WPTT) in 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  $0.36 \text{ year}^{-1}$  was used in final runs for management advice, with average  $M$  across all ages of  $0.4 \text{ year}^{-1}$ . The 2010 MULTIFAN-CL (MFCL) assessment (Langley et al., 2010) applied three alternatives for  $M$ , with high (base  $M=0.8 \text{ year}^{-1}$ ), 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  $0.36 \text{ year}^{-1}$ . The 2015 SS3 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 SS3 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 (Figure 1).

### $M$ for mature females

Many natural mortality ogives used in stock assessments for yellowfin, bigeye and albacore tuna assume higher natural mortality for mature females relative to males. For yellowfin tuna, 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 and Punsly, 1990; Itano, 2000; Schaefer, 1998). This trend in sex ratio at length was assumed to be caused by natural mortality of females increasing after maturity.

Maunder and Watters (2001) estimated female and total natural mortality for yellowfin tuna by assuming 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 (Harley and Maunder, 2003; Watters and Maunder, 2001), and in the WCPO for yellowfin (Hoyle et al., 2009), bigeye (Hoyle and Nicol, 2008) and albacore tunas (Hoyle, 2008). For details of the calculations see Maunder and Aires-da-Silva (2012) and Hoyle et al. (2009).

Until relatively recently, 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 (Schaefer, 1998; Wild, 1986). This work was based on immature and mature fish less than 4 years old, aged using daily increments. 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 ATL (Gulf of Mexico), the oldest male and female were 18 and 17 years respectively (Pacocco et al., 2021), in the WCPO 15 and 13 years (Farley et al., 2020), and in the Indian Ocean 10.9 and 9.7 years (Farley et al., 2021; Jessica Farley, personal communication). It should be noted that there remains some debate about the reliability of the estimates of maximum ages (see below).

However, alternative explanations appear to contribute to, and may be wholly responsible for, the observed changes in sex ratio at length. Female growth rates of most or all species in the genus

*Thunnus* become slower than males after maturity (e.g., Chen et al., 2012; Farley et al., 2006; Farley et al., 2014; Pacicco et al., 2021; Shimose et al., 2009; Williams et al., 2012), and mature females may also become less catchable than males due to changes in their behaviour or spatial distribution. In the ATL, female yellowfin tuna grow to smaller sizes than males (Pacicco et al., 2021), with the difference in length at age between sexes much larger than the small differences observed (albeit without data for older ages) in the EPO (Wild, 1986). Statistically significant growth differences between sexes have not been found in the WCPO (Farley et al., 2020), but there were very few old females in the sample and the confidence limits on female  $L_{\infty}$  were large. Two studies in the IO found a) substantially smaller  $L_{\infty}$  for females based on limited data (Shih et al., 2014), and b) apparently smaller  $L_{\infty}$  for females, though also based on limited data, and not fitted with independent models by sex (Farley et al., 2021).

Reduced vulnerability of large females due to catchability change appears unlikely because sex ratios change with age in both longline (deep gear) and purse seine fisheries (surface gear) (Everett and Punsly, 1990; Maunder and Aires-da-Silva, 2012). However, 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 and 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, and evidence of different size at maturity among areas in the EPO (Schaefer and Fuller, 2022b) and WCPO (Hoyle et al., 2009). These complicate our attempts to understand what causes these patterns, 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.

### Senescence

Senescence is the deterioration of the functional characteristics of an organism with increasing age, which increases risk of disease and decreases ability to repair damage or to respond to stress, leading to higher rates of natural mortality. It is a ubiquitous phenomenon both in terrestrial and aquatic animals (Finch, 1994), but little studied in fish, and there have been no studies in tunas. It has been hypothesised that fish are more inclined to evolve delayed senescence because they have indeterminate growth and thus continuing capacity to replace old cells and increase fecundity with age (Reznick et al., 2002).

Senescence is usually ignored in fish stock assessments, with a few exceptions (Fonteneau and Pallares, 2005). For tunas, the increase of natural mortality after the onset of reproduction as described above would represent a form of senescence. Senescence has been assumed in the tuna simulation model SEAPODYM (Spatial Ecosystem and population Dynamics Model (Lehodey et al., 2008). SEAPODYM is a spatially explicit biophysical model that tracks all life stages. SEAPODYM assumes that natural mortality increases after the senescence threshold, assumed to occur at 7 years for bigeye tuna in the WCPO (Lehodey et al., 2010).

### 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 modelling natural mortality in fishery assessments. The focus was on model specification, parameter estimation, and management consequences. We use the presentations and conclusions of the workshop to develop advice on approaches for implementing natural mortality in stock assessments for yellowfin tuna.

Punt et al. (2021) 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  $M$ , adjusts appropriately for selectivity, 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, RO likelihood component profiles). They recommended examining the final estimates of  $M$  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 outside the range of uncertainty represented by the prior indicates inconsistency between the prior and the data included in the model as evaluated through the model assumptions. Both cannot be true at the same time and the model may be misspecified, so it is reasonable to reject the estimate that includes both.

We 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, and the estimator was structured to be identical to the operating model, except that  $M$  was specified to be independent of age and time. Yellowfin 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 therefore considered to have the best predictive power.

Hamel and Cope (in review) presented a method that used a large database of fish species compiled by 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 review) justified this based on better fit to the data, and 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 number of fish remaining was 1% of  $N_0$  would be  $-\log(0.01)/M$ , or  $4.605/M$  and, for 0.1% of  $N_0$ ,  $-\log(0.001)/M = 6.91/M$ . 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-specific nature of natural mortality, the fishing mortality at age (the age selectivity of the fisheries), the age selectivity of the process used to select fish for ageing, and the number of fish aged. It is also dependent on the age used to define  $N_0$ .

It should be noted that despite  $A_{max}$  being theoretically related to  $M$ , the empirical estimates of  $M$  based on maximum age are not a result of applying theory. They are simply estimates of  $M$  for stocks that are similar to those that are represented in the data set used to develop the relationship. This means that to be used for a specific stock, that stock needs to have similar life-history,

exploitation history, and age sampling history as those stocks used to develop the relationship. The stocks used to develop the relationship have a wide range of characteristics and these will be reflected in the estimated prediction error of the relationship. However, application to a stock that has characteristics substantially different from those used to generate the relationship may produce biased results.

The Then et al. (2015) database includes 3 tropical and one temperate tuna species, suggesting that the results of this meta-analysis might be extended to yellowfin tuna. However, closer examination of these studies demonstrates one of the risks with the meta-analysis approach. The  $M$  estimates for tropical tunas are based on the Hampton (2000) Western Pacific tagging study discussed above, including an  $M$  estimate for yellowfin tuna of  $1.085 \text{ year}^{-1}$ , and  $A_{max}$  of 7 years (Lehodey and Leroy, 1999). The tagging estimates of  $M$  are likely biased (see above) and subsequent ageing using annual increments has more than doubled this estimate of maximum age.

Hamel and Cope (in review) 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 assumed equal variance with a standard deviation of 0.31 for each variance component and proposed that this should be used as the standard deviation of the prior. Alternatively, it could be argued that we cannot separate the variance components and should use the total variance ( $sd = 0.438$ ) for the prior so that it does not influence the data more than it should.

