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A REVIEW AND EVALUATION OF NATURAL MORTALITY FOR THE ASSESSMENT AND MANAGEMENT OF YELLOWFIN TUNA IN THE EASTERN PACIFIC OCEAN

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1. ABSTRACT

Natural mortality (M) is one of the most influential quantities in fisheries stock assessment and the calculation of management advice. Direct estimates from data (e.g. tagging and age-composition) are seldom available and estimates based on relationships with life history parameters such as maximum observed age are unreliable. In addition, the common assumptions that M is constant over age, gender, and time are likely to be violated. We provide a comprehensive review of information about M for yellowfin tuna in the eastern Pacific Ocean (EPO) and evaluate the influence of M on management advice. There is inadequate information in the stock assessment model to estimate the appropriate age and sex specific M for yellowfin tuna in the EPO and the fishing mortality rate reference point (FMSY) used for managing yellowfin in the EPO is highly sensitive to the assumed M. Simulation analysis suggests that it may be possible to estimate some components of M inside the stock assessment model given the current data if M for the youngest ages and the ratio of M between mature females and males are pre-specified. However, the simulation analysis indicates that there may be moderate bias in the estimates of M. A well-designed tagging study with gender identified at recovery and the collection of gender-specific age-composition data should provide the best information to estimate M for yellowfin tuna in the EPO.

2. INTRODUCTION

Natural mortality (M) is one of the most influential quantities in fisheries stock assessment and the calculation of management advice. M relates directly to the productivity of the stock, the yields that can be sustained, and management reference points. Unfortunately, M is highly uncertain for most fish populations. In general, the value of M used in a stock assessment is not based on data from the stock being assessed (e.g. derived from tagging data or catch curves) and it is inferred from similar species, relationships with life history parameters (e.g. Pauly 1980; Jensen 1996; Gunderson 1997), or maximum observed age (e.g. Hoenig 1983). In many cases the value of M was determined historically and its basis is not clear. In addition, M is commonly assumed to be constant over age, time, and gender, an assumption that is likely to be violated (Vetter 1988). It is therefore important to thoroughly evaluate the available information and the current assumptions about M used in all fish stock assessments (e.g. Maunder and Wong 2011).

Here we provide a comprehensive evaluation of M for yellowfin tuna in the eastern Pacific Ocean (EPO). First, we describe how M in the EPO yellowfin tuna assessments has been treated historically. Next, we describe and discuss the available approaches to estimate M and apply them to EPO yellowfin tuna. We then use simulation analysis to test how well M can be estimated inside the stock assessment model. Finally, we evaluate the management consequences of different assumptions about M.

3. HISTORY

In early age structured assessments (cohort analysis) of yellowfin tuna in the EPO, M was assumed to increase for females after they reach the age of 30 months (7-8 quarters) while the male M stayed at the base value of 0.8 y-1 (Anonymous 1999) or equivalently 0.2 q-1 since M is currently reported as a quarterly rate because many yellowfin tuna assessments are conducted on a quarterly time step. Similar assumptions are made in the current statistical age-structured assessments (Aires-da-Silva and Maunder 2012). This assumption is based on the ratio of male to female yellowfin in the catch favoring males as the size of the fish in the catch increases (Orange 1961; Everett and Punsly 1990; Schaefer 1998). This trend can be interpreted in at least three ways (Everett and Punsly1990): 1) large females are less vulnerable to fishing than large males (perhaps because large females do not occur in the main fishing areas or are segregated from males vertically in the water column); 2) females grow more slowly than males; 3) large females die at a more rapid rate than do large males (perhaps because the physiological costs of reproduction are higher for females). The first hypothesis is unlikely because sex ratio changes with age occur in both the longline and purse-seine fisheries (Everett and Punsley 1990). There is a lack of Information on the size at age of large yellowfin, so evaluating (2) is difficult. Despite Wild (1986) reporting gender differences in growth rates (Wild's figure 4 indicates that females may be smaller than males after around age 3), there is no evidence of the accumulation of females (i.e. sex ratio favoring females) at intermediate sizes as would be expected if females grow slower. It should be noted that the energetic cost of reproduction could reduce both growth and survival simultaneously. The third interpretation has been used to support the age specific M used in the stock assessment of yellowfin tuna in the EPO.

A detailed description of the estimation of the natural mortality schedule currently used in the EPO yellowfin tuna assessment is provided in Appendix 1. In early assessments using the A-SCALA stock assessment model (Maunder and Watters 2003) males and females were not treated separately, and M was treated as a rate for males and females combined. M at age was composed of three phases (Figure 1): 1) M is assumed to be high for young yellowfin because both sexes are small and vulnerable to predation by other fishes. As the fish grow they become less vulnerable to predation and M declines; 2) After the onset of sexual maturity, the combined M increases with age. Mature males were assumed to have a constant M of 0.2 q-1, while female M increases; 3) The combined M decreases because the high M for females removes females from the population at a faster rate so the combined M is composed of more males, which have a lower M. The combined M eventually becomes equal to the M assumed for males when all the females have died. These three phases are supported by tagging data for yellowfin in the western and central Pacific (Hampton 2000) and estimates of M for yellowfin in the western and central Pacific from stock assessment models (Hampton and Fournier 2001). The M-at-age was calculated by making the assumptions described above, fitting to sex ratio data (Schaefer 1998), and comparing the values with those estimated for yellowfin in the western and central Pacific Ocean (Hampton 2000; Hampton and Fournier 2001) (See Appendix 1 and Harley and Maunder 2003). The increase in M is assumed to occur 1.5 years (6 quarters) after they mature based on the length at which the proportion females declines (Harley and Maunder 2003). The combined sex M was calculated as the average of male and female M weighted by the number of males and females at age. This method assumes that fishing mortality at age is the same for males and females.

Current assessments (e.g. Aires-da-Silva and Maunder 2012) using Stock Synthesis (Methot and Wetzel in press) explicitly model males and females and therefore can treat M for males and females separately. The sex-specific Ms follow the same assumptions as used in the A-SCALA assessments, but without the need to derive a combined sex M.

4. REVIEW OF APPROACHES TO ESTIMATE M

Maximum age

The lower the mortality rate, the longer individuals live. Therefore, it is logical that the maximum age (amax) observed in the population provides an indication of the morality rate. A simple rule of thumb (M=3/amax) has commonly been used to estimate M from the maximum age (Quinn and Deriso 1999). However, this method has been criticized for a number of reasons (Maunder and Wong 2011). First, it is an estimate of total mortality and can only estimate M if the samples come from an unexploited population or if the fishing mortality is known. The maximum age is dependent on the sample size, and this is not taken into consideration in the rule of thumb. The theory for calculating M using amax assumes a single value of M for all ages, which may not hold, and it is not clear how age-specific M would bias estimates. Based on the empirical relationship of Hoenig (1983), Hewitt and Hoenig (2005) suggest using 4.22/amax. However, Hoenig’s (1983) relationship has large prediction error (Maunder and Wong 2011).

Maximum age is difficult to determine for yellowfin tuna since aging techniques, which are based on counting daily rings in otoliths, are problematic for older yellowfin. The daily rings become too compressed to count for yellowfin about five years old and older (Wild 1986). Times at liberty for tagged yellowfin 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 otolith data. The longest time at liberty for YFT in the EPO is 8 years for a yellowfin tuna released in 2003 at a size of 51 cm (approximately age 1) for an estimated age of 9 years. The next longest time at liberty is 6 years for a yellowfin tuna released in 1981, but the size at release is unknown. Followed by 3 yellowfin at liberty for 5 years released at lengths 133 cm (approximately age 3) and 101 cm (approximately age 2), and one of unknown length at release for estimated ages of 8 and 7 years. Hampton (1992) reported the maximum age yellowfin tuna from tagging data in the western Pacific Ocean as 7.5 years. The EPO yellowfin tuna stock has been exploited for over 50 years and exploitation rates during the time that these yellowfin were at liberty were substantial. Therefore, these estimates of mortality from amax represent the total mortality and not just M. The gender of these tagged fish was not recorded, so gender specific amax cannot be determined.

