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NATURAL MORTALITY USED IN THE EPO BIGEYE TUNA ASSESSMENT

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1. Summary

Natural mortality (*M*) is one of most influential parameters in a stock assessment model. It can have a large influence on estimates of both the current stock status and management reference points. Here we describe the natural mortality currently used in the EPO bigeye tuna stock assessment, other relevant information on natural mortality for bigeye tuna, and the influence of natural mortality on management quantities. The results of this review suggest that there is no definitive information to update the estimates of natural mortality currently used in the assessment. The difference in *M* between mature females and males should be based on the sex ratio data, but more information on gender specific growth rates is vital to interpret gender specific *M*. Fitting the sex-ratio data in the stock assessment model and estimating natural Mortality should also be considered once some of the current issues with the assessment have been resolved.

2. Introduction

Natural mortality (*M*) is one of most influential parameters in a stock assessment model. It can have a large influence on estimates of both the current stock status and management reference points. Here we describe the natural mortality currently used in the EPO bigeye tuna stock assessment, other relevant information on natural mortality for bigeye tuna, and the influence of natural mortality on management quantities.

Much of the information presented here is taken directly from other IATTC documents.

3. Natural mortality currently used in the assessment

The age and sex-specific vectors of natural mortality used in the EPO bigeye tuna stock assessment are described in Aires-da-Silva et al. (2014) and their calculation follows Harley and Maunder (2003). A higher level of quarterly natural mortality ($M = 0.25$) is assumed for fish of both sexes 0 quarters old, decreasing to 0.1 at 5 quarters of age (Figure 3). The model is run using quarters as years in Stock Synthesis, so natural mortality is reported on a quarterly basis. Natural mortality of females increases after they mature (age at 50% maturity is approximately 3 years based on the size at 50% maturity of 135 cm (Schaefer et al. 2005), but the actual age at change is delayed unto age 3.5) to 0.143 at age six and a half quarters. These age-specific vectors of natural mortality are based on fitting to age-specific proportions of females, maturity at age, and natural mortality estimates of Hampton (2000).

The method of Harley and Maunder (2003) is based on the observation that while the sex ratio of catches of small tuna are close to 50/50, males begin to dominate catches of large tuna (Kume and Joseph 1966; Hampton et al. 1998; Miyabe 2002), which could be caused by higher natural mortality for old females. However, before the change in sex ratio can be attributed to sex-specific natural mortality, other assumptions must be considered. Everett and Punsly (1994) speculated that there are three possible causes of the observed changes in sex ratios:

a. • Sex-specific growth, i.e., that females grow to a smaller maximum size than males.
b. • Sex-specific vulnerability, i.e., behavioral differences make large males more vulnerable to fishing gears than females.
c. • Sex-specific mortality, i.e., females die out before they become large.

Though Everett and Punsly (1994) did not have specific data to separate these hypotheses they did provide some discussion of preliminary analyses and other ideas. First they noted that if females grew to a smaller asymptotic size than males one would expect to observe an accumulation of females in smaller size classes. This pattern is not supported by sex ratio data for bigeye tuna (Figure 2, need to update). The limited data available for the length at age by sex for old individuals does not support differences in growth between females and Males (Figure 5). Sex ratios by purse seine for large bigeye are not available so differential vulnerability to fishing mortality cannot not be ruled out, but Harley and Maunder (2003) concluded it unlikely for yellowfin tuna.

Within the hypothesis for which differences in natural mortality are the cause of the change in sex ratio there are a number of sub-hypotheses that are confounded, e.g., does male mortality decline and female mortality remain constant? or does mortality for both sexes increase with size but the rate for females increase faster? It is assumed that the increase in mortality occurs some period of time after an individual becomes mature. This is based on the observation in yellowfin tuna, that the decline in the proportion of females in catches occurs about 1.5 years after the age at 50% maturity (K. Schaefer, IATTC, pers. comm.).

The data used in the model for *M* are estimates of the proportion of males in the population by size class (as determined by sampling catches), the proportion of females that are mature in a size class, estimates of mean length-at-age (to convert length-based estimates to age-based), and the estimates of natural mortality at age estimated from tagging data by Hampton (2000).

There are three parts to the model (Figure 1):

a. Part 1: mortality is the same for males and females and declines linearly from some first age (min age) to some breakpoint (break age).
b. Part 2: mortality is constant and the same for males and immature females from this breakpoint until females begin to mature.
c. Part 3: mortality for males remains constant but mortality for mature females is higher than immature females. The overall mortality for females increases with age as proportion of mature females increases. The increase in natural mortality for mature females can either occur as soon as they become mature, or at some lag after becoming mature.

The details of the method can be found in Harley and Maunder (2003) and the estimates of natural mortality used in the stock assessment are presented in Figure 3. Stock Synthesis uses a broken stick form to represent estimable natural mortality, so what is used is somewhat different from Figure 1, which uses maturity at age to weight the female natural mortality.

