NATURAL MORTALITY ESTIMATES OF YELLOWFIN TUNA (*Thunnus albacares*) IN THE INDIAN OCEAN

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SUMMARY

Natural mortality (M) is considered one of the most influential parameters in fisheries stock assessment and management, as it relates directly to stock productivity and reference points used for fisheries management advice. M is very uncertain and difficult to estimate reliably and directly, and often other life history parameters such as growth or maximum observed age are used as proxies to get an estimate of M. Here we use 3 different theoretical estimators (one longevity-based and two growth-based) to calculate M values for Indian Ocean yellowfin tuna (Thunnus albacares). Obtained M values were 0.462, 0.542 and 0.351. However, all three methods are likely subject to bias and/or imprecision, mainly due to incomplete data focused on specific study areas and/or lack of sufficient data from the largest size classes, among others. We then combined the results obtained from the three approaches to obtain a median composite M value, estimated at 0.45 year^{-1}*, that was then scaled across age classes to calculate the age-dependent natural mortality. Estimated M-at-age values were higher than those used in the latest 2021 IOTC assessment for the first two years of life, being lower thereafter. Overall, the present study highlights the current information gaps that prevent obtaining more accurate estimates of M and calls for the need for a dedicated sampling that allows the estimate of M more effectively.*

KEYWORDS: Natural mortality, M-at-age, yellowfin tuna, stock assessment, IOTC

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1. Introduction

Natural mortality (M) represents the removal of fish from the stock that is not attributed to fishing activities, that is, the rate at which fish die due to natural causes such as predation, starvation, disease, senescence, or environmental stressors, among others (Punt et al., 2021). M estimates play a crucial role in tuna stock assessment models, serving as a fundamental parameter for estimating the maximum sustainable yield, productivity, and overall health of a stock (Maunder et al., 2023). In practice, the direct estimation of M is difficult to achieve, and there is often insufficient information regarding the actual extent of natural mortality. Alternatively, there are other indirect methods that can be used as proxies to estimate M. These methods are based on the relationship between M and other life-history parameters, such as maximum age, growth parameters and age-at-maturity (Cope and Hamel, 2022; Maunder et al., 2023). However, this information is not always up to date or is not truly representative of the whole population, and its variability may be significant enough to influence the estimation of M and, in consequence, to influence the results of the stock assessment (Brown et al., 2005). All methods are subject to bias and or imprecision due to incorrect assumptions and/or incomplete data (Hamel et al., 2023). Hence, rather than relying solely on a single estimate or approach for M, considering a range of feasible approaches is often recommended (Hamel et al., 2023; Maunder et al., 2023).

Here, (1) we estimated different baseline M values for Indian yellowfin tuna stocks based on three distinct estimators (one longevity-based and two growth-based), (2) we identify important issues for estimating M associated with each type of estimator and highlight current information gaps, and (3) we propose alternative M-at-age estimates to complement those already used by the IOTC.

2. Data and methods

2.1 Natural mortality estimations (M)

Three different estimators were used to calculate point estimates of M values for yellowfin tuna of the Indian Ocean (**Table 1**). For longevity-based M estimates, the maximum age (A_{max}) inverse relationship from Hamel and Cope (2022) was used. For von Bertalanffy growth-based M estimates, two approaches were used, one of which only uses relative growth rate (k) and another which uses both k and mean asymptotic length (L_∞), with equations described in Hamel and Cope, (2022) and Then et al., (2015), respectively. These three equations for estimating M were selected following recommendations from Maunder et al., (2023). Entry values used were A_{max} = 11.7 years, k = 0.35 year^{-1} and L_∞ = 169.8 cm according to the von Bertalanffy growth function (VBGF) model from Farley et al., (2023).

Finally, all three approaches were combined into a weighted density function to estimate a composite median M using the "*Natural Mortality Tool*" from Cope and Hamel, (2022). The contribution of each method in the composite M distribution was weighted as follows: a value of 1 (full weighting) for the longevity-based method and 0.5 for each of the two growth-based methods (due to redundancies of methods, so weighted together equal 1). Default prior sample number and density bandwidth were used in the density plot (1000000 and 1, respectively). An CV of 0.31 with lognormal error type was used to add additional uncertainty to the point estimates (Cope and Hamel, 2022; Hamel et al., 2023).