Life history

Ecological theory suggests that there should be a relationship between M and other life history characteristics. Jensen (1996) used the Beverton-Holt life history invariants to determine relationships between M and the von Bertalanffy growth rate parameter (K) and the age at maturity (amat). Relationships have also been derived from empirical data (Beverton 1963; Charnov and Berrigan 1990; Jensen 1996). Pauly (1980) regressed M on the von Bertalanffy growth rate, asymptotic size (either in weight (Winf) or length (Linf)), and water temperature. Gunderson (1997) regressed M on the gonad index. However, the predictions are generally imprecise (Pascual and Iribarne, 1993) and there is uncertainty in the life history parameters used as explanatory variables in the regressions (e.g. Chang and Maunder 2012).

EPO yellowfin tuna growth does not follow the von Bertalanffy curve (Aires da Silva et al. this workshop). There appears to be linear growth for individuals up to about age 4 and then growth slows rapidly. 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). In addition, the estimates of the asymptotic length are poorly defined due to the inability to age large yellowfin from otoliths and the lack of large yellowfin in the tagging data.

Tagging studies

Well-designed tagging studies are probably the most promising method to estimate M (Vetter 1988; Hampton 1992; Fonteneau and Pallares 2005). There are variety of methods that can be used to estimate M from tagging data, but tag-attrition and related methods are probably the most appropriate (e.g. Kleiber et al. 1987; Hampton 2000). In general, the model needs to incorporate catch or effort to separate M from F (Hampton 1992). The tagging analysis also needs to account for tag shedding, tagging mortality, non-reporting, and emigration (Hampton 1992). Hampton (2000) applied tag-attrition analysis to estimate natural mortality by size groups for yellowfin, bigeye and skipjack tuna in the western Pacific Ocean. 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. 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. Nonmixing may be a substantial issue for tropical tunas like skipjack, yellowfin, and bigeye based on restricted movement indicated by archival tagging (Schaefer et al. 2011). 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. The analysis did not use the additional location information available from archival tag data. Whitlock et al. (2012) estimated age-specific M for Pacific bluefin tuna using archival tags taking advantage of the additional location information between release and recapture to model movement among areas. However, the tagging study was not designed to estimate natural mortality and the lack of tag releases in the western Pacific Ocean may have biased results. Integrating the tagging data into the stock assessment model is preferable because tag growth-increment data should help resolve age-composition estimates, return rates will improve estimates of total mortality; catch (or effort) data will allow the separation of mortality into M and F, and the inclusion of indices of abundance to resolve time-series trends in abundance (Hampton 1992; see below).

Bayliff (1971) provided crude estimate of M for EPO yellowfin tuna from tagging data (Table 1). Recently collected tagging data for yellowfin in the EPO is limited and has not yet been used for estimating natural mortality.

Estimating M inside the stock assessment model

M can also be estimated within the stock assessment model (Lee et al. 2011). Modern integrated stock assessment models use all the available data in as raw a form as appropriate and therefore can extract all the information about M while keeping assumptions consistent (Maunder and Punt in press). Hence, estimates of M from an integrated stock assessment model should generally be superior to estimates using only a single source of data (e.g. catch curve analysis) that make many assumptions that may be violated. Using simulation analysis, Lee et al. (2011) showed that M could be estimated reliable for some stocks. In some cases the estimates included M that varied with age or sex. However, Francis (2012) question their results because Lee et al. (2011) analyzed simulated data under ideal conditions (e.g. the structure of the model was known). Bias and variance in estimates of M from actual data is expected to be higher than that found by Lee et al. (2011). Estimation of M within the stock assessment model should be improved with the inclusion of tagging data (e.g. Maunder 1998; Hampton and Fournier 2001).

The assessment of yellowfin tuna in the EPO and of other tropical tunas is particularly problematic due to the inability to age large individuals and the limited amount of age-length data. Mean length-at-age and the variation of length-at-age are used (internally in the stock assessment model) to convert length-composition data into age-composition data. Therefore, estimates of M from the stock assessment model will be sensitive to the assumptions about growth.

The Stock Synthesis program used to assess EPO yellowfin tuna has the capability of including tag-recaprure data (converted to age outside the model) in the assessment (Methot and Wetzel in press), but not tag growth increment data. However, the limited tagging data available for the timeframe of the stock assessment (1975-2011) has yet to be integrated into the assessment.

Age, sex, and time specific M

Several studies have derived empirical relationships of declining M with age or size (e.g. McGurk, 1987; Lorenzen, 1996) and Lorenzen (2000) suggests that M is inversely proportional to length. M is higher for young individuals due to predation and physiological factors (Lorenzen, 1996). M may also increase for older individuals due to the costs of reproduction or other senescent factors (Siler, 1979, Fonteneau and Pallares 2005). In general, changes in M for ages younger than observed in the data do not have to be modeled because they only scale the estimated average recruitment. Vetter (1988) suggests that the impact of age-structured M is difficult to predict, but in general the overall magnitude of M is probably more important than the age-specific variability.

Many studies have shown differences in M between males and females (e.g. flatfish, Maunder and Wong 2012). Often, the differences in M are apparent in amax observed for each gender or the sex ratios with age. Species with gender differences in M often also show gender differences in other biological characteristics (e.g. size at age, age at maturity). For example, M is related to age at maturity (Jensen 1996) and gender differences in age at maturity may explain differences in M.

Use of predation in multi-species and ecosystem models has been advocated as a way to estimate natural mortality. This is particularly relevant to the young smaller individuals and may cause M to vary over time. Hampton (1992) suggests that this has low potential for yellowfin tuna due to the lack of reliable information on the abundance of predators of yellowfin tuna and that yellowfin vulnerable to the fisheries are of a size that is less vulnerable to predation. Fonteneau and Pallares (2005) suggest that a time trend in M may have occurred due to the depletion of large predators by industrial fisheries. Predation may be more relevant for looking at temporal variation in recruitment to the fishery.

Natural mortality for yellowfin and other tuna has been estimated to vary with size (e.g. Hampton 2000) and age (Whitlock et al. 2012). Due to limited aging and gender information for yellowfin in the EPO, amax is not available for each gender. 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. However, pre-spawning courtship 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 yellowfin in the EPO favors males at large sizes (Schaefer 1998) suggesting that female M is higher than male M. In contrast, males mature at shorter lengths (L50% = 69.0 cm, age = 1.3) than do females (L50% = 92.1 cm, age = 2.0) (Schaefer 1998) suggesting that males have a higher natural mortality than females based on life history theory (Jensen 1996).

The current EPO yellowfin 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 1.5 years (6 quarters) in EPO yellowfin because that is when the sex ratio changes (Harley and Maunder 2003). The same 1.5 year lag was also estimated for EPO bigeye tuna (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.

Reviews of M for other stocks and species

There is very little direct information on M for tunas with tagging data probably providing the best information. Hampton (2000) applied tag-attrition analysis to estimate natural mortality by size groups for yellowfin, bigeye and skipjack tuna in the western Pacific Ocean. Maunder et al. (2010) applied a cohort analysis to conventional and archival tag data to estimate age- and sex-specific natural mortality for bigeye tuna in the eastern Pacific Ocean. The analysis did not use the additional location information available from archival tag data and the estimates of M were highly imprecise. Whitlock et al. (2012) estimated age-specific M for Pacific bluefin tuna using archival tags taking advantage of the additional location information between release and recapture to model movement among areas. However, the tagging study was not designed to estimate natural mortality and lack of tag releases in the western Pacific Ocean may have biased results. These and other studies may provide information that can be used to infer M EPO yellowfin tuna. Meta-analysis has been applied to other population dynamics parameters (e.g. steepness of the stock-recruitment relationship, Myers et al. 1999) and a similar approach, that takes the estimation uncertainty into consideration, could be used for M. Previous approaches using M have focused on correlations with other quantities.

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 2). 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 2) 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 (Figure 3). 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; Figure 5). 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.

Previous estimates of M for yellowfin tuna in the Pacific Ocean have been summarized by Cole (1980), Suzuki (1991), Wild (1991), and Hampton (1992) (see Table 1). These estimates are mainly based on catch-curve analysis, but a few more recent estimates have been based on tagging data. The catch-curve analyses were probably based on converting length-composition to age-composition and will therefore be sensitive to the assumptions about growth, particularly for older individuals (Hampton 1992).