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. (submitted), a development of Maunder et al. (2010) and Maunder (2011). It is described in the updated SS user manual (Methot Jr and Wetzal, 2012; Methot et al., 2021). 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). Natural mortality is assumed to increase equally for both sexes after individuals become reproductively mature, and this increase is linked to the proportion of mature females. This contrasts with the approach described earlier which increases only female natural mortality, and includes a lag between maturation and increased natural mortality. Senescence is assumed to be either small or to occur at an age when too few fish are alive to affect dynamics. The new model is specified as follows for length-based (equation 1) or age-based (equation 2) maturity:

$$M_a = M_{juv} \left( \frac{L_a}{L_{mat*}} \right)^\lambda + \frac{M_{mat} - M_{juv} \left( \frac{L_a}{L_{mat*}} \right)^\lambda}{1 + \exp[\beta(L_a - L_{50})]} \quad (1)$$

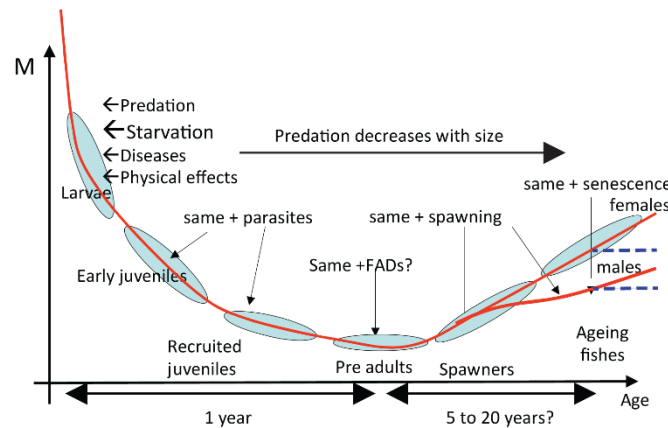
$$M_a = M_{juv} \left( \frac{L_a}{L_{mat*}} \right)^\lambda (1 - mat_a) + M_{mat} \cdot mat_a \quad (2)$$

The following values are proposed by Maunder et al. (submitted) as defaults: The rate of decline in natural mortality with size  $\lambda = -1.5$  (Gulland, 1987). Natural mortality for mature adults is based on the analysis by Hamel and Cope (in review):  $M_{mat} = 5.4/t_{max}$  if  $t_{max}$  is available, otherwise  $M_{mat} = 4.118 K^{0.73} Linf^{0.33}$  (Then et al., 2015).  $M_{juv} = 3W_{mat*}^{-0.288}$  (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.

The resulting pattern of  $M$  at age resembles the conceptual model of Fonteneau and Pallares (2005, Figure 3), but with constant  $M$  after reaching maturity.



*Conceptual model of the changes in natural mortality by age for tunas according to the main biological processes determining mortality (red line) modified from Figure 3 in Fontenau and Pallares (2005). The proposed model for yellowfin tuna is similar except that no senescence is included (blue dashed line).*

An alternative approach follows Walter and Sharma (2017) in applying the shape of the Lorenzen (1996) curve to all age classes without differentiating by maturity status, and adjusting the mean natural mortality of mature age classes to be equal to the level suggested by  $A_{max}$  (Hamel and Cope in review).

## Application to yellowfin tuna

Implementing these approaches for yellowfin tuna requires estimates of maximum age. Ageing of yellowfin tuna has been relatively limited. For the EPO the age estimates result from counts of daily rings in otoliths for individuals up to 4 years old and about 150 cm, which have twice been validated (Wild and Foreman, 1980; Wild et al., 1995). Counts of annual increments in yellowfin tuna otoliths have produced estimates of maximum age of 10.9 years in the IO (Farley et al., 2021), 18 years in the ATL (Andrews et al., 2020; Pacicco et al., 2021), and 15 years in the WCPO (Farley et al., 2020). Yellowfin tuna in the EPO have been aged up to about 5 years based on counts of daily increments in otoliths (Wild 1986), while the maximum age based on tagging data is about 8 years, given 5 years at liberty for a fish with length at release consistent with an age of about 3 years (Schaefer and Fuller, 2022a). Conventionally tagged fish were previously reported with longer times at liberty (Maunder and Aires-da-Silva, 2012), but these data are considered to be erroneous (Daniel Fuller IATTC personal communication).

Ogives were not calculated separately for males and females, but maximum observed ages are higher for males in all oceans, suggesting that male total mortality is slightly lower than females. Maximum ages for males and females in the ATL are 18 and 17 respectively, suggesting mature male and female natural mortality of 0.3 and 0.32 year<sup>-1</sup>. The WCPO  $A_{max}$  observations of 15 for males and

13 for females suggest  $M = 0.36$  and  $0.42 \text{ year}^{-1}$ . For the IO,  $A_{max}$  of 10.9 for males and 9.9 for females suggest  $M = 0.50$  for males and  $0.55 \text{ year}^{-1}$  for females.

Growth curves and maturity ogives were obtained for each stock, based on the following sources, representing either the values used in the latest stock assessments, or more recent updates if considered appropriate. ATL analyses used the Richards growth curve for both sexes combined (Pacocco et al., 2021) and length weight relationship  $W_L = 2.1527 \times 10^{-5} L^{2.976}$  (Caverivière, 1976). Diaha et al. (2016) found L50 to be 99.2 cm when females with ovaries at the cortical alveoli formation (CA) stage and onward were considered mature, and 124.6 cm FL when females with advanced vitellogenic oocytes (AV) were considered mature, and the latest assessment used the average, 115 cm (Walter et al., 2020). For consistency with other stocks we used the AV-stage estimate, refitting the original data (Diaha et al., 2016, Table 3) with a logistic regression in R to obtain the parameters  $\alpha = -10.67$ ,  $\beta = 0.0843$ , and  $L50 = 126.6$ . Parameters for CA-stage maturity were  $\alpha = -11.40$ ,  $\beta = 0.1127$ ,  $L50 = 101.2$ .

WCPO analyses used the WCPO-wide estimates of growth (nominally for both sexes but dominated by males) (Farley et al., 2020) and female maturity at length (Hoyle et al., 2009) with  $L50 = 106$  cm, and length-weight relationship  $W_L = 2.01 \times 10^{-5} L^{2.986}$  (Vincent et al., 2020a). IO analyses used the Richards growth curve for both sexes combined (Farley et al., 2021), maturity at length from Zudaire et al. (2013) with  $L50$  for AV-stage oocytes = 102.4 cm (CA-stage maturity gave  $L50$  of 76.58 cm), and length-weight relationship  $W_L = 2.459 \times 10^{-5} L^{2.9667}$  (Chassot et al., 2016). EPO analyses used the von Bertalanffy growth curve from Table 5 of Wild (1986), maturity at length from Schaefer (1998) with  $L50 = 91.8$  cm, and length-weight relationship  $W_L = 1.387 \times 10^{-5} L^{3.086}$  (Table 9, Wild, 1986). Plots of length at age (Figure 2), weight at age (Figure 3), and maturity at age (Figure 4) are provided for comparison across stocks. Patterns of length and weight at age are similar for IO, WCPO and ATL stocks, but the shape of the EPO yellowfin growth curve is very different: slower initially and then increasing, reaching a higher asymptotic length and weight. Patterns of maturity at age are generally similar across all stocks.

We calculated the natural mortality implied by the maximum age observed in each yellowfin tuna stock, as  $M_{mat} = 5.4/A_{max}$ . Uncertainty in the prediction was assigned using a SD of 0.438 on the log scale (Hamel and Cope, in review). The estimates of  $M$  used in developing the empirical relationship were derived from various age classes, but generally excluded the youngest age classes since they mostly (79%, Then et al., 2015) came from age-based catch-curve analyses of age classes fully recruited to the fishery. They were assumed to represent the natural mortality of mature fish,  $M_{mat}$ .

We set  $M_{juv}$  equal to the mortality predicted by the Lorenzen equation at weight  $W_{mat*}$ , the weight at which female maturity was 5%, calculated from the maturity ogives.  $M_A$  using the two-stage method was then estimated for each stock using equation (2).

For estimates using the scaled Lorenzen method, weights at age at quarterly intervals were predicted for each stock, and natural mortality predicted based on  $M_A^{Lor} = 3W_A^{-0.288}$ . Each ogive was adjusted so that mean mortality of mature fish was equal to  $5.4/A_{max}$ .  $M_A^{scaledLor} = M_A^{Lor} \frac{5.4}{A_{max}} \cdot \frac{\sum_A mat_A}{\sum_A (M_A^{Lor} \cdot mat_A)}$ .

Estimates of natural mortality according to each approach and for each stock are provided in Tables 2 and 3, and Figures 5 and 6.