2.2 Natural mortality at age estimations (M_a)

Composite M value was then scaled across age classes to calculate the age-dependent natural mortality (M_a) following Lorenzen (2005), as IOTC used this method in previous data preparatory meetings (Fu et al., 2021):

$$M_a = \ln\left(\frac{La}{(L_a + L_\infty \times (e^k - 1))}\right) \times \left(\frac{M1}{L_\infty\ x\ k}\right)$$

where M_a is mortality at age, L_a is mean length at age, L_∞ is mean asymptotic length, k is relative growth rate and M1 is mortality by size unit. Growth parameters were from Farley et al., (2023) VBGF model. Baseline M was fixed at age 4.07, when 95% of individuals are assumed to be sexually matured according to maturity ogives in Zudaire et al., (2022). We considered mature females, those in advanced vitellogenic (AV) oocytes stage or atresia of yolked oocytes, as it is the most reliable threshold for determining if a female is mature and contributing to egg production (Schaefer, 2001).

3. Results and Discussion

3.1 Natural mortality estimates (M)

The decision to estimate M inside or outside stock assessment models can depend on various factors and the specific context of the assessment. For example, Punt et al., (2021) proposed that estimating M within the stock assessment model, rather than pre-specifying M. This allows for the possibility of accounting for temporal and spatial variability of M, as well as age and size-dependent mortality. A successful estimation of M within a stock assessment model will vary among stocks and will depend on the amount and type of available data, as well as on the assumptions that are made in the assessment and how M is modelled (Maunder et al., 2023). In this regard, it has been noted that yellowfin tuna (*Thunnus albacares*) data are prone to being less informative and more conflicting, thus diminishing the ability to successfully estimate M inside the model (Hoyle et al., 2023). For this kind of situation, the use and evaluation of multiple methods are recommended (Cope and Hamel, 2022; Maunder et al., 2023). In the present work, we proposed three alternative point estimates of M values and used a composite median M value derived from them for representing M-at-age of yellowfin tuna in the Indian Ocean.

M values varied depending on the estimator used and substantial differences were found between the two growth-based methods (**Table 1**). The lowest M estimates, M=0.351, were obtained when both *k* and L_∞ were considered following the Then et al. (2015) method. When only *k* was considered following Hamel and Cope, (2022) method, M increased to 0.542. Growth parameters for yellowfin tuna are fairly up-to-date (Farley et al., 2023) and the ageing method has been recently validated (Fraile et al., 2024). However, the samples used for the growth model development (N=386) may not yet be fully representative of the whole population. For example, samples used in the growth model are mostly (95%) west-centred (west of 80ºE), with fewer samples (5%) obtained from the eastern Indian Ocean (east of 80ºE). Studies have shown that there may be considerable uncertainty in the estimate of *k* for the same species across regions (Maunder et al., 2023). Farley et al. (2023) state that there are no clear regional differences in growth, but that region-specific sample sizes remain too small to be conclusive and recommend that additional otoliths from the northern and eastern regions of the Indian Ocean should be collected and aged to provide further information on growth and longevity. Another uncertainty in applying growth parameters to obtain M estimates is the fact that there may be sexual dimorphism in growth and how this should be treated. Data available in Farley et al., (2023) indicates that growth for males and females was similar up to 3-4 years of age, after which males seem to grow slightly faster and reach slightly larger sizes, on average, than females. Estimates of *k* were 0.34 for males and 0.42 for females, while mean asymptotic length was estimated to be 171.6 cm for males and 155.8 cm for females (Farley et al., 2023). The independent review of the recent IOTC yellowfin tuna assessment recommended the implementation of a two-sex model that considers different longevities for males and females and that is consistent with different growth between sexes in the mortality section (Anon, 2023). Another uncertainty in using the growth parameters to estimate M is that both Hamel and Cope, (2022) and Then et al., (2015) used parameters of the VBGF model to develop the equations, while it has been observed that the best-fitting model for growth in yellowfin tuna in the Indian Ocean is the 2-stage VB model (Farley et al., 2023).