Different assumptions about M have been made in the different oceans (Table 2, Figure 6). M for the assessment of yellowfin tuna in the Atlantic is assumed to be higher for juveniles than for adults based on tagging studies in other oceans (ICCAT 2011). M is assumed to be 0.2 q-1 for ages 0 and 1, and 0.15 q-1 for ages 2+ years. The natural mortality rate for yellowfin in the western Pacific Ocean is strongly variable with size (Hampton 2000). Tag recapture data in the western Pacific Ocean indicate that significant numbers of yellowfin reach four years of age and the longest period at liberty for yellowfin tagged at about 1 year of age, is 6 years (Langley et al. 2011a; note the difference in age (7.5) stated in Hampton (1992)). Age specific M used for the assessment of yellowfin in the western and central Pacific Ocean was calculated using the approach also applied to bigeye (Watters and Maunder 2001; Harley and Maunder 2003) and yellowfin (Maunder and Watters 2001) tunas in the EPO, and to albacore (Hoyle 2008) and bigeye (Hoyle and Nicol 2008) tunas in the WCPO (see Appendix 1). The increase and consequent decrease in the gender aggregated M with age is a consequence of the increase in M of females, associated with sexual maturity and the onset of reproduction, and is estimated by predicting the increasing proportion of males in the catch with increasing size. Details of the calculations are provided in Hoyle et al. (2009). There are no direct estimates of M for yellowfin in the Indian Ocean (Langley et al. 2011b). M used in the Indian Ocean yellowfin tuna stock assessments varies with age and the relative trend in age-specific natural mortality is based on the values used in the Pacific Ocean (western and central; eastern) yellowfin tuna stock assessments. The overall level of natural mortality was fixed at a lower level, which is more consistent with tag recoveries in the Indian Ocean (Langley et al. 2011b). Further analysis of the Indian Ocean tagging data should provide better estimates of M in the future.

Management consequences

M is one of the most influential quantities on the calculation of management advice (Clark 1999). M relates directly to the productivity of the stock, the yields that can be sustained, and management reference points. Optimal exploitation rates are particularly sensitive to M (Maunder 2012). Higher M generally implies that the biomass corresponding to MSY is a lower fraction of the unexploited biomass (Maunder 2003). When M is misspecified in a stock assessment, the magnitude of the impact depends on values estimated for the other model parameters due to interactions among parameters and the data (Tyler et al. 1985). The management impact of age-structured M is difficult to predict, but the overall magnitude of M may be more important than the age-specific variability (Vetter 1988). Harley and Maunder (2003) showed that management quantities for EPO bigeye tuna were sensitive to the assumptions about age and sex-structured natural mortality.

Natural mortality influences yield-per-recruit (YPR) and, consequently, equilibrium yield (e.g. after the stock-recruitment relationship is taken into consideration). The yield obtained from a yellowfin tuna population is dependent on the selectivity of the gears used (Maunder 2002). In general, fisheries that capture small yellowfin produce smaller optimal yields than fisheries that capture large yellowfin. Therefore, it could be argued that fisheries should use gear that catch large yellowfin. However, the relative differences in yield that can be obtained by the different gears may be highly dependent on the assumption about natural mortality for small yellowfin, which is highly uncertain (Fonteneau and Pallares 2005).

5. METHODS

Indirect methods

Natural mortality is estimated using relationships with life history parameters and maximum observed age (Table 3). We use the amax based rule of thumb, Hoenig's (1983) regression with amax, Jensen's (1996) relationships with K and amat, Pauly's (1980) regression on Linf, K, and temperature, and Gunderson's (1997) regression with the gonad index (see Table 3). The longest time at liberty for a tagged yellowfin adjusted for the age at release was used for the maximum age (9 years). The age at maturity is 1.3 and 2.0 for males and females, respectively. K and Linf are taken from both the von Bertalanffy and the Richards growth curves to determine the sensitivity to growth model assumptions (Aires da Silva this workshop). GSI has not yet to be determined for this report.

Simulation analysis

We follow the simulation analysis approach of Lee et al. (2011). The current stock assessment model (Aires da Silva and Maunder 2012), which is implemented in Stock Synthesis 3 (Methot and Wetzel in press), was used both as the simulator and the estimator. The data is the same as used by Aires da Silva and Maunder (2012b).

Stock assessment model

The Stock Synthesis (SS) software (Methot and Wetzel in press) is used to assess the status of yellowfin tuna in the EPO (Aires da Silva and Maunder 2012). SS is an integrated statistical age-structured stock assessment model (Maunder and Punt in press). The EPO yellowfin tuna application is sex structured and uses quarterly time steps to describe the population dynamics with recruitment occurring every quarter. The model is fitted to indices of relative abundance based on CPUE and to size compositions by finding a set of population dynamics and fishing parameters that maximize a penalized (for recruitment temporal deviates) likelihood, given the amount of catch taken by each fishery. Sixteen fisheries are defined on the basis of gear type (purse seine, pole and line, and longline), purse-seine set type (sets on schools associated with floating objects, unassociated schools, and dolphin-associated schools), and IATTC length-frequency sampling area or latitude. CPUE data is not used for fisheries that do not direct their effort at yellowfin or that have too much variability in the fishery. Parameters estimated include average recruitment and quarterly recruitment deviates, catchability coefficients for the five CPUE time series that are used as indices of abundance, coefficients of variation (CV) for likelihood functions for four of the CPUE indices used as indices of abundance (the CV of the southern longline fishery, which is assumed to be the most reliable index of abundance, is fixed at 0.2), selectivity curves for 11 of the 16 fisheries, and initial population size and age structure (recruitment offset, initial fishing mortality, and deviates for ages 1 to 16 quarters). Several parameters are assumed known including the mean length at age, parameters of a linear model relating the coefficient of variation of length at age to age, fecundity of females at age, selectivity curves for the discard fisheries, the steepness of the stock-recruitment relationship (steepness = 1; no relationship between stock size and recruitment). M is sex- and age-specific and different scenarios are used in the simulation analysis. Estimates of management quantities and future projections are computed based on the average of the 3 most recent years (2009-2011) fishing mortality rates by gear.

M parameterization

One option to model age-specific M in Stock Synthesis is a broken stick with a user defined number of breaks. M is constant before and after the minimum and maximum break points. A three break point model for each gender is used to mimic the age specific M use in the current EPO yellowfin tuna stock assessment (Figure 7). The match is not perfect, but the stock assessment results are similar although the likelihood is worse (Table 4).

$$M_{g,a} = \begin{cases} M_{g,1} & a \le a_1 \\ M_{g,1} + \dfrac{(a - a_1)\left(M_{g,2} - M_{g,1}\right)}{a_2 - a_1} & a_1 < a < a_2 \text{—} \\ M_{g,2} + \dfrac{(a - a_2)\left(M_{g,3} - M_{g,2}\right)}{a_3 - a_2} & a_2 \le a < a_3 \text{—} \\ M_{g,3} & \overline{a \ge a_3} \end{cases}$$

Where Mg,x is the natural mortality at the fixed age ax for gender g and the same ages are used for both genders.

The parameters of the M model can be estimated directly or estimated as multiplicative exponential offsets of other parameters in two ways: 1) the parameters of one gender can be made an exponential offset of the other gender or 2) offset of the parameter value for the previous younger age for the same gender. The ages selected for the three break points are defined to bracket the ages when yellowfin become mature (Table 5). To implement the current stock assessment assumptions it is desirable for the mortality rates for the males and females to be the same until they start maturing, the natural mortality is constant for some ages before they mature, and that the male natural mortality does not change when they mature. However, this is not possible with the current implementation in SS. Therefore, we make the male M an offset of the female M and allow the Male M to change when they mature (Table 5). The problem with this formulation is that there is no period where M is constant before they mature, but we assume that the formulation is adequate for the purposes of our investigation.

The scenarios and what parameters are estimated or pre-specific are described in Table 6.