Both approaches generate patterns of natural mortality at age that are very different from those used to date by most tuna RFMOs (Figure 1), apart from the ICCAT assessment which has used the

scaled Lorenzen approach. In most cases both priors indicate much lower levels of natural mortality at most ages.

## Discussion and recommendations

This paper develops a proposal for several alternative natural mortality ogives to consider as prior distributions and/or fixed values in yellowfin tuna stock assessments. The proposal combines alternative patterns for representing natural mortality at age with the results of an empirical meta-analysis of the relationship between the maximum observed age and natural mortality estimates from a database of over 200 stocks. Most of the proposed mean levels of natural mortality are lower than those in recent assessments of most stocks, and outside the range of the values considered in most assessments. These lower  $M$  estimates are a direct consequence of new aging methods based on counts of presumed annual increments in transversely sectioned otoliths (Farley et al., 2020; Farley et al., 2021; Pacicco et al., 2021; Williams et al., 2013), which have resulted in age estimates up to 18 years. Daily increment methods could not age fish older than 4 to 5 years, while the oldest yellowfin based on time at liberty in a mark-recapture experiment was 11 years (ICCAT, 2020).

However, these annual-increment methods are not universally accepted for yellowfin tuna, partly due to contrasting results with daily increments for the EPO, for which ageing of fish up to the age of 4 years has been validated (Wild and Foreman, 1980; Wild et al., 1995). Mark-recapture-based validation using otolith marking is available for only two individual fish that have been aged annually, of which just one was at liberty for more than a year (Farley et al., 2019). Edge-type analysis has been used to corroborate the periodicity of annual increment formation (Farley et al., 2019). Further support for annual ageing is provided by radiocarbon dating based on declines in  $^{14}\text{C}$ , which has been shown to be consistent with estimates of birth year from annual ageing in both absolute estimates and trends through time for 34 yellowfin and 12 bigeye tuna (Andrews et al., 2020), indicating that ages on average may be unbiased. Inter-reader error has also been shown to be low (<10%) with no evidence of bias between readers (Williams et al., 2013) indicating that age estimates from this approach are repeatable. Age estimates derived from annual increment counts are also consistent with otolith growth, with a very strong relationship ( $R^2 = 0.95$ ) between annual age and otolith weight (Farley et al., 2021). Estimates of age from annual increments are also consistent with the time at liberty and age at release for recaptured yellowfin (Farley et al., 2021). Validation of annual ageing for other *Thunnus* species has been carried out for WCPO bigeye (Farley et al., 2018), south Pacific albacore (Farley et al., 2011), southern bluefin tuna (Clear et al., 2000), and Atlantic bluefin tuna (Neilson and Campana, 2008), providing a foundation for the presence of annual increments in the otoliths of all species in this genus.

Nevertheless, comparisons of annual increment counts with daily counts using recent methods for individuals of 1-4 years of age showed substantial differences both between ageing methods and between daily agers (Williams et al., 2013, Farley et al., 2019; IATTC, 2019). Furthermore, counts by IATTC scientists of daily rings deposited post-release in otoliths of two bigeye and two yellowfin tuna tagged with  $\text{SrCl}_2$  in the WCPO, and one Atlantic yellowfin tuna tagged with OTC, substantially underestimated the numbers of days at liberty (Farley et al., 2019). The reasons for these conflicting results are unknown and may be linked to differences in aging techniques or species characteristics differing between oceans. The disagreements about ageing methods make the interpretation of maximum age from presumed annual aging of otoliths uncertain, particularly for the EPO. Therefore, these estimates may be considered preliminary and uncertain until further age validation work is conducted. The differences in natural mortality estimates (and associated growth estimates) have

huge impacts on the estimates of management quantities and improving and validating aging estimates should be a priority.

Although average natural mortality can be expected to differ between stocks, the large differences observed here are likely to be at least partly due to other effects, in addition to aging methods. For example, natural mortality in the EPO could be overestimated, because tagging-based maximum ages are expected to be lower than those based on otoliths due to low sample sizes, low tag return rates from the longline fisheries that catch the largest fish (although the purse-seine fishery on dolphins also catch large fish, see Minte-Vera et al. (2020)), tag loss, and the effects of tagging on survival. Estimates for each stock may be affected by fishing mortality, to varying degrees.

It should be noted that the assumed relationship between maximum age and natural mortality ( $M=5.4/A_{max}$ ) 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 stock was assessed in 2018 and 2021 to be overfished and experiencing overfishing, which would reduce the expected value of  $A_{max}$ . The EPO, WCPO, and ATL populations have also been fished relatively heavily compared to most of the stocks in the Then et al. (2015) database. Fishing mortality truncates the age distribution and will reduce the value of  $A_{max}$ , unless samples can be obtained from spatial refuges. The Atlantic stock may be more likely to have sampled such refuges given that most age sampling was by recreational line fishers, and there are areas in the Gulf of Mexico with restricted access to industrial fishing. Age sampling for other stocks was from industrial fisheries.

Past assessments have assumed higher natural mortality for mature females based on sex ratio at length, but such differences are likely overestimated given the reduced female growth rate after sexual maturity seen in many stocks, although the availability of lengths across age classes by sex is limited. The approach used in this study assumes that both sexes have the same natural mortality at all ages, whereas the reality may lie somewhere in between. The potential for mature females to have higher natural mortality than males should be explored in future, but these analyses will require reliable data on sex ratio at length and length at age by sex, and with good spatial resolution since both relationships appear to vary spatially (Hoyle et al., 2009). In the interim it may be reasonable to assume the same ogive for both sexes.

The natural mortality ogives developed here can be applied in yellowfin stock assessments as fixed values or as priors with  $M$  estimated in the model. Punt et al (2021) recommend a range of diagnostics to check models in which  $M$  is estimated.

While acknowledging the uncertainties with aging and determining maximum age, for most stocks we suggest, in the meantime, four alternative hypotheses for the base value of natural mortality: two based on the local  $A_{max}$  and either annual ageing or mark-recapture, and two based on the global  $A_{max}$  of either 11 years based on mark recapture, or 18 years based on annual ageing.

This study also provides two alternative approaches for determining the natural mortality ogive. The two-stage approach proposes  $M$  for immature fish that is lower than for adult fish and does not vary for different values of  $A_{max}$ . This approach may need further development, given (for example) 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 older immature yellowfin tuna are in most stocks caught in large numbers by purse seine fisheries and their natural mortality rate can be influential. The scaled Lorenzen approach is easier to understand and to apply, and consistent with the approach used recently in the Atlantic.

Simulation studies are recommended to test the feasibility of reliably estimating  $M$  within tuna assessments, and to explore what kinds of datasets and model configurations might work best. The spatial population model (SPM) approach (Dunn et al., 2020) could be adapted for this purpose. This simulation approach could be used to explore the potential to obtain further value from the tagging datasets, such as by completing the Brownie-Petersen analyses for the Indian Ocean (Bousquet et al., 2012; Eveson et al., 2012).

Given the importance of estimates of  $A_{max}$  for developing natural mortality prior distributions, and the influence of natural mortality estimates in determining stock status, population-wide biological sampling must be a high priority for tropical tunas. Scientific sampling within spatial refuges may be particularly useful, given the growing evidence for limited movements of fish in some areas (e.g., Schaefer and Fuller, 2022a). Such data could also inform issues such as spatial patterns in growth, sex ratio, and maturity, and their causes. The use alternative aging techniques, such as measuring DNA methylation (Maulani and Auerkari 2020, Mayne et al 2020, Mayne et al 2021a,2021b), should also be explored for tunas.

This approach for developing priors for natural mortality is applicable to all tuna and billfish species for which reliable ageing is available. Ageing samples should come primarily from fisheries that catch the largest fish, which are usually the longline fisheries. Following Hoenig's (1983) recommendation that maximum age tends to increase slowly above a sample size of about 200, only moderate sample numbers are required.