4. Other information on natural mortality

There has not been an extensive review of natural mortality for bigeye tuna in the EPO. However, natural mortality was reviewed for yellowfin tuna by Maunder et al. (2012) and many of the issues are similar for bigeye tuna.

Maximum age is difficult to determine for bigeye tuna since aging techniques, which are based on counting daily rings in otoliths, are problematic for older bigeye. The daily rings become too compressed to count for bigeye about four years old and older (Schaefer et al. 2006). Times at liberty for tagged bigeye can be used to estimate maximum age. The time at liberty is an under estimate of the age and needs to be adjusted by the age at release. The age at release can be estimated by converting the length at release into age at release based on the age-length relationship from the otolith data. The longest time at liberty for bigeye in the EPO is thirteen and a half years for a bigeye tuna released in 2002 at a size of 84 cm (approximately one and a half years old) for an estimated age of 15 years. The gender of this individual was unknown. The next oldest individuals were two females at twelve and a half years old, unknown gender individuals at 10 and ten and a half years old, and a male at 9 years old. The two oldest sexed individuals are female and the next five are males. Unfortunately, there are very few long term recovered sexed individuals, so the information is not very informative, but it does not support female natural mortality being higher than male. The annual natural mortality estimates using the rule of thumb (M = 3/amax) for all (amax = 15), females (amax = 12.5), and males (amax = 9) is 0.2, 0.24, and 0.33, respectively. The EPO bigeye tuna stock has been heavily exploited since the mid 1990s. Therefore, these estimates of mortality from maximum age probably also represent some fishing mortality and not just *M*. Other estimators based on maximum age could also be used, but given the confounding between natural mortality and fishing mortality they are all unreliable.

Ecological theory suggests that there should be a relationship between *M* and other life history characteristics and many theoretical or empirical relationships have been developed between *M* and life history parameters (e.g. von Bertalanffy growth rate parameter (K), and the age at maturity (amat), the gonad index). However, the predictions are generally imprecise and there is uncertainty in the life history parameters used as explanatory variables in the regressions. EPO bigeye tuna growth does not follow the von Bertalanffy curve (Aires da Silva et al. 2015; Maunder et al. 2018) and it is not clear how applicable the life-history methods are to estimates from von Bertalanffy parameters when this model is incorrect or if parameters are taken from other models (e.g. the Richards growth curve). We do not provide natural mortality estimates based on these relationships because they are unreliable.

Maunder et al. (2010) applied a cohort analysis to conventional and archival tag data to estimate age-specific natural mortality for bigeye tuna in the eastern Pacific Ocean (Figure 6). The cohort analysis approach is not biased by nonmixing of tagged fish with the untagged fish as long as the total number of recaptures are known and most tagged fish are dead by the end of the recovery collection period. The model was fit simultaneously to tagging data, estimates of natural mortality from Hampton (2000), and sex ratio data. The estimates were highly uncertain and dependent on the reporting rate of archival tags by the longline fleet.

Schaefer (1996; 2001) found that the energetic costs of spawning were higher for female yellowfin (0.7% of body weight/day) compared to male yellowfin (0.3% of body weight/day) suggesting that reproduction might cause *M* to be higher for females. This is expected to be the same for bigeye tuna. However, pre-spawning courtship of yellowfin involves both females and males and can last for several hours presumably at a high energetic cost (Margulies at al. 2007). Sex ratio data for bigeye in the EPO favors male's at large sizes suggesting that female *M* is higher than male *M*. Information on male maturity is not available.

The current EPO bigeye tuna assessment model assumes that *M* is age and sex-specific (see above). It assumes that female *M* increases after they mature, while male *M* does not. An alternative may be that male *M* also increases, but at a lower rate than females (Harley and Maunder 2003), as estimated by Maunder et al. (2010) for bigeye tuna and as indicated by the high energetic cost of extensive pre-spawning courtship (Margulies et al. 2007). The change in female *M* was assumed to occur at 3.5 years in EPO bigeye because that is when the sex ratio changes (Harley and Maunder 2003). The reason for the lag is unknown. Hoyle et al. (2009) showed how uncertainty in the growth curve that is used to calculate maturity and sex-ratio at age and differences in sex-ratio at age can influence the estimated age-specific *M* for yellowfin in the western Pacific Ocean. Fonteneau and Pallares (2005) suggest that schooling behavioral changes in tuna that occur as tuna age (e.g. disassociation with floating objects) might also influence natural mortality. Fonteneau and Pallares (2005) suggest that a time trend in *M* may have occurred due to the depletion of large predators by industrial fisheries.