Actual estimates

The assessment is repeated with the addition that natural mortality is estimated. The parameters estimated are the same as used in the simulation analysis with alternative parameters fixed and estimated in the different scenarios (Table 6). Likelihood values for each data component are presented to determine which components of the data are informative about M.

Management consequences

The influence of M on management quantities is evaluated by reruning the assessment with the different pre-specified M assumptions and re-estimating the other parameters of the model. This approach takes into consideration both the influence of M and the updated parameter estimates on the management quantities. The results can also be used to investigate the uncertainty in the estimates of M. We vary the age zero M, the pre-mature M, the female mature M, the male mature M, age of the pre-mature M, age of the mature M all by plus or minus 25% (see Table 7 and Figure 8 for scenarios).

To compare the results we estimate the following management quantities:

1. Maximum sustainable yield (MSY)
2. The biomass and spawning biomass corresponding to MSY (BMSY, SMSY)
3. The biomass and spawning biomass corresponding to MSY as a ratio of the unexploited spawning biomass (BMSY/B0, SMSY/S0).
4. Recent catch as a proportion of MSY (Crecent/MSY).
5. Recent biomass and spawning biomass as a proportion of SMSY (Brecent/BMSY , Srecent/SMSY)
6. The multiplier that would make the current fishing mortality (or effort) equal to the fishing mortality corresponding to MSY (Fmultiplier).

6. RESULTS

Indirect methods

The estimates of natural mortality vary widely among the indirect methods and range from 0.035 q-1 for the Jensen (1996) method based on the von Bertalanffy estimate of K to 0.3175 q-1 for the Jensen (1996) method based on male age at maturity (Table 3). The von Bertalanffy estimate of K is unrealistically low (0.09) and the Richards K (0.69) gives a much higher M (0.275 q-1). The age at maturity for females is higher than males producing a lower M, which is inconsistent with the sex ratio data. Pauly's (1980) estimate of M based on the Richards growth parameters is the most consistent with the pre-mature M and the mature male M used in the current assessment (0.2 q-1).

Simulation analysis

The simulation scenarios that estimate M at age zero (scenarios 1 and 3) perform poorly, some model runs did not converge while others had much lower estimates of M for age zero (Figure 9). The model is unable to estimate the difference in M between mature females and males (scenarios 1 and 2) except for one data set. The model appears to be able to estimate M for age 7 and for mature males and females, if M for age zero and the difference between mature female and male M are pre-specified.

Actual estimates

Convergence issues occurred for all runs that estimated M at age 0 and age 7. The exception is scenario E that estimates pre-mature M and mature M that is the same for both males and females. However, the biomass estimates for this run are unrealistically high. In general, the estimated mature M is higher than assumed in the assessment, either the male M is much higher and similar to female or both are higher (Table 4; Figure 10). The model prefers (lower negative log likelihood) natural mortality to be the same for mature males and mature females than the difference based on the sex ratios (Table 4). Most of the difference in the negative log likelihood is from the length composition data. Similar results are seen in the negative log likelihoods of the scenarios used to investigate the sensitivity of management quantities to M in which the three lowest negative log likelihood scenarios have M for mature males higher and the same as that for mature females (Table 8). The scenario with the next lowest negative log likelihood has the second break point at age 9 quarters.

Management consequences

Most of the scenarios that investigate the influence of M on management quantities investigate a 25% change in a specific M parameter or in an age of one of the breaks in the broken stick model. Therefore, a change greater than 25% in a management quantity indicates that that management quantity is hyper sensitive to the parameter. The sensitivity of management quantities to changes in M depend on the management quantity and what part of the age-specific M vector is changed (Table 8). MSY and recent catch as a ratio of MSY (these should be similar since recent catch is assumed to be known without error) are not very sensitive to changes in M except for when large increases are made in mature male M to make it equal to female M (e.g. scenarios 14 and 16). The amount that fishing mortality needs to be adjusted to reach FMSY is sensitive to M, particularly to increases in M for mature males. The SMSY/S0 reference point and current spawning biomass relative to this SMSY are moderately sensitive to M and the sensitivity is generally greater when M changes for pre-mature and mature yellowfin compared to juveniles.

7. DISCUSSION

Natural mortality (M) is one of the most influential quantities in fisheries stock assessment and the calculation of management advice. Unfortunately, it is notoriously difficult to estimate from standard fisheries data. Although, recent studies show promise (e.g. Lee et al. 2011). The standard indirect approaches based on relationships with life history parameters (e.g. Pauly 1980; Jensen 1996; Gunderson 1997) or maximum observed age (e.g. Hoenig 1983) are notoriously imprecise or biased (Maunder and Wong 2011). In addition, M is not constant over age, time, or gender (Vetter 1988). The ability to estimate M for EPO yellowfin tuna, and other tunas in general, is particularly poor given the lack of good aging data. However, tagging studies have been applied to tuna (e.g. Hampton 2000) and they represent the most promising approach to estimate M for yellowfin tuna in the EPO and tunas in other oceans (Hampton 1992; Fonteneau and Pallares 2005).

Application to yellowfin tuna in the EPO is another illustration of the inadequacy of indirect methods to estimate M. The estimates of M vary widely among the methods and estimates based on gender specific ages at maturity are in conflict with the sex ratio information. This is not surprising given the imprecision of the predictions from life-history (Pascal and Iribarne 1993) and maximum age regressions (Maunder and Wong 2012), the assumptions about sampling design for the maximum age methods (Maunder and Wong 2012), and the imprecision in estimates of some life history parameters (e.g. growth parameters (Chang and Maunder 2012). Use of these methods to estimate M for use in stock assessments and management should be seriously questioned for any species.

Given the importance of M for stock assessment estimates and management advice, it is surprising the lack of research and data collection to determine natural mortality for the major fish stocks of the world. Age composition and tagging data are probably the most informative standard data sets for estimating natural mortality. These data sets should be integrated into stock assessment models to reduce the number of assumptions made about the population and fishing processes (Hampton 1992; Maunder 1998, Hampton and Fournier 2001; Goethel et al 2011, Maunder and Punt in press). Collecting these two data types for yellowfin tuna in the EPO is problematic due to the difficulty in aging yellowfin and the wide-spread nature of the stock. Some progress has been made in recent years to tag yellowfin in the EPO and comprehensive programs have been conducted in other oceans. Tagging data has been integrated into stock assessment models of yellowfin tuna in other oceans, which have attempted to estimate natural mortality (Hampton and Fournier 2001; Langley et al. 2011b). However, aging yellowfin tuna is still problematic and these models use length composition data rather than age composition data. Integrating tag-increment data into the stock assessment model, particularly for large yellowfin, should improve the estimates of growth and therefore the estimates of natural mortality (Hampton 1992; Aires da Silva this workshop). Sex composition data and sex-specific tagging data should also be collected to enable the estimation of different natural mortality between the genders as well as sex specific growth and selectivity if appropriate. If these types of data are not collected, substantial uncertainty will remain in the assessment and management of yellowfin tuna in the EPO and in most tuna species of all oceans. Current tagging programs are impeded by uncertain and the possibility of low reporting rates of large individuals caught in the longline fisheries (Maunder et al. 2010) and this needs to be addressed in any tagging program designed to estimate M for yellowfin tuna. Other biases common to tagging programs also need to be addressed such as tag shedding, tagging mortality, non-reporting, and emigration (Hampton 1992; Fonteneau and Pallares 2005).

Fonteneau and Pallares (2005) suggest that senescence is universal and should apply to tuna species. Unfortunately, very little information is available on senescence for yellowfin tuna. In a general age and sex specific model for M, Maunder (2009) suggested ignoring senescence and assuming that by the time senescence was important few individuals would be alive and it would not influence the stock assessment. However, if age (or length) composition data is used in the stock assessment, the proportion of old individuals in the data may have a large influence on the estimates of total mortality (and thus biomass and depletion). One way to overcome the influence of these old individuals that are subject to senescence might be to ignore the catch-at-age of old individuals and only fit to individuals of an age for which the natural mortality is thought to be estimable (e.g. fit to proportions at age using a multinomial for ages 5 to 10 in the model where these proportions sum to one for both the observed (with appropriate sample size) and predicted data) and not have the standard plus groups at age 5 and 10). Alternatively, plus groups or aging error matricies could be used. Ignoring the lower ages might overcome issues with time varying selectivity. Assumptions about selectivity for the older and younger ages would have to be made such as simply extending the functional form or making them equal to the selectivity at the lowest and oldest ages in the age composition data used in the model.