Finally, in the medium to long term the development of close-kin mark-recapture for yellowfin tuna should be considered (Bravington et al., 2016; Kolody and Bravington, 2019). If viable for a species with such wide-ranging spawning, this technique offers the prospect of estimating natural mortality more effectively than other methods.

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## Tables

Table 1: Estimates of natural mortality ( $M$ ) for yellowfin tuna stocks that were influential in determining the values of  $M$  assumed in stock assessments.

Region	$M$ (year <sup>-1</sup> )	ages/sizes	Method	Caveats	Reference
Eastern Pacific Ocean	0.77 (0.6 - 1.0)	2-4 years	catch curve analysis	only use baitboat data, which catches the smallest fish, the fishery was coastal	Hennemuth 1961
Eastern Pacific Ocean	0.55 - 1.05	2-4 years	catch curve analysis	As above	Schaefer 1967
Western and Central Pacific Ocean	0.68	51-60 cm	tagging	Reporting rates vary with size, time, location; slow mixing	Hampton 2000
Western and Central Pacific Ocean	0.44	61-70 cm	tagging	As above	Hampton 2000
Western and Central Pacific Ocean	0.69	71-80 cm	tagging	As above	Hampton 2000
Western and Central Pacific Ocean	0.44-0.6		meta-analysis	Stocks in the meta-analysis may not represent well tuna stocks	Vincent et al 2020a
Indian Ocean	0.5	1.00	tagging	Brownie-Petersen models are sensitive to misspecification around issues such as the spatial and seasonal patterns	Bousquet et al 2012
Indian Ocean	0.27	2	tagging	As above	Bousquet et al 2012
Indian Ocean	0.22	3	tagging	As above	Bousquet et al 2012
Indian Ocean	0.27	4	tagging	As above	Bousquet et al 2012
Indian Ocean	0.28	5	tagging	As above	Bousquet et al 2012
Indian Ocean	0	1.5	tagging	Re-analysis of Bousquet et al (2012), preliminary analysis, lack of tag returns from the longline fisheries	Eveson et al (2012)

Table 2: Natural mortality ogives by stock, calculated based on two-part equations and Amax.

Quarters	Years	IO	ATL	WCPO	EPO
1	0.25	0.714	1.163	0.986	1.269
2	0.5	0.462	0.454	0.551	0.897
3	0.75	0.335	0.316	0.382	0.649
4	1	0.267	0.253	0.296	0.482
5	1.25	0.235	0.218	0.246	0.367
6	1.5	0.227	0.196	0.217	0.292
7	1.75	0.240	0.183	0.202	0.282
8	2	0.267	0.176	0.202	0.346
9	2.25	0.301	0.174	0.217	0.436
10	2.5	0.336	0.176	0.245	0.515
11	2.75	0.367	0.180	0.282	0.570
12	3	0.394	0.187	0.315	0.605
13	3.25	0.414	0.195	0.337	0.627
14	3.5	0.430	0.204	0.348	0.640
15	3.75	0.442	0.212	0.354	0.648
16	4	0.452	0.220	0.357	0.653
17	4.25	0.459	0.228	0.358	0.656
18	4.5	0.464	0.235	0.359	0.659
19	4.75	0.468	0.241	0.359	0.660
20	5	0.472	0.247	0.360	0.661
21	5.25	0.474	0.252	0.360	0.662
22	5.5	0.476	0.256	0.360	0.663
23	5.75	0.478	0.260	0.360	0.663
24	6	0.480	0.263	0.360	0.663
25	6.25	0.481	0.266	0.360	0.664
26	6.5	0.482	0.269	0.360	0.664
27	6.75	0.482	0.271	0.360	0.664
28	7	0.483	0.273	0.360	0.664
29	7.25	0.484	0.275	0.360	0.664
30	7.5	0.484	0.276	0.360	0.664
31	7.75	0.485	0.278	0.360	0.664
32	8	0.485	0.279	0.360	0.664
33	8.25	0.485	0.280	0.360	0.664
34	8.5	0.486	0.281	0.360	0.664
35	8.75	0.486	0.282	0.360	0.664
36	9	0.486	0.283	0.360	0.664

Table 3: Natural mortality ogives by stock, calculated based on the scaled Lorenzen equation.

Quarters	Years	IO	ATL	WCPO	EPO
1	0.25	1.780	1.307	1.417	3.622
2	0.5	1.386	0.764	1.015	2.949
3	0.75	1.145	0.621	0.823	2.435
4	1	0.986	0.547	0.710	2.041
5	1.25	0.873	0.499	0.634	1.736
6	1.5	0.791	0.466	0.580	1.499
7	1.75	0.728	0.440	0.540	1.314
8	2	0.679	0.420	0.509	1.169
9	2.25	0.640	0.404	0.484	1.054
10	2.5	0.608	0.391	0.464	0.963
11	2.75	0.583	0.379	0.447	0.890
12	3	0.561	0.370	0.433	0.831
13	3.25	0.543	0.361	0.422	0.784
14	3.5	0.528	0.354	0.412	0.746
15	3.75	0.516	0.348	0.403	0.716
16	4	0.505	0.342	0.396	0.691
17	4.25	0.495	0.337	0.389	0.670
18	4.5	0.487	0.332	0.384	0.654
19	4.75	0.480	0.328	0.379	0.640
20	5	0.474	0.325	0.375	0.629
21	5.25	0.469	0.321	0.371	0.620
22	5.5	0.465	0.318	0.367	0.612
23	5.75	0.461	0.315	0.364	0.606
24	6	0.457	0.313	0.362	0.601
25	6.25	0.454	0.310	0.359	0.597
26	6.5	0.451	0.308	0.357	0.593
27	6.75	0.449	0.306	0.355	0.591
28	7	0.447	0.304	0.354	0.588
29	7.25	0.445	0.303	0.352	0.586
30	7.5	0.444	0.301	0.351	0.585
31	7.75	0.442	0.300	0.349	0.584
32	8	0.441	0.298	0.348	0.582
33	8.25	0.440	0.297	0.347	0.582
34	8.5	0.439	0.296	0.346	0.581
35	8.75	0.438	0.295	0.346	0.580
36	9	0.437	0.294	0.345	0.580