The main tuna species skipjack, yellowfin, bigeye, albacore, and bluefin have very different life histories (e.g. age and size at maturity) and therefore it is not expected that they will have the same natural mortality rates. Analysis of tagging data for skipjack, yellowfin, and bigeye tuna from the same tagging study in the western Pacific Ocean (Hampton 2000) provides similar estimates of natural mortality, particularly for small and moderate sized yellowfin and bigeye (Figure 4). Fonteneau and Pallares (2005) argue that because small skipjack, yellowfin, and bigeye mix in the same schools, live in the same habitat, show similar behavior, eat the same prey, and are vulnerable to the same predators, they should have similar levels of natural mortality, which is consistent with studies that find *M* is a function of size (e.g. McGurk, 1987; Lorenzen, 1996). The biggest difference in the estimates of *M* for yellowfin and bigeye in the western Pacific Ocean occurs when *M* increases at older ages (Figure 4) and may be related to the differences in the age and size at maturity. The growth rates of EPO yellowfin and bigeye are similar for sizes that can be aged and do not appear to decrease when the individuals mature. Therefore, energy used for spawning does not appear to be taken from energy used for growth. The length composition data for yellowfin tuna is similar for all four floating object fisheries and they appear to leave the floating objects by about 75 cm (Figure 4). In contrast, the length composition data for bigeye tuna differs among the four floating object fisheries with larger bigeye caught at floating objects in the coastal and central fisheries. The difference in the sizes of bigeye and yellowfin caught at floating objects may be related to ontogenetic behavior changes that could influence natural mortality (Fonteneau and Pallares 2005) and could be related to the differences in age at maturity. The natural mortality assumed for small bigeye and yellowfin used in the EPO assessments are very different (age zero *M* is arbitrarily pre-specified at 0.25 and 0.7 q^{-1} for bigeye and yellowfin, respectively). Although, the comparisons should be made for tuna vulnerable to the fisheries and not for younger ages. The relationship with age or the difference among genders for other species of tuna may be more appropriate to use compared to the absolute levels of natural mortality. Due to differences in energy expenditure, tropical tunas (skipjack, yellowfin, and bigeye) which spawn continuously may have different patterns of natural mortality than temperate tunas (albacore and bluefin) that spawn seasonally and make large transoceanic migrations.

5. Influence of natural mortality on management quantities

Many studies (e.g. Watters and Maunder 2001; Harley and Maunder 2003; Harley and Maunder 2005; SARM-9-INF-B1) have shown that that different levels of natural mortality have a large influence on the estimates of absolute population size and on the population size relative to that corresponding to the maximum sustainable yield. The management quantities generally show little sensitivity when higher levels of *M* were assumed for young fish 0-5 quarters of age, probably because natural mortality of young individuals is confounded with recruitment.

6. Discussion

The results of this review suggest that there is no definitive information to update the estimates of natural mortality currently used in the assessment. The difference in M between mature females and males should be based on the sex ratio data, but more information on gender specific growth rates is vital to interpret gender specific M. Fitting the sex-ratio data in the stock assessment model and estimating natural Mortality should also be considered once some of the current issues with the assessment have been resolved.

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TABLE 1. Estimates of management-related quantities for bigeye tuna for the base case and the sensitivity analysis to higher values of juvenile natural mortality (M0; see Figure 7). The sensitivity analyses were conducted assuming one of two values of M0 (0.25 and 0.50 quarter-1), and a linear decreasing trend of *M* between age-0 and one of three possible young ages (5, 10 and 13 quarters) (see Figure E.1 to compare *M* schedules). The sensitivity analyses were done for both data-weighting configurations of the size-composition data (λ = 0.05 for all fisheries, as in the base case, and with the original sample sizes for all fisheries, λ = 1). See Aires da Silva et al. (2018) for details.