The management quantity MSY and therefore recent catch as a ratio of MSY tends to be less sensitive to natural mortality compared to the evaluation of reference points (Fmultiplyer = FMSY/Fcur and Scur/FMSY) suggesting that MSY might be a more robust quantity for basing management than the current used FMSY. However, yellowfin recruitment and biomass is highly variable and catching MSY every year would not be appropriate. Future analyses should investigate the consequences on management of assuming the wrong natural mortality in the assessment model. For example, the equilibrium yield could be calculated by applying FMSY calculated from the current assumptions about M when the assumptions in the scenarios presented in Table 7 are true.

The results of this review suggest that the best approach to estimate M for EPO yellowfin tuna given the current data is within the stock assessment model while pre-specifying M at age zero and the difference in M between mature females and males. The difference in M between mature females and males should be based on the sex ratio data as already done in the current assessment. Fitting the sex-ratio data in the stock assessment model should also be considered (this has been done in past EPO yellowfin tuna assessments using Stock Synthesis). When this analysis is conducted, the estimated M increases for mature males, which is consistent with the high energetic costs of pe-spawning courtship, which lasts for hours, for both males and females (Margulies et al. 2007). However, convergence problems are a concern with the EPO yellowfin tuna assessment when estimating M and pre-specifying the pre-mature M based on the average of M (0.1625 q-1) for yellowfin and bigeye from Hampton (2000) might be prudent.

ACKNOWLEDGEMENTS

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APPENDIX 1: Estimation of natural mortality currently used in the EPO yellowfin tuna stock assessment.

The following describes the current method used to estimate M for yellowfin tuna in the EPO and is similar to the method described by Harley and Maunder (2003) that has been used to estimate M for both bigeye and yellowfin tuna in the EPO. Male M is pre-specified based on the ASCALA M for ages 1.5 and younger and set at 0.2 for older ages (by quarter). M at age zero is set to 0.7, but this is not important because no fish are caught of this age. M for females is equal to the M for males for immature females and equal to an estimated parameter (Mfmature) for mature females. Since for some ages there are both mature and immature females, the following equation is used

$$M_{f,a} = M_{m,a}(1-\varphi_a) + M_{fmature}\varphi_a$$

Where the proportion mature is (not sure where this comes from, probably Schaefer)

$$\varphi_a = (1-(1-Rm) * EXP(-RK * (l_a - Rxstar)))\text{^}(1/(1-Rm))$$

Where Rm=0.871,RK=0.056, and Rxstar=84.508.

And the length at age comes from the growth curve.

The parameter Mfmature is estimated by fitting the predicted sex ratio at age to the “observed” sex ratio at age using least squares. The predicted sex ratio is calculated as

$$\hat{\theta}_a = \frac{exp\left(-\sum_1^{a-1} M_{f,i}\right)}{exp\left(-\sum_1^{a-1} M_{f,i}\right) + exp\left(-\sum_1^{a-1} M_{m,i}\right)}$$

The “observed” sex ratio is based on a logistic model fit to the sex ratio data (Schaefer xxxx).

$$\theta_a = 1 - (d + (1/(1 + EXP(LN(19) \ * \ (l_a - a)/(a - b)))) * (1 - d))$$

Where a=152.3192524, b=189.4370147, d=0.493775113

The logistic model is used because the model is based on age, but the sex ratio data is collected by length and a continuous model is needed to convert from length to age.

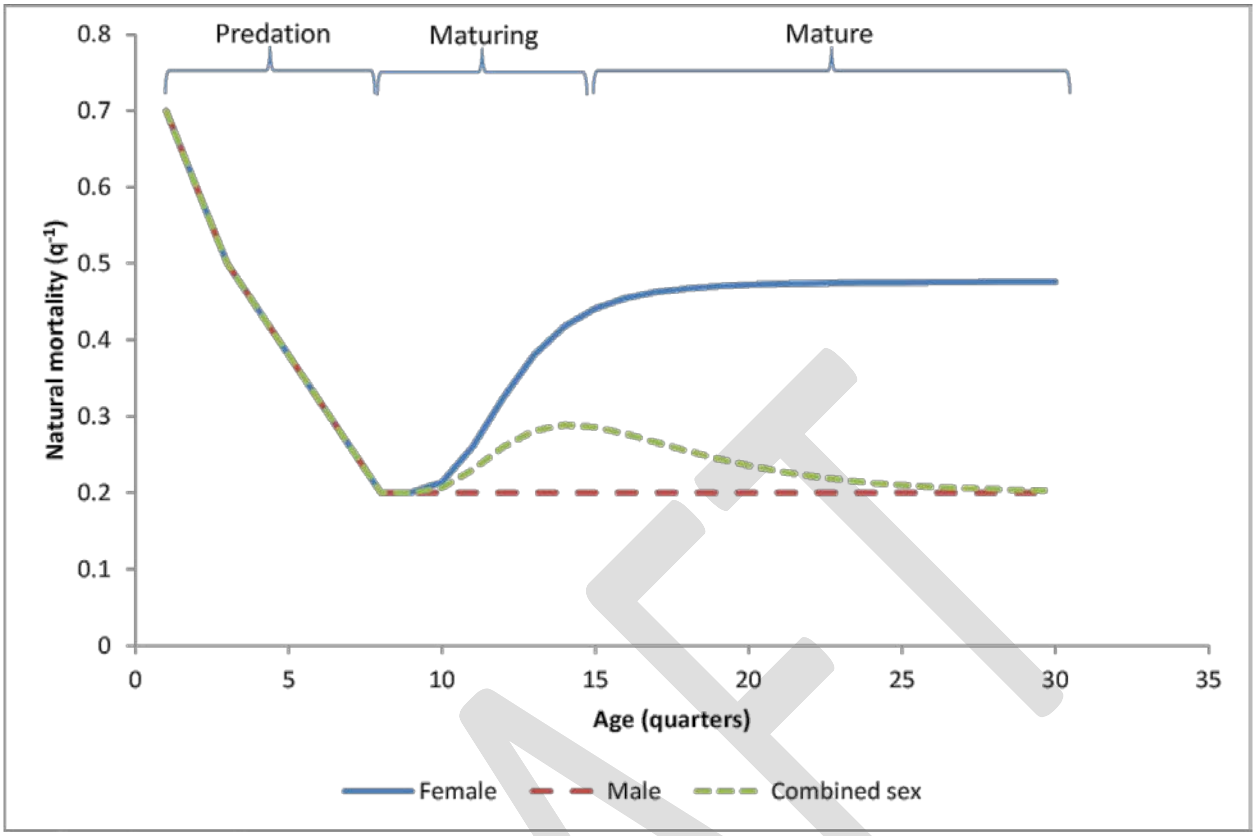

Figure 1. Natural mortality (q-1) used in the stock assessments for yellowfin tuna in the EPO with the three M categories.