Figures

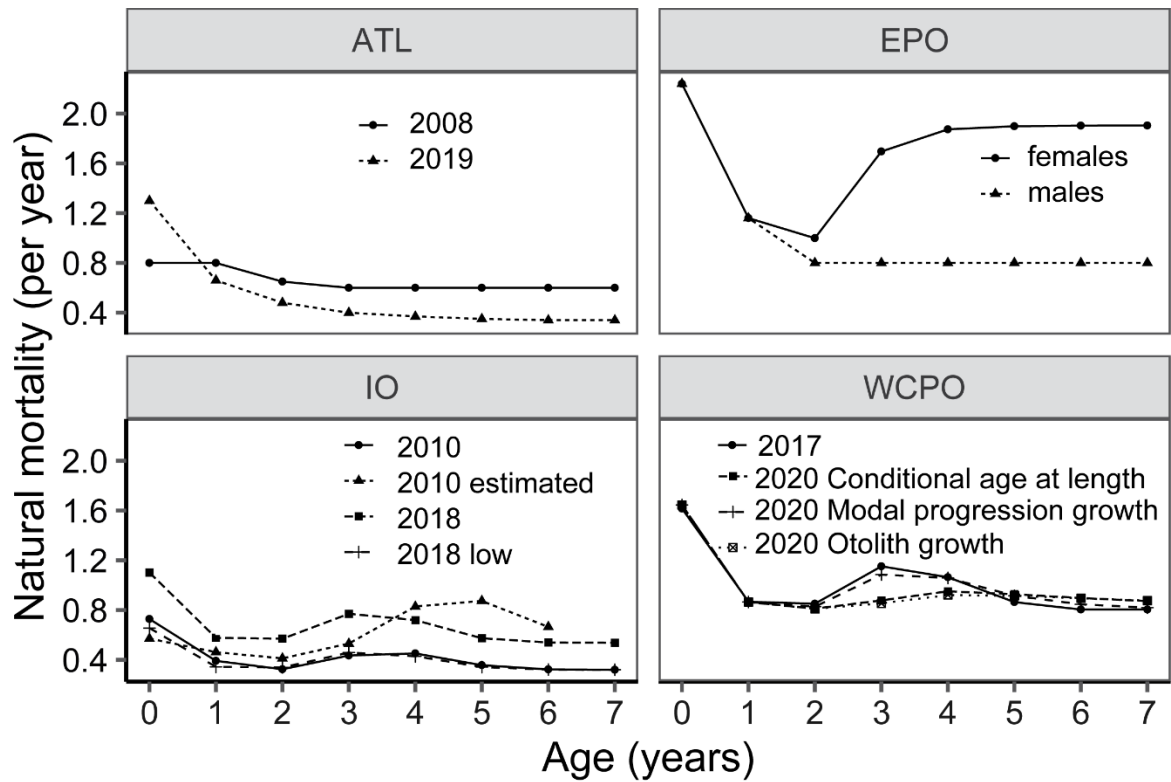


Figure 1: Ogives of natural mortality at age assumed in one or more of the most recent yellowfin tuna assessments for each tuna RFMO.

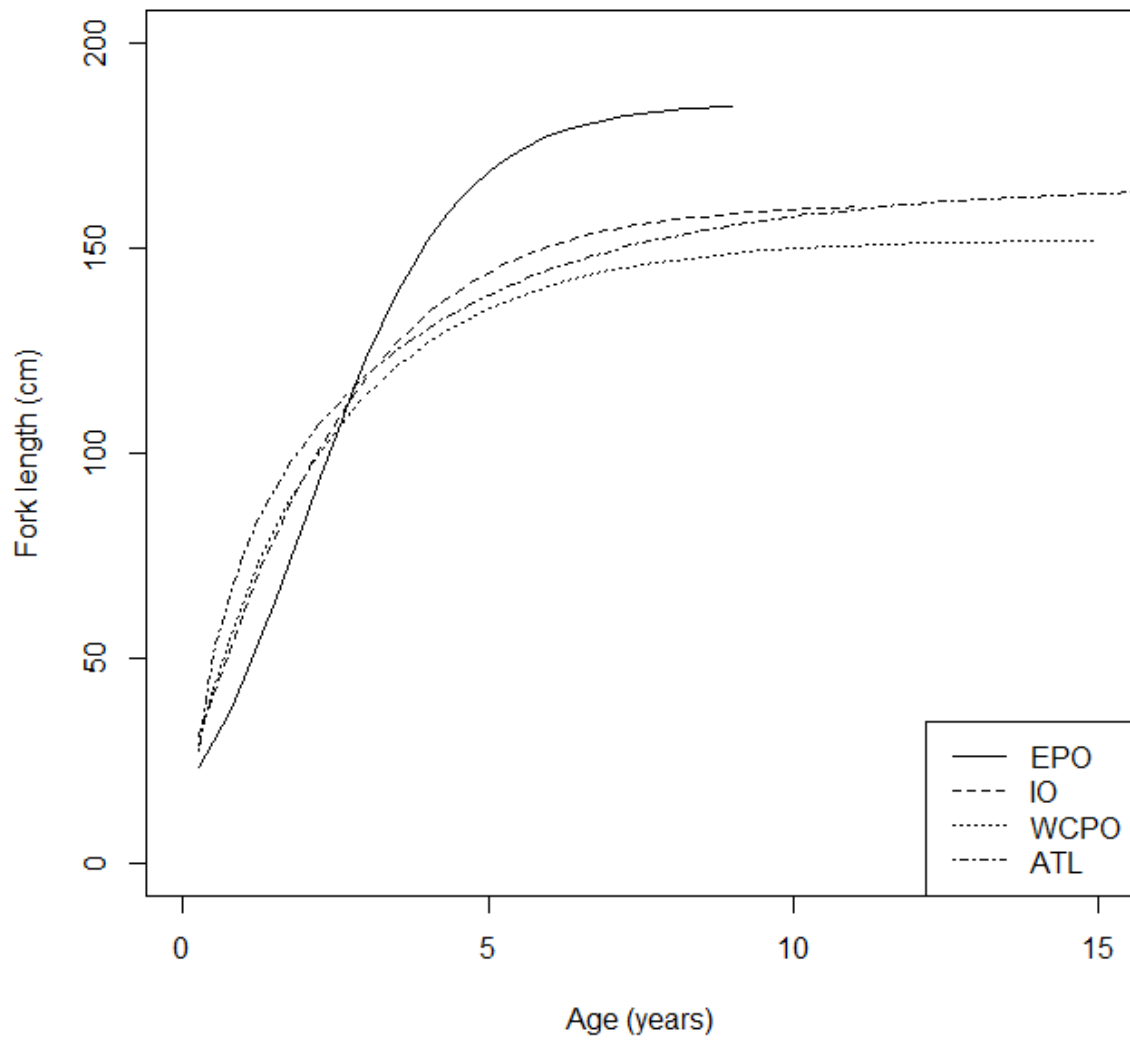


Figure 2: Mean length at age assumed in the stock assessments of each stock for all ages up to the observed  $A_{max}$ .