λ = 0.05, all fisheries—todas pesquerías	**M_0 = 0.25**	**M_0 = 0.5**	**M_0 = 0.25**	**M_0 = 0.5**	**M_0 = 0.25**	**M_0 = 0.5**
Age (quarters) Edad (trimestres)	**5**	**5**	**10**	**10**	**13**	**13**
MSY-RMS	107,864	107,692	108,830	111,450	112,312	126,262
B_{MSY}- B_{RMS}	389,211	374,742	326,723	281,092	305,120	211,981
S_{MSY}- S_{RMS}	95,101	90,427	71,794	52,902	60,632	16,596
B_{MSY}/B_0- B_{RMS}/B_0	0.26	0.26	0.26	0.26	0.25	0.22
S_{MSY}/S_0- S_{RMS}/S_0	0.21	0.21	0.19	0.16	0.17	0.064
C_{recent}/MSY- C_{recent}/RMS	0.97	0.97	0.96	0.94	0.93	0.83
B_{recent}/B_{MSY}- B_{recent}/B_{RMS}	1.00	0.99	0.97	1.00	1.06	1.55
S_{recent}/S_{MSY}-S_{recent}/S_{RMS}	0.96	0.95	0.9	0.91	1.01	2.22
F multiplier-Multiplicador de *F*	1.05	1.04	1.01	1.03	1.11	1.77
λ = 1, all fisheries—todas pesquerías	**M_0 = 0.25**	**M_0 = 0.5**	**M_0 = 0.25**	**M_0 = 0.5**	**M_0 = 0.25**	**M_0 = 0.5**
Age (quarters) Edad (trimestres)	**5**	**5**	**10**	**10**	**13**	**13**
MSY-RMS	95,544	102,822	105,136	109,484	107,477	126,703
B_{MSY}- B_{RMS}	340,276	345,811	319,633	286,226	301,285	225,595
S_{MSY}- S_{RMS}	82,911	82,195	70,235	54,692	60,012	19,854
B_{MSY}/B_0- B_{RMS}/B_0	0.29	0.3	0.29	0.28	0.28	0.23
S_{MSY}/S_0- S_{RMS}/S_0	0.23	0.23	0.21	0.18	0.19	0.076
C_{recent}/MSY- C_{recent}/RMS	1.09	1.01	0.99	0.95	0.97	0.82
B_{recent}/B_{MSY}- B_{recent}/B_{RMS}	0.59	0.66	0.81	1.03	0.94	1.88
S_{recent}/S_{MSY}-S_{recent}/S_{RMS}	0.41	0.42	0.51	0.66	0.6	1.93
F multiplier-Multiplicador de *F*	0.57	0.59	0.68	0.84	0.78	1.7

TABLE 2. TABLE F.1. Estimates of management-related quantities for bigeye tuna for the base case and adult natural mortality (*M*) sensitivity analysis (see Figure 8). See Aires da Silva et al. (2018) for details.

λ = 0.05, all fisheries—todas pesquerías	***Mad*-sens1**	***Mad*-sens2**	**Base case Caso base**	***Mad*-sens3**	***Mad*-sens4**	***Mad*-sens5**	***Mad*-sens6**	***Mad*-sens7**
MSY-RMS	123,379	105,537	107,864	114,673	121,037	126,395	130,515	134,010
B_{MSY}- B_{RMS}	565,617	425,993	389,211	406,529	416,454	421,992	424,606	426,046
S_{MSY}- S_{RMS}	169,233	115,829	95,101	97,768	97,168	96,336	94,607	92,750
B_{MSY}/B_0- B_{RMS}/B_0	0.28	0.27	0.26	0.26	0.26	0.26	0.26	0.27
S_{MSY}/S_0- S_{RMS}/S_0	0.27	0.23	0.21	0.21	0.2	0.2	0.2	0.2
C_{recent}/MSY- C_{recent}/RMS	0.84	0.99	0.97	0.91	0.86	0.82	0.8	0.78
B_{recent}/B_{MSY}- B_{recent}/B_{RMS}	0.31	0.58	1.00	1.21	1.35	1.44	1.5	1.55
S_{recent}/S_{MSY}-S_{recent}/S_{RMS}	0.2	0.47	0.96	1.22	1.39	1.5	1.58	1.63
F multiplier-Multiplicador de *F*	0.4	0.64	1.05	1.29	1.48	1.62	1.72	1.81
λ = 1, all fisheries—todas pesquerías	***Mad*-sens1**	***Mad*-sens2**	**λ = 1**	***Mad*-sens3**	***Mad*-sens4**	***Mad*-sens5**	***Mad*-sens6**	***Mad*-sens7**
MSY-RMS	133,834	111,103	95,544	100,851	102,766	108,296	115,942	122,755
B_{MSY}- B_{RMS}	663,082	454,769	340,276	338,034	337,600	350,831	371,995	388,208
S_{MSY}- S_{RMS}	205,439	126,585	82,911	78,926	76,612	78,414	81,777	83,760
B_{MSY}/B_0- B_{RMS}/B_0	0.3	0.3	0.29	0.29	0.29	0.28	0.28	0.28
S_{MSY}/S_0- S_{RMS}/S_0	0.3	0.26	0.23	0.22	0.22	0.21	0.21	0.21
C_{recent}/MSY- C_{recent}/RMS	0.78	0.94	1.09	1.03	1.01	0.96	0.9	0.85
B_{recent}/B_{MSY}- B_{recent}/B_{RMS}	0.21	0.39	0.59	0.83	1.03	1.24	1.43	1.56
S_{recent}/S_{MSY}-S_{recent}/S_{RMS}	0.11	0.22	0.41	0.59	0.8	1.02	1.22	1.36
F multiplier-Multiplicador de *F*	0.27	0.4	0.57	0.73	0.91	1.12	1.34	1.52