Longevity-based approach from Hamel and Cope, (2022) leads to an M estimate of 0.462, when maximum age of 11.7 years is considered. Compared to other life-history parameters, A_{max} is expected to own a more consistent relationship with M across different taxa and had the lowest residual variance compared to other empirical methods, therefore considered to have the best predictive power (Hamel and Cope, 2022; Hoyle et al., 2023). However, there is some concern regarding the extent to which the observed maximum age for a fish represents the longevity of the species or the population. In many cases, these observations refer to a very small number of fish, and there is some debate over the possible magnitude of the effective sample size and its influence (Hamel and Cope, 2022; Hoening, 2017; Maunder et al., 2023). The relationship of $M=5.4/A_{max}$ 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 and the process used to select fish for ageing, as well as the number of fish aged (Hoyle, 2021). For instance, in the Indian Ocean, A_{max} of 11.7 years has been described for an individual of 184 cm FL (Farley et al., 2023) but fishery data show that yellowfin tuna can reach maximum lengths of 198 cm in the Indian Ocean (**Figure 1**). In the Atlantic Ocean, A_{max} of yellowfin tuna has been reported to be 18 years, for 191 cm and 181 cm FL individuals (Andrews et al., 2020; Pacicco et al., 2021), which leads to a substantially lower M of 0.300 year^{-1}. As it can be seen, the choice of the value of A_{max} has a strong influence on the M estimate, leading to serious doubts regarding where to set the maximum age when estimating mortality for yellowfin tuna and consequent implications for the perception of the stock. However, extrapolating A_{max} out of the basis of observations (both up and down) cannot just happen without scientific evidence to support it. Then et al., (2015) stated that A_{max} estimates from their study correspond empirically to the age where 0.6% of the population survives. It should be noted that despite A_{max} being theoretically related to M, species data of interest needs to be similar to that used to develop the relationship (Hoyle et al., 2023). The Hamel and Cope, (2022) relationship between A_{max} and M was determined by fitting to data from populations that were mostly unfished or where the fishing impact has been small, excluding heavily exploited populations (Then et al., 2015). This may not represent the reality of yellowfin tuna stocks, with the Indian stock considered to be overfished and subject to overfishing (ISSF, 2023). In this regard, Maunder et al., (2023) caution that for cases where fishing mortality is significant, selectivity, refugia and sampling approach are important factors to be considered for applying A_{max} for M estimations.

The best method for estimating M outside the stock assessment model will be stock-specific (Hamel et al., 2023). In the case of Indian Ocean yellowfin tuna, both growth-based and longevity-based methods are likely subject to a certain degree of bias and/or imprecision. Besides, it is difficult to establish a criterion for determining which M to stick with as there is no one superior approach, and, in these cases, the application of multiple empirical estimators is likely recommended rather than assuming just one estimator or approach for M (Maunder et al., 2023). Here, the composite median M value for yellowfin tuna was estimated at 0.45 year^{-1} (**Figure 2**).

3.2 M-at-age estimations (M_a)

Estimates of M-at-age are provided in **Table 2**, which were similar for the first two years of life to those values used in the 2021 reference model from the IOTC (**Figure 3**). For older ages, M-at-age values from the current study were lower than those used in the 2021 reference model from the IOTC, which only extended up to age 7. Besides, the current study does not consider the ‘hump’ assumed in the 2021 stock assessment M-at-age values. Two other scenarios based on Hoyle (2021) were also included in the uncertainty grid, following Hamel and Cope (2022) equation, one based on a maximum age of 10.5 years observed for Indian Ocean yellowfin tuna according to Shih et al., (2014), and the other based on the validated maximum age of 18 years the Atlantic Ocean yellowfin tuna. For A_{max}=18 years the range of M-at-age estimates were substantially lower than M ogives presented in the current study and in the 2021 stock assessment basic model. There is no evidence to show that the maximum age observed for Atlantic yellowfin tuna can be extrapolated to the Indian stock, as both stocks may be exposed to different predation rates, different environmental stressors and subject to different local pressures and diseases. Moreover, both stocks form genetically distinct populations that own different life history traits (Murua et al., 2017; Pecoraro et al., 2018, 2016). For A_{max}=10.5, the range of M-at-age estimates were slightly higher than those presented in the current study. Nevertheless, this approach should be revisited as new data has extended the maximum age of yellowfin tuna in the Indian Ocean to 11.7 years (Farley et al., 2023). Hoyle et al., (2023) also proposed an alternative two-stage approach for representing M-at-age of yellowfin tuna in the Indian Ocean, as well as in other oceans. They assumed an A_{max} of 10.9 years and growth parameters from the Richards growth curve described in Farley et al., (2021), maturity data from Zudaire et al., (2013) at AV stage and length-weight relationship from Chassot et al., (2016). The estimated M-at-age pattern using the two-stage approach was very different from those used in the 2021 assessment, with lower levels of M at all ages (**Figure 3**). The M-at-age values from the two-stage approach were significantly lower for immature fish than those derived in the current study up to age 4 (where they converge), being between 0.04-0.10 higher thereafter. Authors acknowledge that this approach may need further development (Hoyle et al., 2023). It can now also be updated with new growth and maturity parameters available for Indian Ocean yellowfin tuna (Farley et al., 2023; Zudaire et al., 2022).