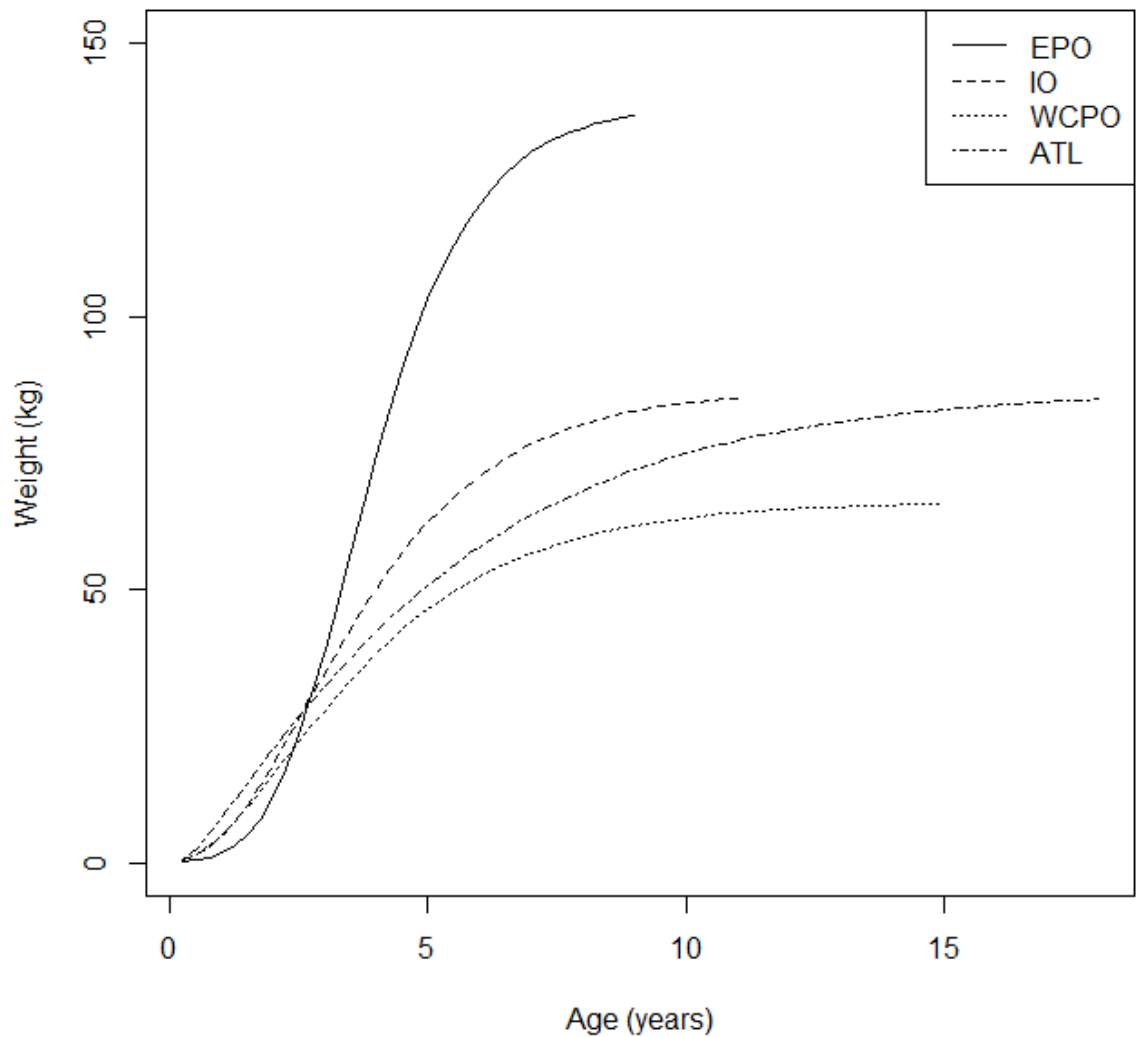


Figure 3: Mean weight at age assumed in the stock assessment for each stock for all ages up to the observed  $A_{max}$ .

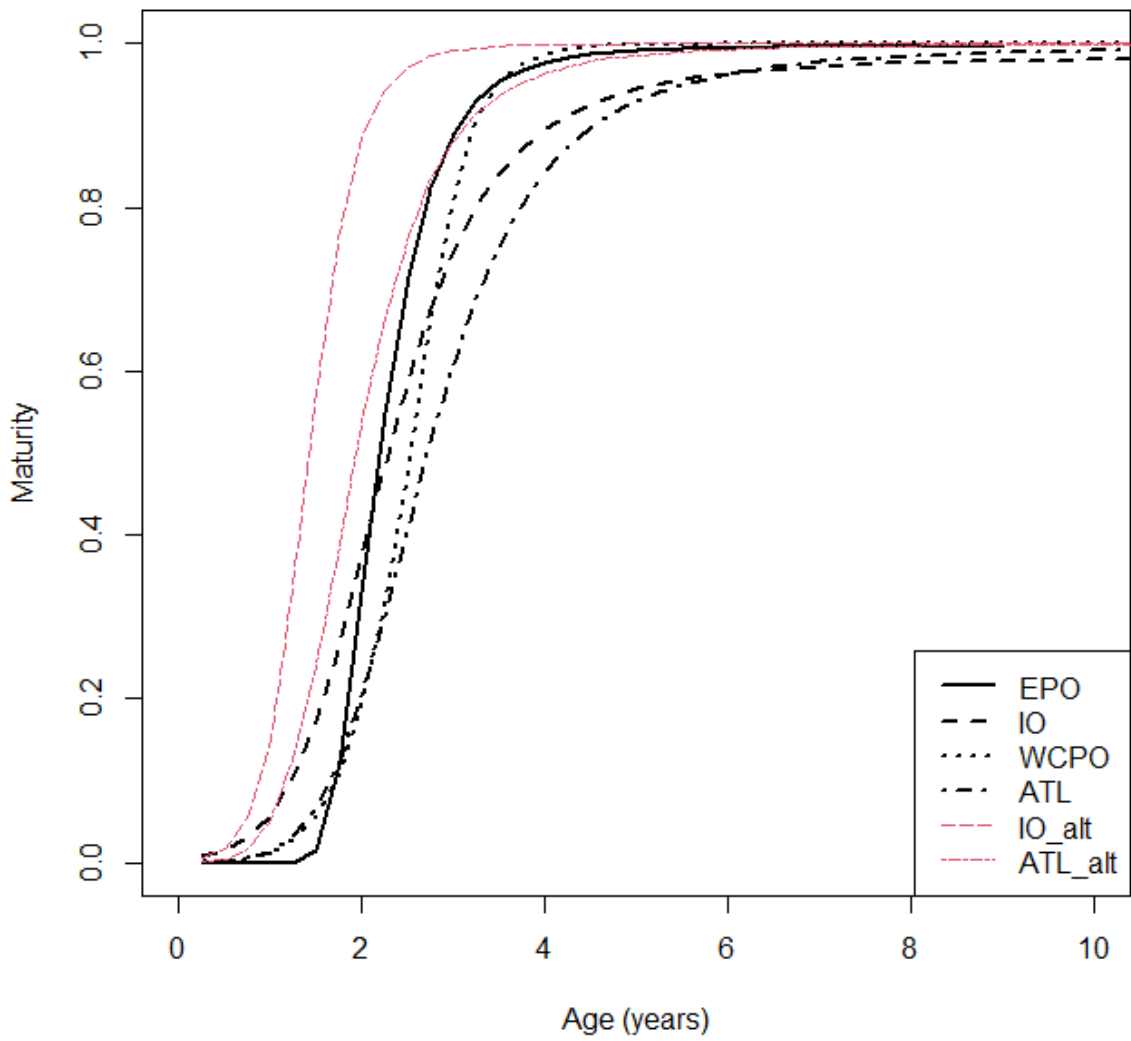


Figure 4: Proportion of females mature at age, for each stock. The alternative ogives in red for IO and ATL are based on CA-stage rather than AV-stage oocytes.