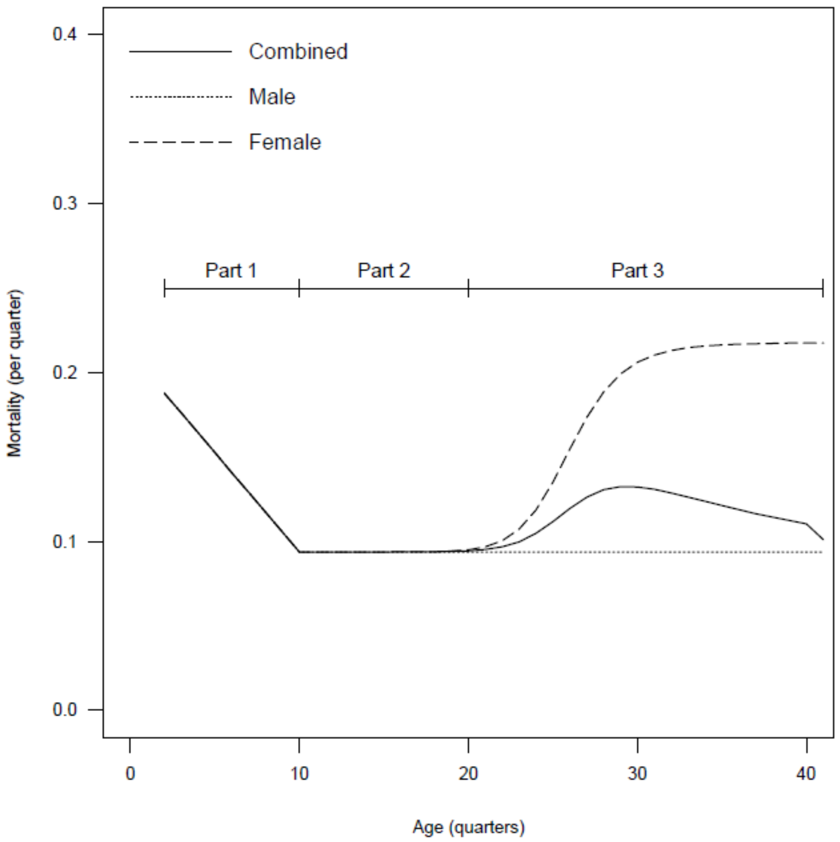

FIGURE 1. Schematic showing how male, female, and combined natural mortality varies in our three-part model (from Harley and Maunder 2003).

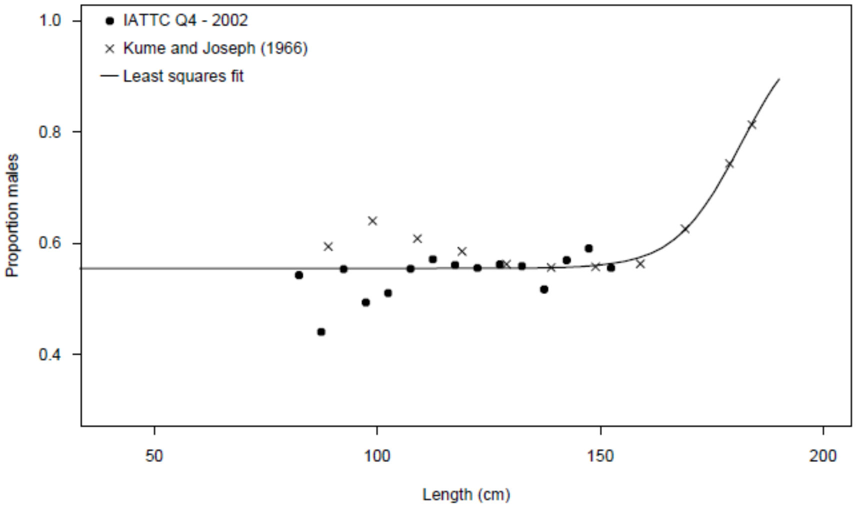

FIGURE 2. Data for the two studies, with the fit of a logistic curve, from Harley and Maunder (2003).