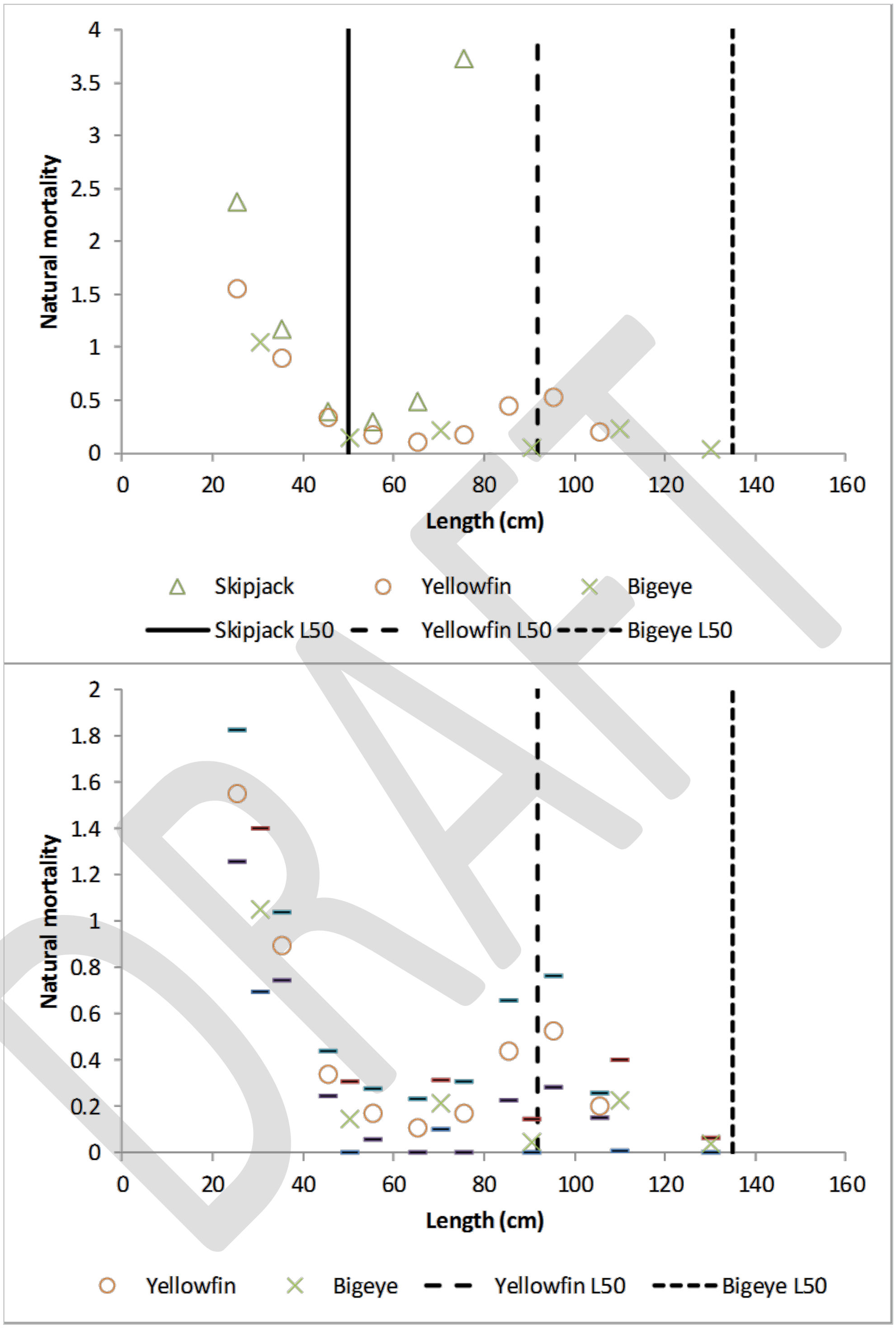

Figure 2. Estimates of natural mortality (q-1) from tagging data for skipjack, yellowfin and bigeye tuna in the western Pacific Ocean (Hampton 2000). The vertical lines are the lengths at 50% maturity. The lower panel shows yellowfin and bigeye tuna on a more restricted scale with 95% Confidence intervals.

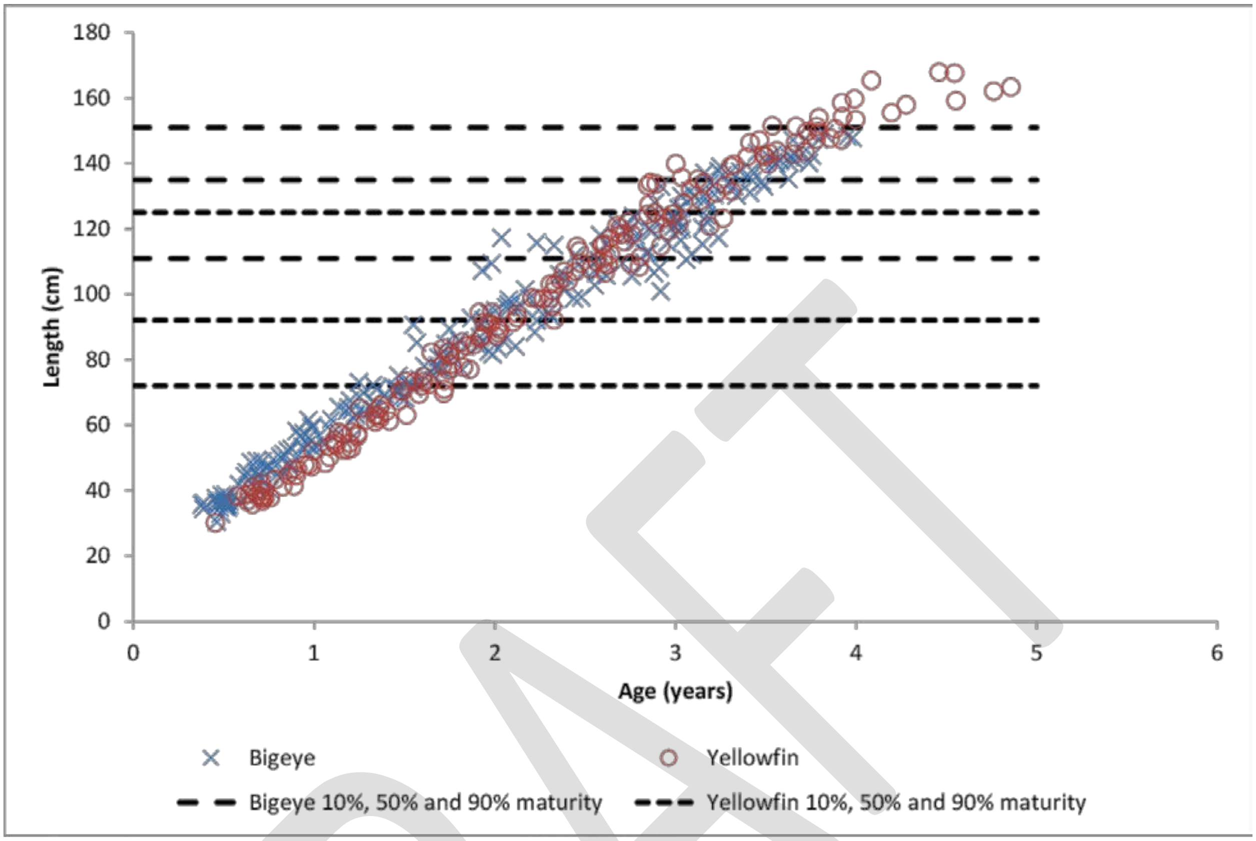

Figure 3. Age-length data from otoliths and estimates of maturity at length from tagging data for yellowfin and bigeye tuna in the EPO.