Two-stage

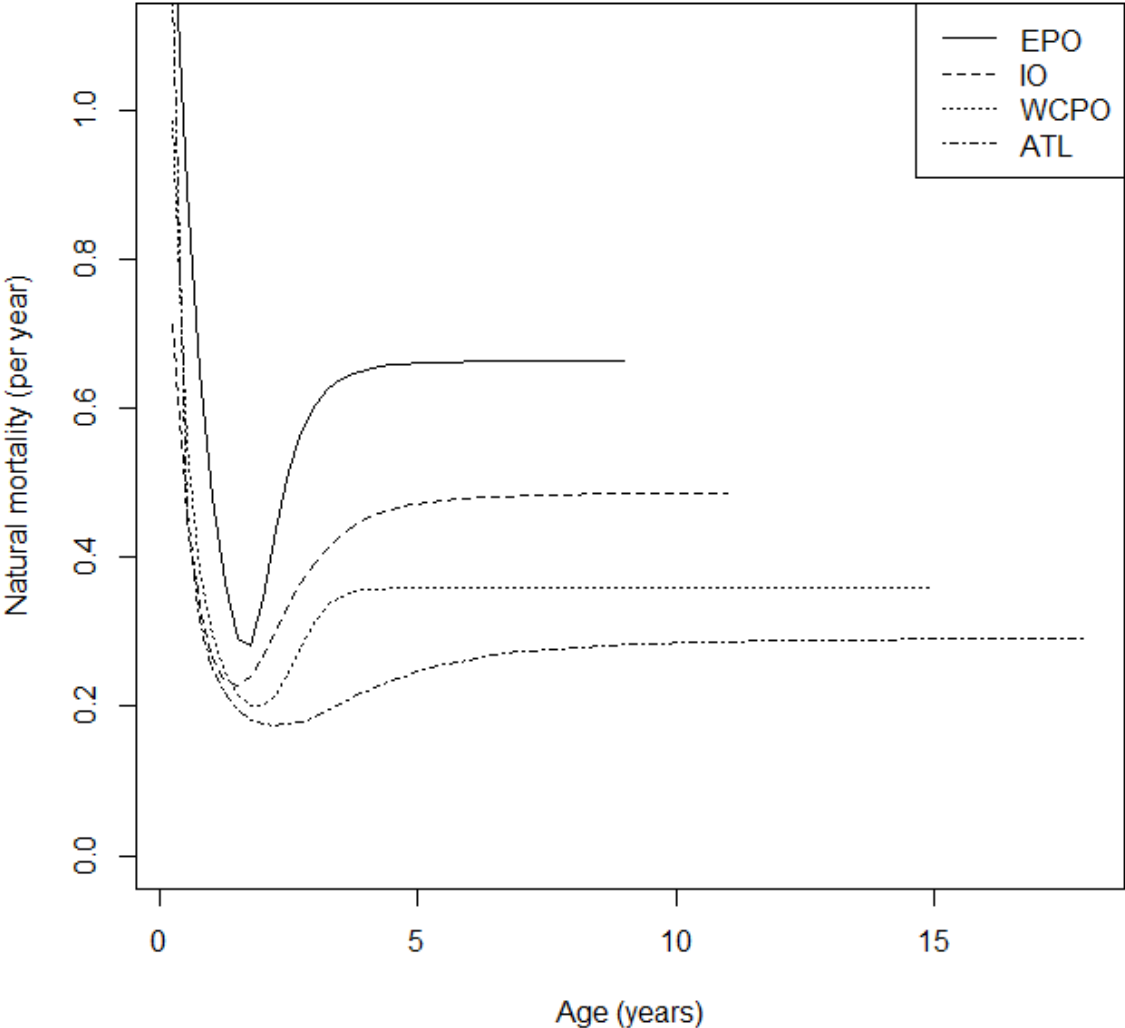


Figure 5: Estimated ogives of natural mortality at age, calculated from maximum observed age  $A_{max}$ , based on the two-stage natural mortality function in Stock Synthesis.