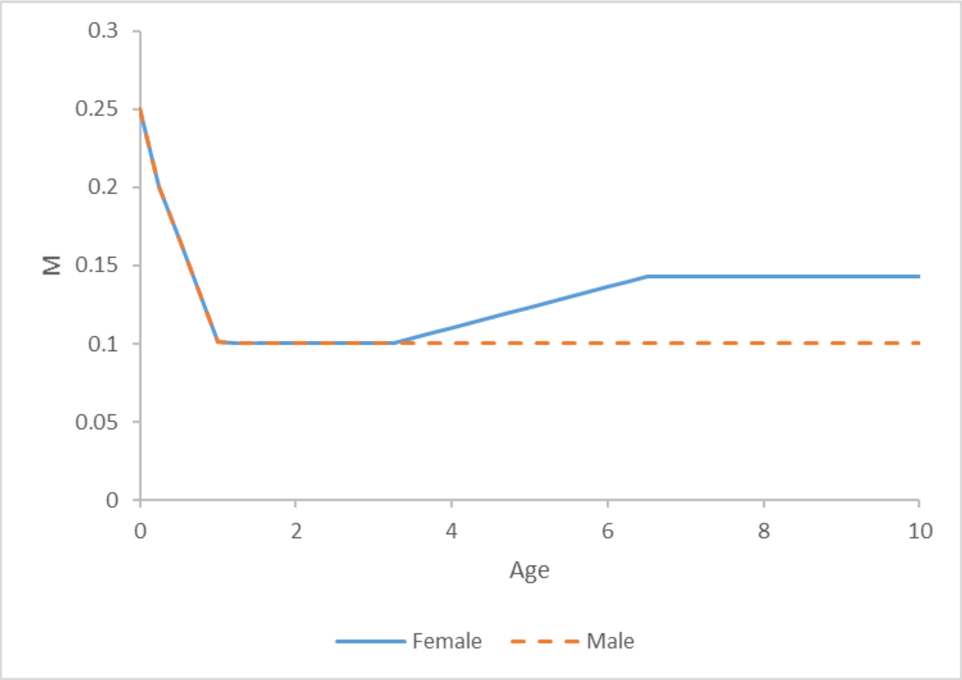

FIGURE 3. Natural mortality used in the EPO bigeye tuna stock assessment.

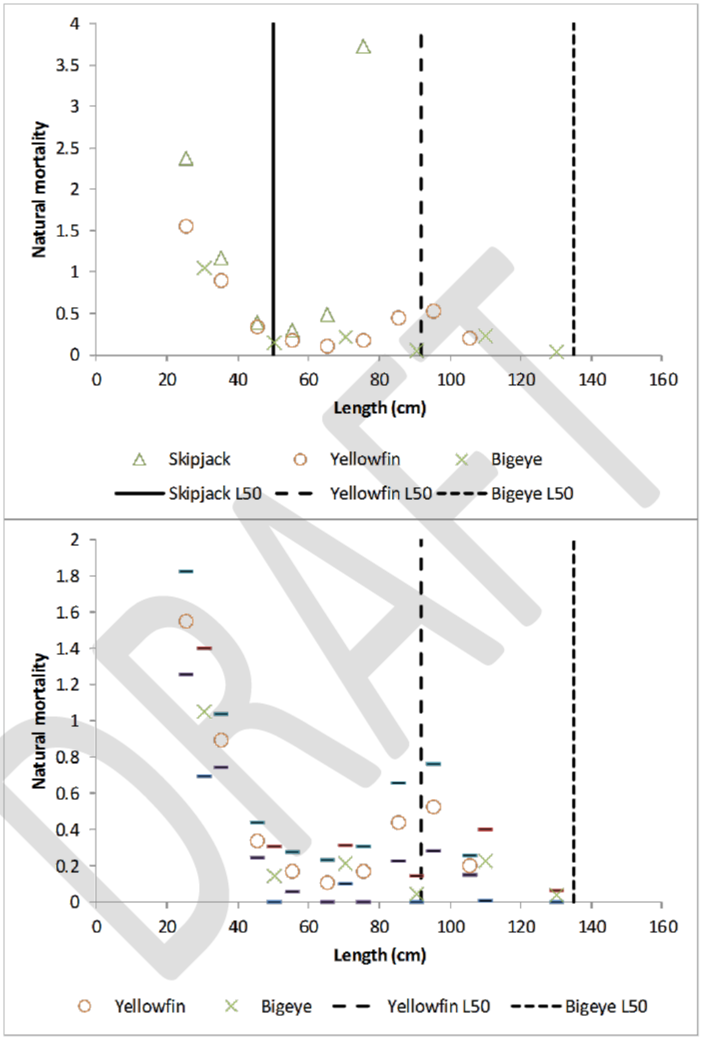

FIGURE 4. Estimates of natural mortality (q-1) from tagging data for skipjack, yellowfin and bigeye tuna in the western Pacific Ocean (Hampton 2000). The vertical lines are the lengths at 50% maturity. The lower panel shows yellowfin and bigeye tuna on a more restricted scale with 95% Confidence intervals. From Maunder et al. 2012.