4. Conclusions

Improving the precision of natural mortality estimates is paramount for enhancing the effectiveness of conservation measures and promoting the resilience of tuna populations in the face of increasing anthropogenic pressures. Although estimating M directly is challenging, empirical methods can help to better understand the relationship between M and other life cycle parameters. However, accurate estimates of M based on life history theory rely on accurate estimates of the associated life history parameters, as any error or bias in these estimators may affect the predictions. Moreover, the magnitude of error when estimating M can be substantial and can be affected by ignoring its variation over time, space, age, sex, and size (Hamel et al., 2023).

The current uncertainty associated with the life history parameters of yellowfin tuna in the Indian Ocean, due mainly to the availability and representativeness of the samples, may prevent obtaining reliable estimates of natural mortality. To make progress in this field, ocean-wide biological sampling (e.g., otoliths, spines, gonads, muscle tissue, etc.) must be a priority for yellowfin tuna. Sampling focused on the highest size ranges available may be particularly useful for estimating A_{max} from otolith readings, as well as focusing on both spatial refuges under low fishing conditions and areas where fishing pressure is known to be high. Sampling must also account for and explore potential regional differences in growth, intensifying the effort in areas where current sample sizes are low, such as the northern and eastern regions of the Indian Ocean. Sex of the fish should also be recorded whenever possible to allow estimation of sex-specific growth, $A_{max,}$ and M. Such reference sample collections, covering the full-size range and the distribution of the species, are also necessary for the development of other, more novel age estimation methods such as an epigenetic ageing clock. Being able to estimate the age of a fish genetically can speed up the process and lower the costs, but it requires first a robust calibration with a reference collection of fish from known age. Similarly, a better understanding of the development of length/age at maturity in different regions will also help to have more accurate estimates of M-at-age. Finally, it should be bear in mind that both mortality and the parameters used to calculate it empirically are dynamic and will change depending on the suite both extrinsic (predators, resource competition, environmental stressors, etc.) and intrinsic (sex, growth, maturity, etc.) factors, and that they may be temporal and/or geographically variable, and it is therefore advisable to review them periodically.

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Table 1. Approaches and equations used for estimating natural mortality (M) of yellowfin tuna *(Thunnus albacares*) in the Indian Ocean, where A_{max} is maximum age (years), *k* is the growth rate ($year^{-1}$), and L_∞ is the asymptotic length (cm). Entry values used were A_{max} = 11.7 years, *k* = 0.35 $year^{-1}$ and L_∞ = 169.8 cm according to the von Bertalanffy growth function (VBGF) model from Farley et al. (2023).

Approach	Equation	M	Reference
Maximum age (Amax)	M= 5.4/Amax	0.462	Hamel and Cope (2022)
Growth rate (k)	M=1.55k	0.542	Hamel and Cope (2022)
Growth rate (k) and asymptotic length ($L\infty$)	$M= 4.118k^{0.73} L\infty^{-0.33}$	0.351	Then et al. (2015)

Table 2. Natural mortality ogives by quarters and years of age estimated for yellowfin tuna (*Thunnus albacares*) from the Indian Ocean.