### Scaled Lorenzen

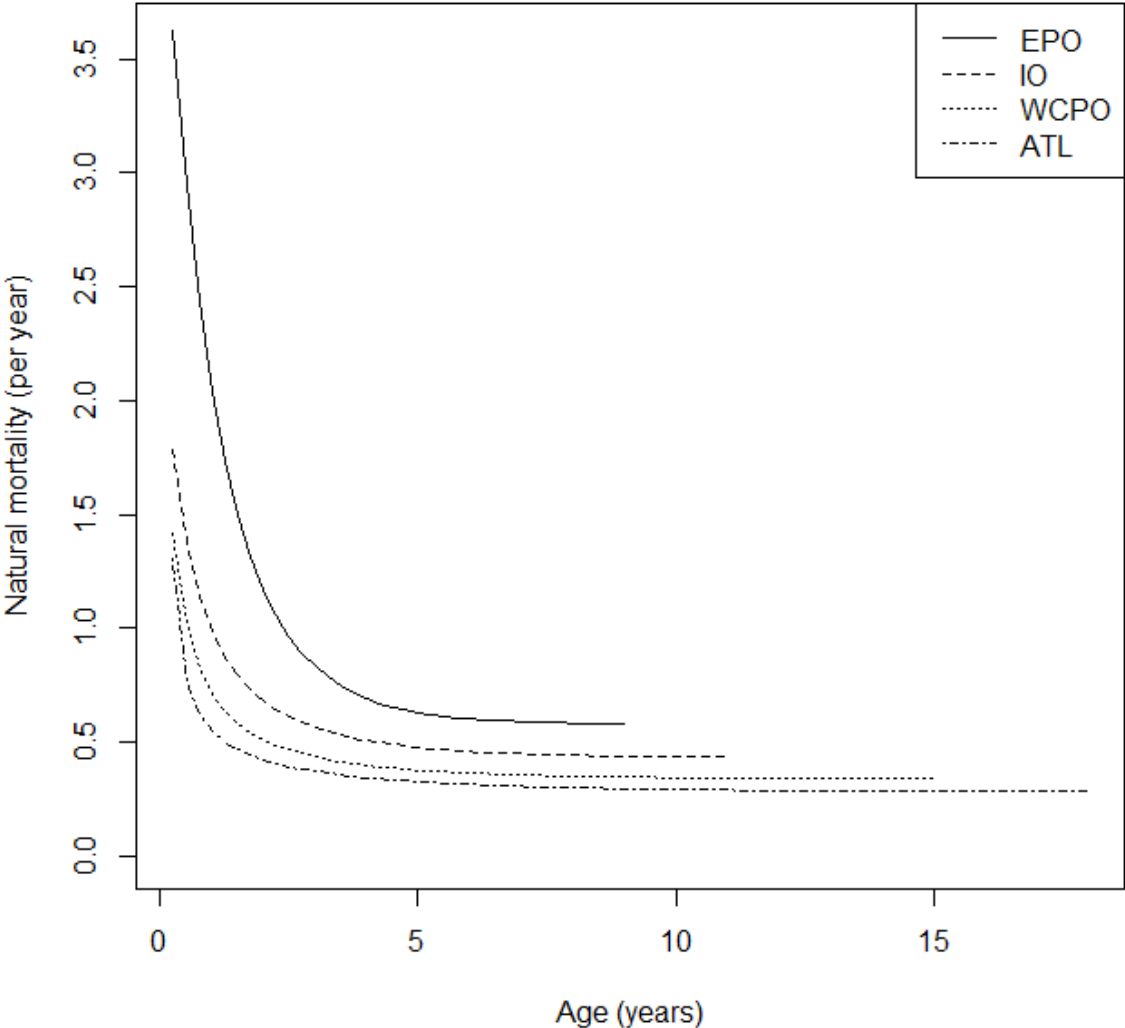


Figure 6: Estimated ogives of natural mortality at age for each stock, based on the scaled Lorenzen approach.





```
stock <- ICCAT2
```

```
ICCAT3 <- list()
ICCAT3$ages <- iccata <- seq(0.25,18,.25)
ICCAT3$LW1 <- 2.1527e-5
ICCAT3$LW2 <- 2.976
ICCAT3$mat_alpha <- mod2$coefficients[1]
ICCAT3$mat_beta <- mod2$coefficients[2]
ICCAT3$mat_L50 <- -ICCAT3$mat_alpha / ICCAT3$mat_beta
ICCAT3$beta <- -0.11
ICCAT3$Rich_Linf <- 165.8
ICCAT3$Rich_k <- 0.23
ICCAT3$Rich_a <- 1.04
ICCAT3$Rich_b <- 0.45
ICCAT3$lengths <- richcalc(ICCAT3)
ICCAT3$mat_age <- 1 - 1/(1 + exp(ICCAT3$mat_beta * (ICCAT3$lengths - ICCAT3$mat_L50)))
ICCAT3$amax_all <- 18
ICCAT3$amax_loc <- 18
ICCAT3$amax_loc_F <- 17
#ICCAT3$Lmat_star <- 80
ICCAT3$Lmat_star <- spline(x=ICCAT3$mat_age, y=ICCAT3$lengths, xmin=0.05)$y[1]
stock <- ICCAT3
```

```
EPO <- list()
EPO_bio <- read_csv("YFT_biology_EPO.csv")
EPO$ages <- seq(0, 9, 0.25)
EPO$lengths <- EPO_bio$length
Linf=188.2
kk=.724
tz=1.825
mm=1.434
EPO$lengths <- Linf * (1-(1-mm)*exp(-kk*(EPO$ages - tz)))^(1/(1-mm))
L1=18.3686; L2=182.307; A1=0; A2=29/4; KK=0.192286*4; BB=-0.542255
EPO$lengths <- richgr2(ages=EPO$ages, L1=L1, L2, A1, A2, KK, BB)
EPO$LW1 <- exp(-11.186)
EPO$LW2 <- 3.086
EPO$mat_L50 <- 91.8
EPO$mat_m <- 0.871
EPO$beta <- -0.11 # do not use
EPO$mat_kappa <- 0.056
EPO$mat_chi <- 84.508
EPO$mat_age <- EPO_bio$mat_at_L
EPO$mat_age <- (1-(1-EPO$mat_m) * exp(-EPO$mat_kappa*(EPO$lengths - EPO$mat_chi)))^(1/(1-
EPO$mat_m))
EPO$mat_age[is.nan(EPO$mat_age)] <- 0
#EPO$Lmat_star <- 65
EPO$Lmat_star <- spline(x=EPO$mat_age[6:30], y=EPO$lengths[6:30], xmin=0.05)$y[1]
EPO$amax_all <- 18
EPO$amax_loc <- 8.1
EPO$amax_loc_F <- NA
```

```

stock <- EPO

richgr_wcpo <- function(a, linf, bb, kk, astar) linf*(1-(1/bb) * exp(-kk*(a-astar)))^bb
WCPO <- list()
WCPO$ages <- seq(0.25,15, 0.25)
WCPO$Rich_Linf <- 152.2
WCPO$Rich_k <- 0.397
WCPO$Rich_a <- 0.847
WCPO$Rich_tz <- -0.548
WCPO$lengths <- richgr_wcpo(a=WCPO$ages, linf = WCPO$Rich_Linf, bb=WCPO$Rich_a,
kk=WCPO$Rich_k, astar = WCPO$Rich_tz)
WCPO$LW1 <- 2.01e-5
WCPO$LW2 <- 2.986
WCPO$mat_L50 <- 106
WCPO$beta <- -0.11 # do not use
WCPO$mat_m <- 3.7
WCPO$mat_kappa <- 0.244
WCPO$mat_chi <- 108.9
WCPO$mat_age <- (1-(1-WCPO$mat_m) * exp(-WCPO$mat_kappa*(WCPO$lengths -
WCPO$mat_chi)))^(1/(1-WCPO$mat_m))
#WCPO$Lmat_star <- 70
WCPO$Lmat_star <- spline(x=WCPO$mat_age, y=WCPO$lengths, xmin=0.05)$y[1]
WCPO$amax_all <- 18
WCPO$amax_loc <- 15
WCPO$amax_loc_F <- 13

#####
make_mort <- function(nsamp=10000, Lorp1, Lorp1_sd, stock) {
  stock$Wmat_star <- stock$LW1 * stock$Lmat_star ^ stock$LW2
  Mjuv_samp1 <- rnorm(nsamp, Lorp1, Lorp1_sd) * (1000*stock$Wmat_star) ^ rnorm(nsamp, Lorp2,
Lorp2_sd)
  Mjuv_samp <- exp(rnorm(nsamp, log(Mjuv_samp1), Msd))
  stock$Mjuv <- Lorp1 * (1000*stock$Wmat_star) ^ Lorp2
  stock$Mmat_loc <- 5.4 / stock$amax_loc
  stock$Mmat_all <- 5.4 / stock$amax_all
  stock$Mmat_loc_F <- 5.4 / stock$amax_loc_F
  stock$Mmat_loc_then <- thencalc(stock$amax_loc)
  stock$Mmat_all_then <- thencalc(stock$amax_all)
  stock$Mmat_loc_F_then <- thencalc(stock$amax_loc_F)

  Msd2 <- sd(log(Mjuv_samp1))
  Mmat_loc_samp <- exp(rnorm(nsamp, log(5.4/stock$amax_loc), Msd))
  Mmat_all_samp <- exp(rnorm(nsamp, log(5.4/amax_all), Msd))
  lambda_samp <- rnorm(nsamp, lambda, .1)
  lenmat <- matrix(stock$lengths, nrow=nsamp, ncol = length(stock$lengths), byrow=T)
  mj <- stock$Mjuv * (stock$lengths / stock$Lmat_star) ^ lambda
  mj_samp <- Mjuv_samp * (lenmat / stock$Lmat_star) ^ lambda_samp
  MM_loc_samp <- mj_samp + (Mmat_loc_samp - mj_samp) / (1 + exp(stock$beta * (lenmat -
stock$mat_L50)))

```



```

MM_all_samp <- mj_samp + (Mmat_all_samp - mj_samp) / (1 + exp(stock$beta * (lenmat -
stock$mat_L50)))
stock$MM_loc <- mj + (stock$Mmat_loc - mj) / (1 + exp(stock$beta * (stock$lengths -
stock$mat_L50)))
stock$MM_all <- mj + (stock$Mmat_all - mj) / (1 + exp(stock$beta * (stock$lengths -
stock$mat_L50)))
MM2_loc_samp <- mj_samp + t((Mmat_loc_samp - mj_samp)) * stock$mat_age)
MM2_all_samp <- mj_samp + t((Mmat_all_samp - mj_samp)) * stock$mat_age)
stock$MM2_loc <- mj + (stock$Mmat_loc - mj) * stock$mat_age
stock$MM2_all <- mj + (stock$Mmat_all - mj) * stock$mat_age
#apply(MM_IO_samp, 2, quantile, 0.1)
stock$MM_loc_lo <- apply(MM_loc_samp, 2, quantile, 0.1)
stock$MM_loc_hi <- apply(MM_loc_samp, 2, quantile, 0.9)
stock$MM_all_lo <- apply(MM_all_samp, 2, quantile, 0.1)
stock$MM_all_hi <- apply(MM_all_samp, 2, quantile, 0.9)
stock$MM2_loc_lo <- apply(MM2_loc_samp, 2, quantile, 0.1)
stock$MM2_loc_hi <- apply(MM2_loc_samp, 2, quantile, 0.9)
stock$MM2_all_lo <- apply(MM2_all_samp, 2, quantile, 0.1)
stock$MM2_all_hi <- apply(MM2_all_samp, 2, quantile, 0.9)

apply(mj_samp, 2, quantile, 0.1)
apply(t((Mmat_all_samp - mj_samp)) * stock$mat_age, 1, quantile, 0.1)
apply((Mmat_all_samp - mj_samp), 2, quantile, 0.1)
apply((mj_samp), 2, quantile, 0.1)

stock$weights <- stock$LW1*stock$lengths^stock$LW2
MLornz <- 3*(1000*stock$weights)^-0.288
meanLr <- mean(MLornz[12:length(stock$mat_age)])
meanLr2 <- sum(MLornz * stock$mat_age) / sum(stock$mat_age)
gm_mean = function(x, na.rm=TRUE){
  exp(sum(log(x[x > 0])), na.rm=na.rm) / length(x)
}
gmeanLr <- 1-gm_mean(1-MLornz[12:28]) # works out the same as meanLr

stock$MLornz_loc_Amax <- 3*(1000*stock$weights)^-0.288 * stock$Mmat_loc / meanLr2
stock$MLornz_all_Amax <- 3*(1000*stock$weights)^-0.288 * stock$Mmat_all / meanLr2
stock$MLornz_loc_Amax_then <- 3*(1000*stock$weights)^-0.288 * stock$Mmat_loc_then /
meanLr2
stock$MLornz_all_Amax_then <- 3*(1000*stock$weights)^-0.288 * stock$Mmat_all_then /
meanLr2
return(stock)
}
#####

WCPO <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, WCPO)
ICCAT <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, ICCAT)
ICCAT2 <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, ICCAT2)
ICCAT3 <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, ICCAT3)
EPO <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, EPO)
IO <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, IO)
IO2 <- make_mort(nsamp = 10000, Lorp1, Lorp1_sd, IO2)

```

```
for(stocknm in c("WCPO", "ICCAT3", "EPO", "IO2")) {  
  windows()  
  stock <- get(stocknm)  
  plot(stock$ages, stock$MM2_loc, type = "l", ylim = c(0,1.1), xlab = "Age (years)", ylab = "Natural  
mortality (per year)", main = stocknm)  
  lines(stock$ages, stock$MM2_loc, type = "l", col = 1, lty = 1)  
  lines(stock$ages, stock$MM2_all, type = "l", col = 2, lty = 1)  
  lines(stock$ages, stock$MLornz_all_Amax, type = "l", col = 3, lty = 1)  
  lines(stock$ages, stock$MLornz_loc_Amax, type = "l", col = 4, lty = 1)  
  legend("topright", legend = c("Two-stage local", "Two-stage global", "Lorenzen local", "Lorenzen  
global"), col = 1:4, lty = 1, lwd = 1)  
  savePlot(paste0("Natural mortality_options_",stocknm,".png"), type = "png")  
}
```