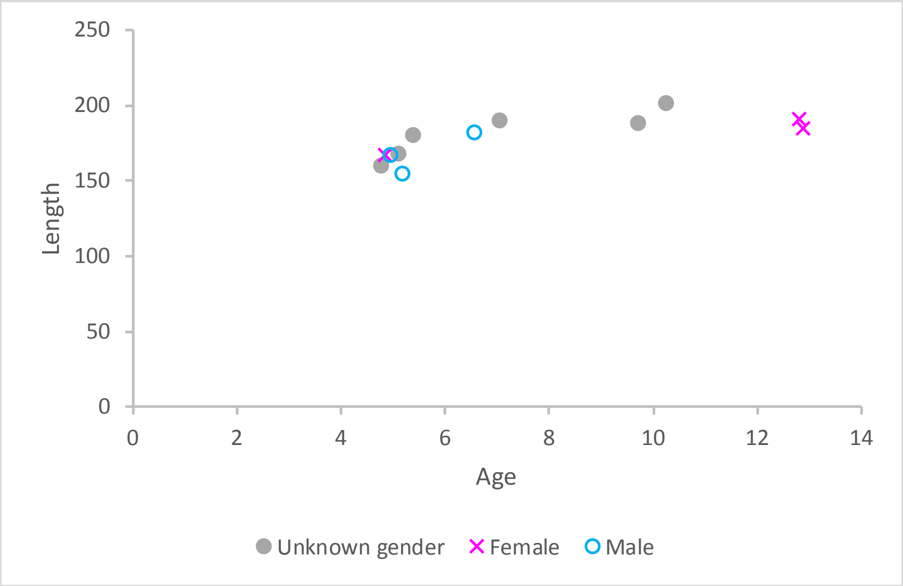

FIGURE 5. Length at age by gender for the long time at liberty tag recoveries.

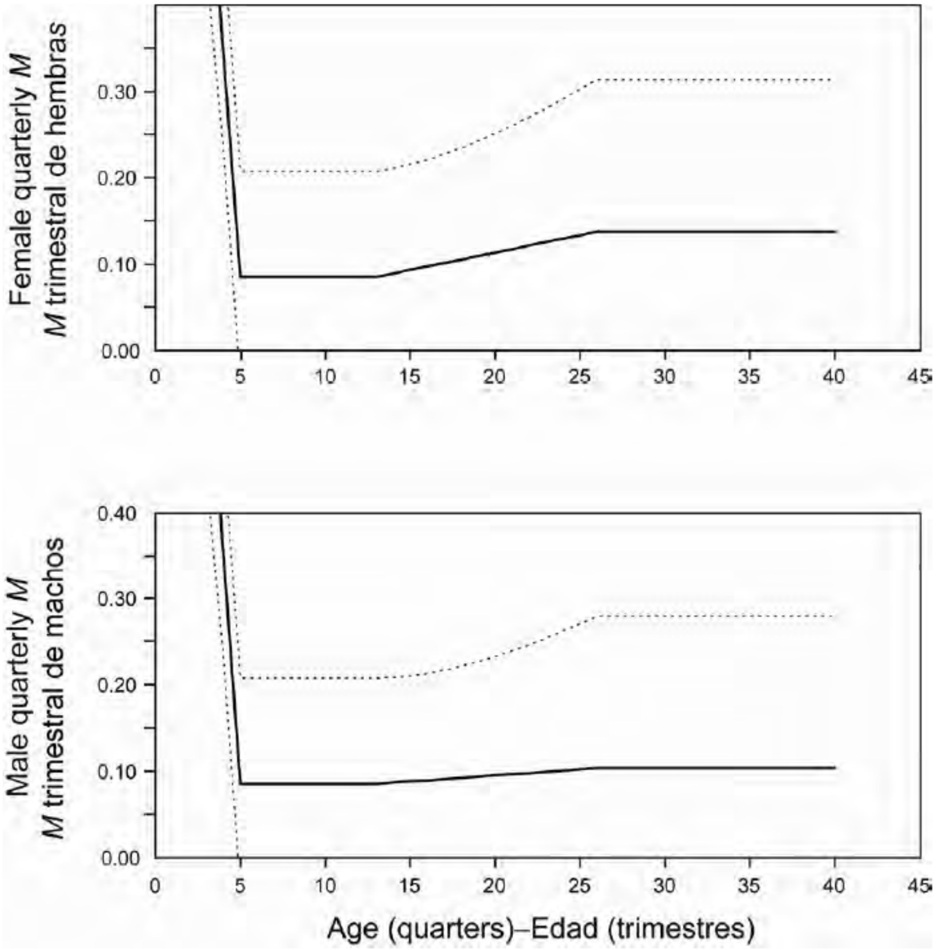

FIGURE 6. Estimates of age-specific natural mortality by gender using tagging data from Maunder et al. (2010).