Quarter	Age (years)	M-at-age
1	0.25	1.301
2	0.5	1.064
3	0.75	0.915
4	1	0.813
5	1.25	0.738
6	1.5	0.681
7	1.75	0.637
8	2	0.601
9	2.25	0.571
10	2.5	0.546
11	2.75	0.526
12	3	0.508
13	3.25	0.493
14	3.5	0.480
15	3.75	0.469
16	4	0.459
17	4.25	0.450
18	4.5	0.442
19	4.75	0.435
20	5	0.429
21	5.25	0.424
22	5.5	0.419
23	5.75	0.415
24	6	0.411
25	6.25	0.407
26	6.5	0.404
27	6.75	0.401
28	7	0.399
29	7.25	0.396
30	7.5	0.394
31	7.75	0.392
32	8	0.391
33	8.25	0.389
34	8.5	0.388
35	8.75	0.386
36	9	0.385

37	9.25	0.384
38	9.5	0.383
39	9.75	0.382
40	10	0.381
41	10.25	0.381
42	10.5	0.380
43	10.75	0.379
44	11	0.379
45	11.25	0.378
46	11.5	0.378
47	11.75	0.377
48	12	0.377

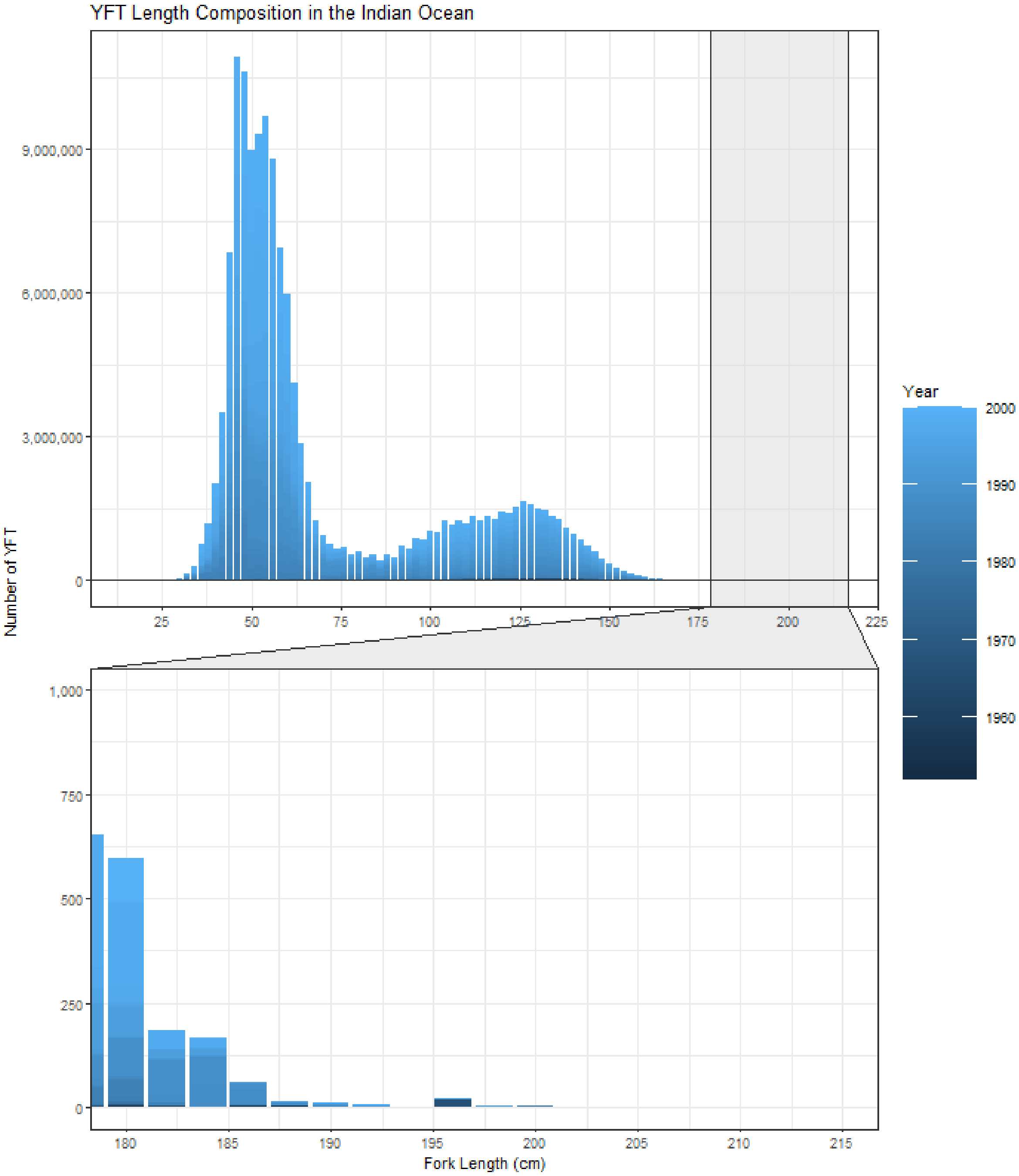

Figure 1. Length composition of yellowfin tuna (*Thunnus albacares*) caught in the Indian Ocean.