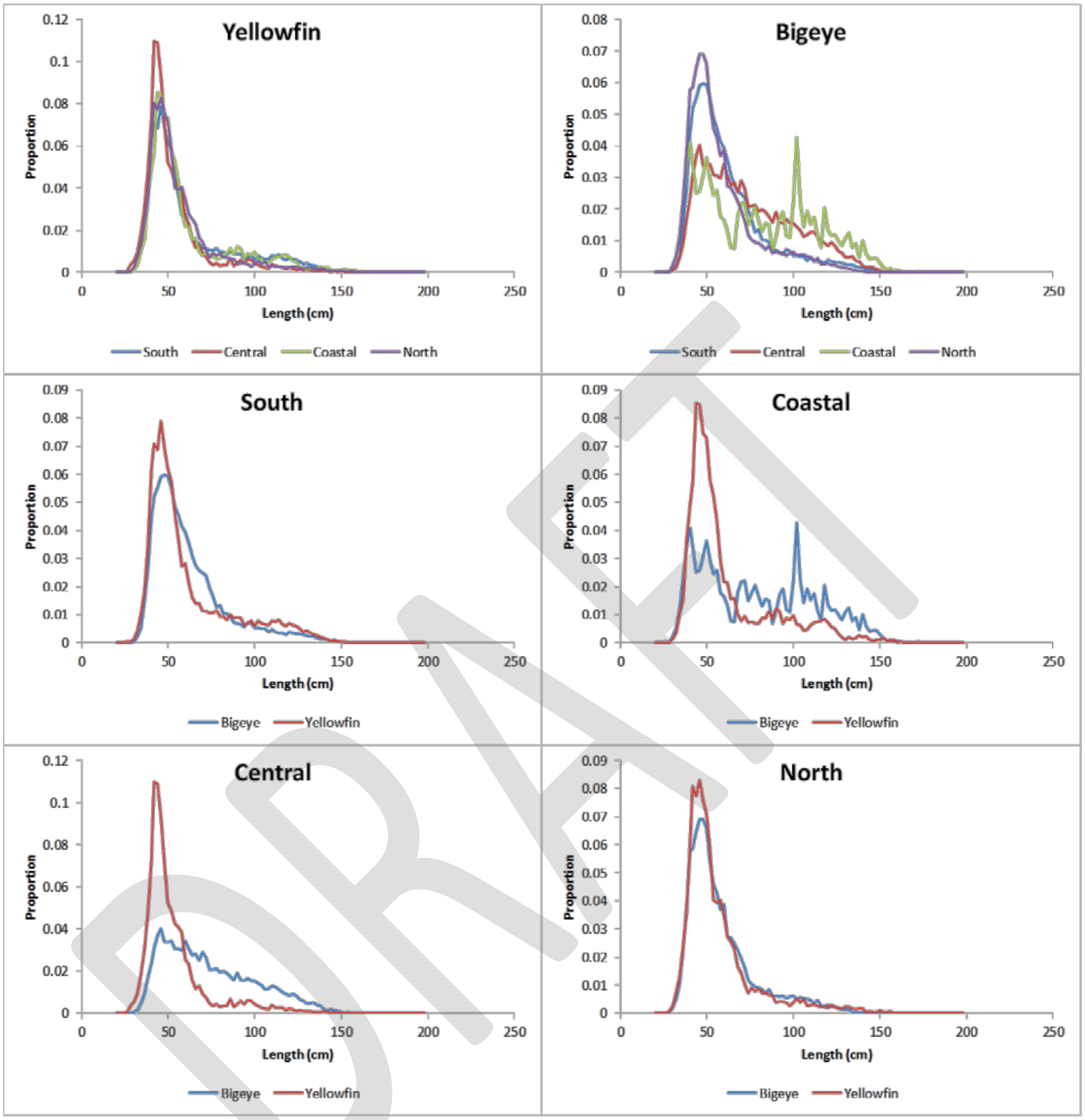

Figure 4. Comparison of length composition data from the floating object fisheries in the EPO for bigeye and yellowfin tuna.

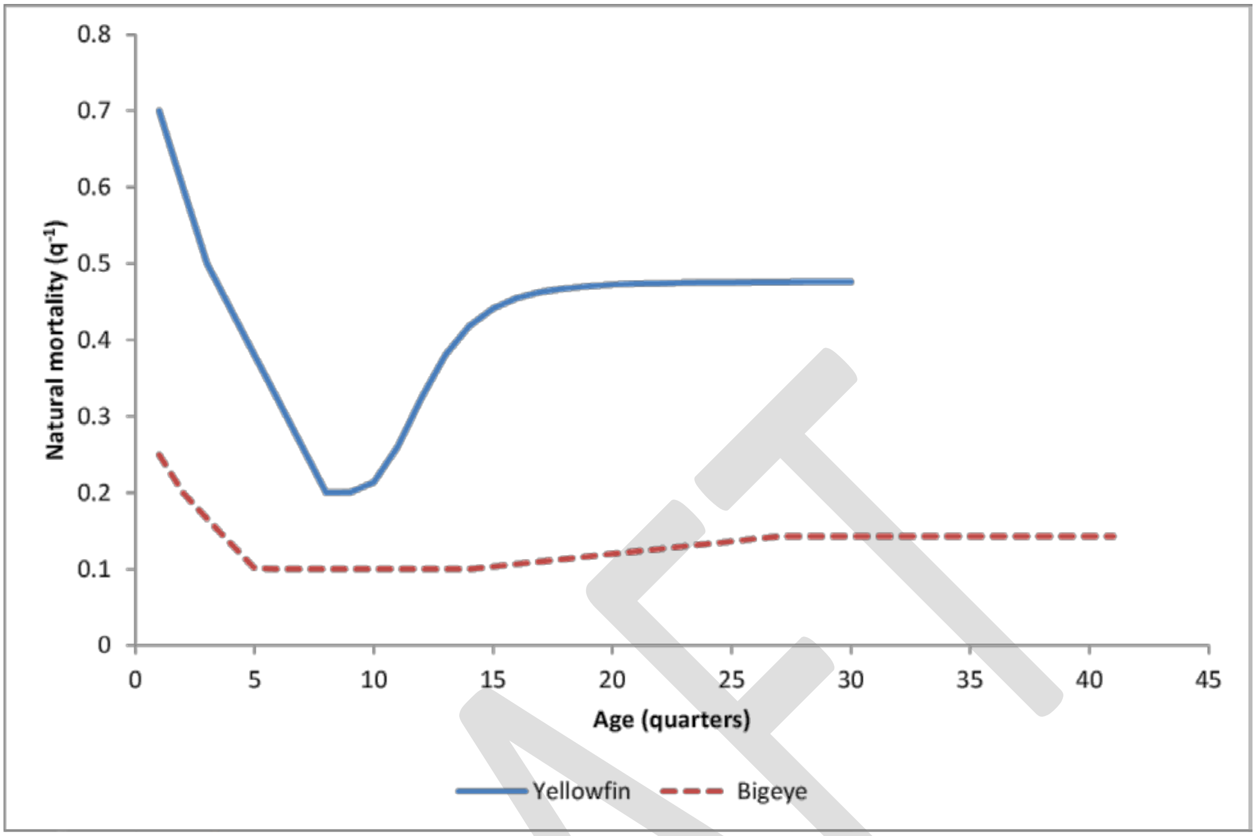

Figure 5. Comparison of natural mortality used in the EPO yellowfin and bigeye tuna assessments.