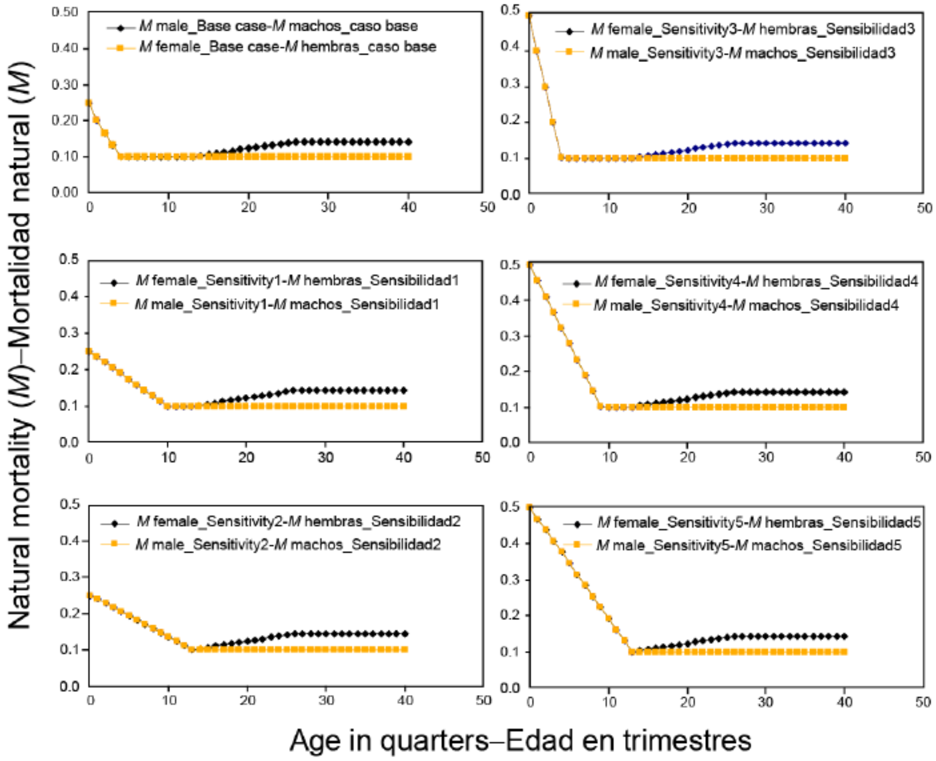

FIGURE 7. Natural mortality (*M*) curves for female and male bigeye tuna investigated in the analyses of sensitivity to higher rates of juvenile natural mortality. From Aires da Silva et al. (2018).

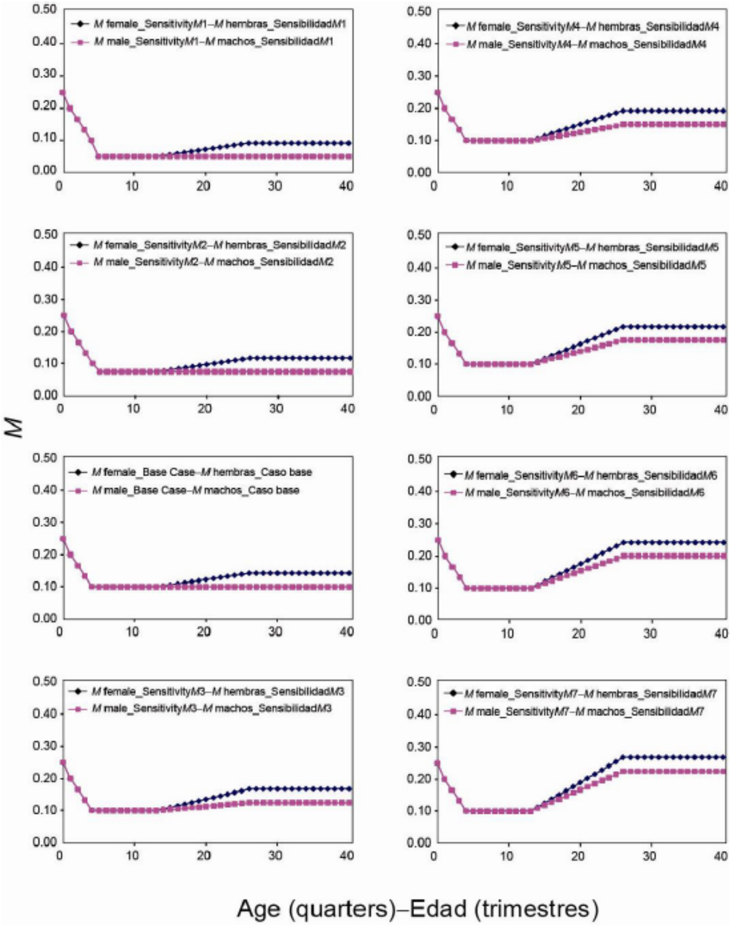

FIGURE 8. Natural mortality (*M*) schedules for female and male bigeye investigated in the sensitivity analysis to lower and higher *M* values for adults. From Aires da Silva et al. (2018).