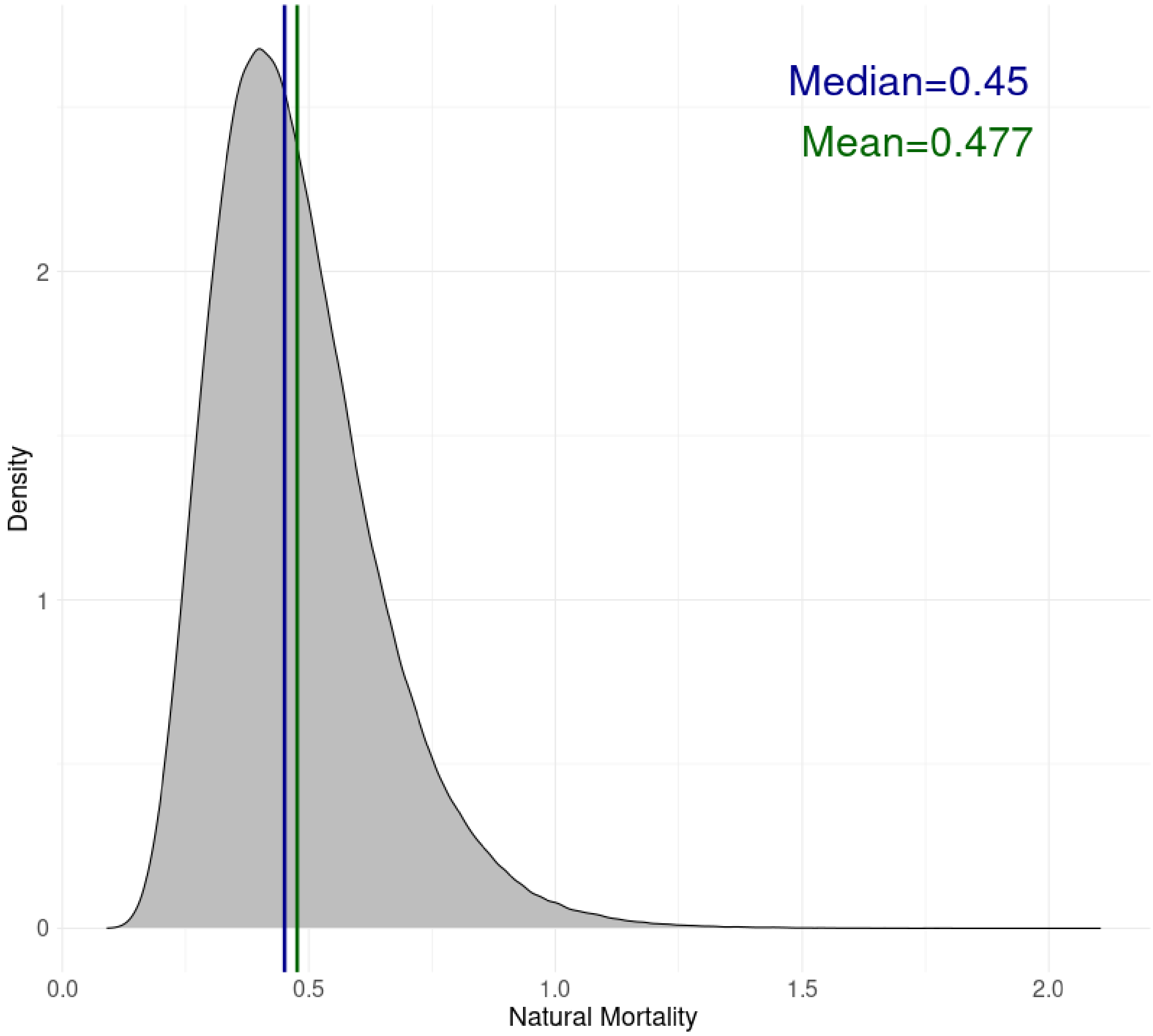

Figure 2. Composite M density distribution. Blue line indicates median value and green line indicates mean value.

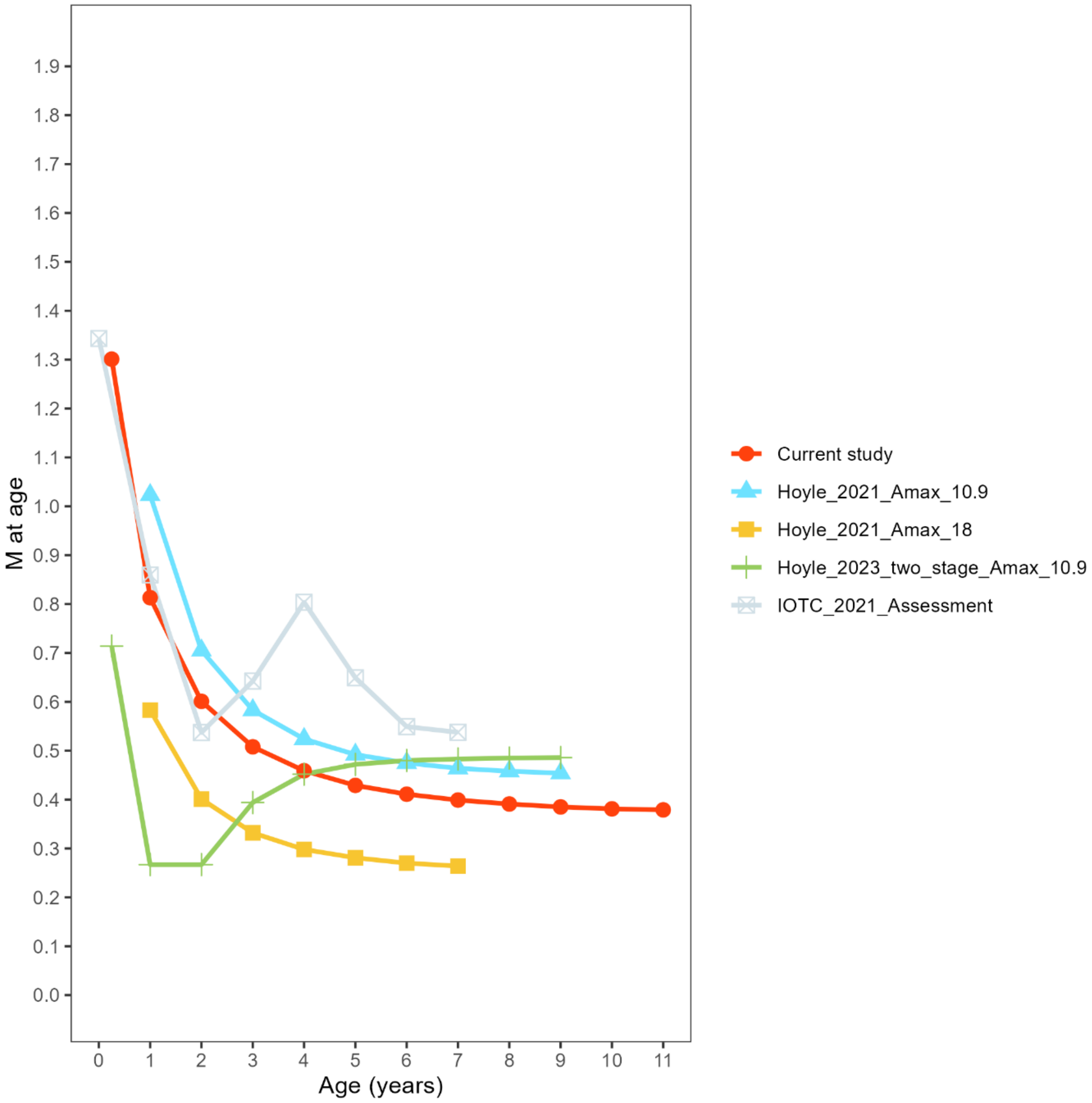

Figure 3. Natural mortality at age estimated for yellowfin tuna (*Thunnus albacares*) from the Indian Ocean in the current study (red line), adopted in 2021 IOTC stock assessment (grey line), described in Hoyle et al. (2023) for two part equation based on maximum age of 10.9 years (green line) and described in Hoyle et al. (2021), based on a maximum age of 10.9 (blue line) and based on maximum age of 18 years (yellow line).