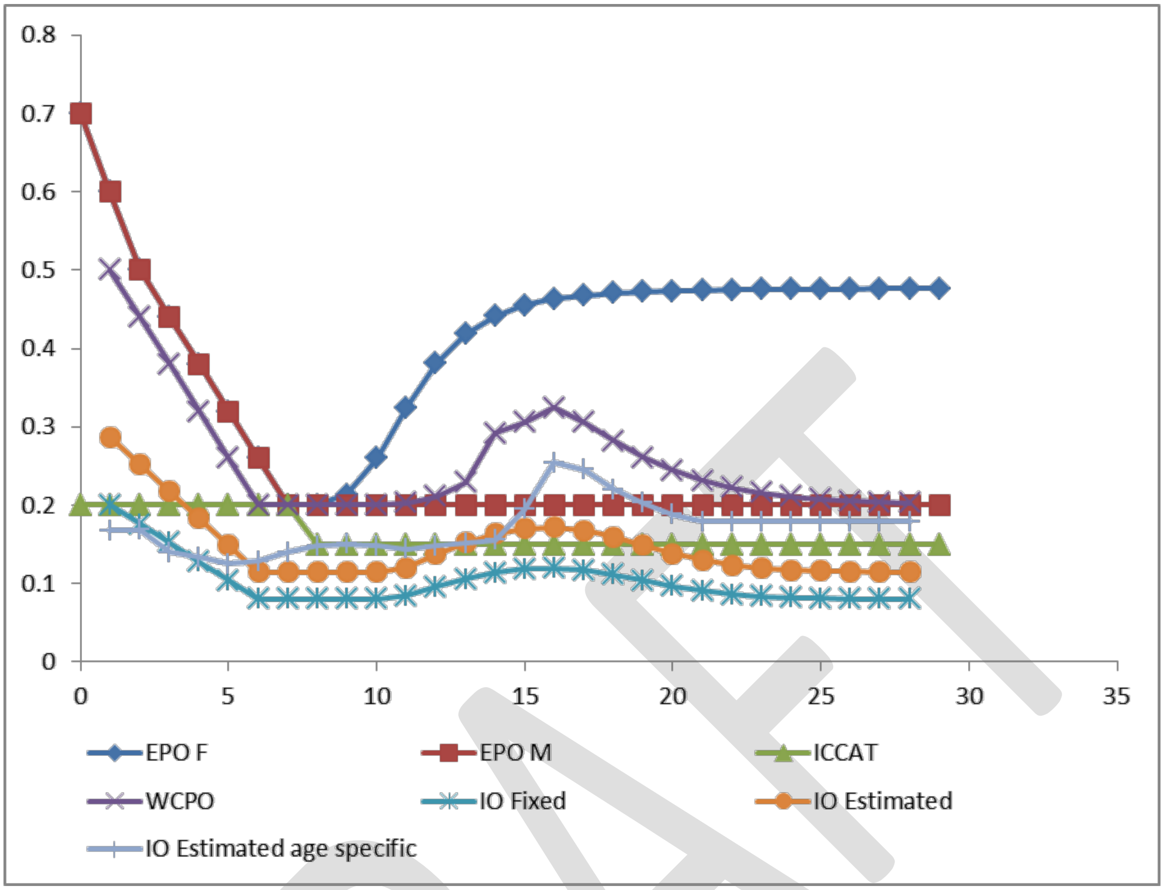

Figure 6. Age (and sex) specific values of M (q-1) used in the yellowfin stock assessments conducted by the four tuna RFMOs.

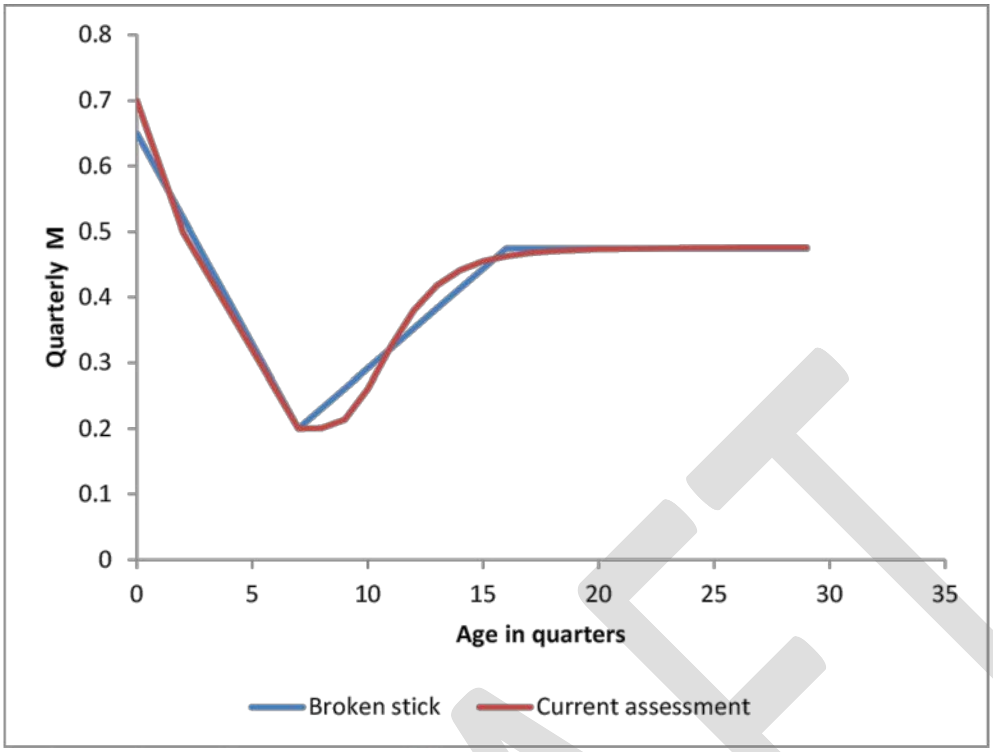

Figure 7. M q-1 at age (in quarters) used the most recent stock assessment (Current assessment; Aires-da-Silva 2012) and the approximation using the broken stock model with three breaks (Broken stick).

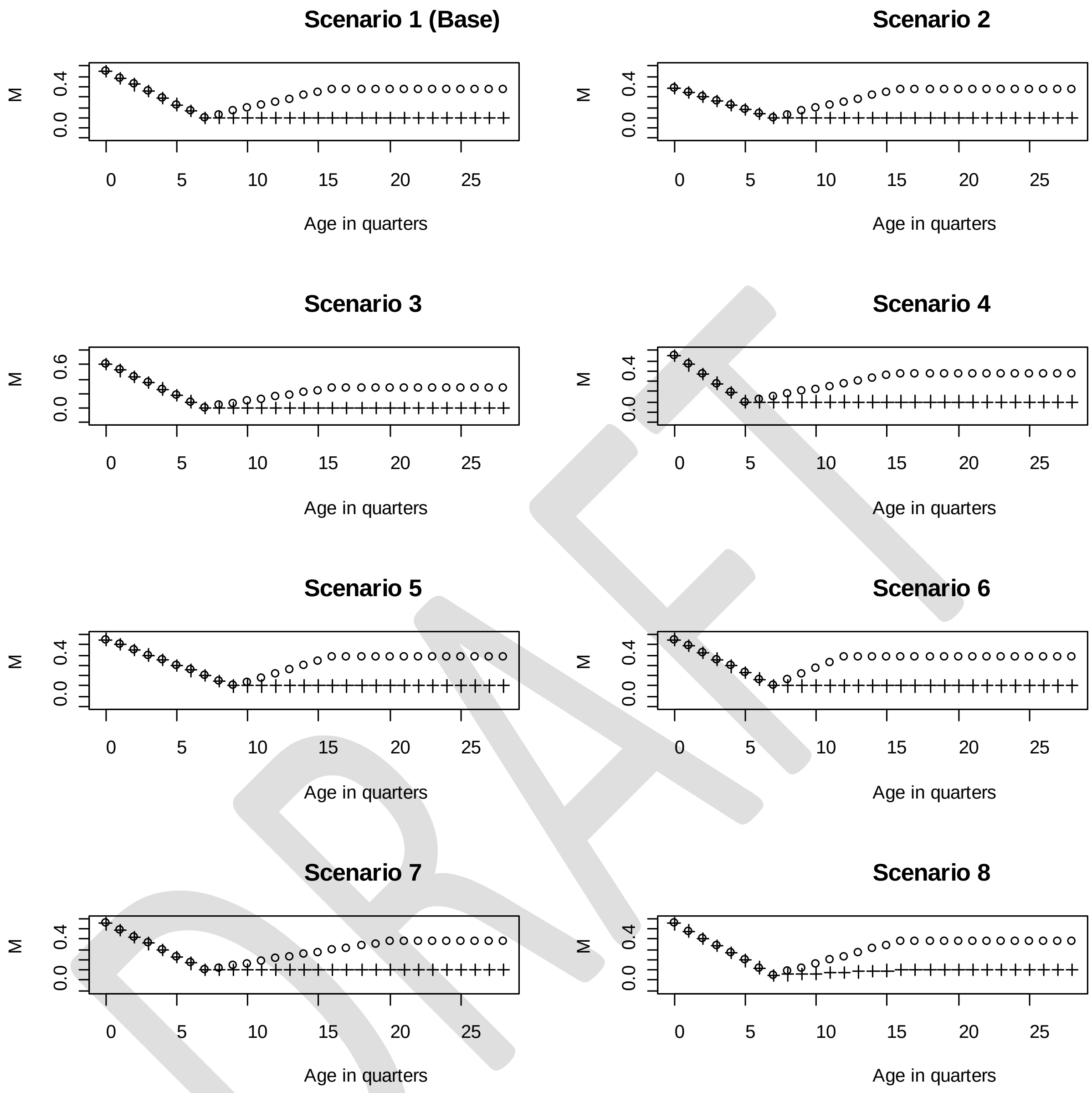

Figure 8a. Age and sex-specific M (q-1) scenarios used to investigate the influence of M on management quantities.

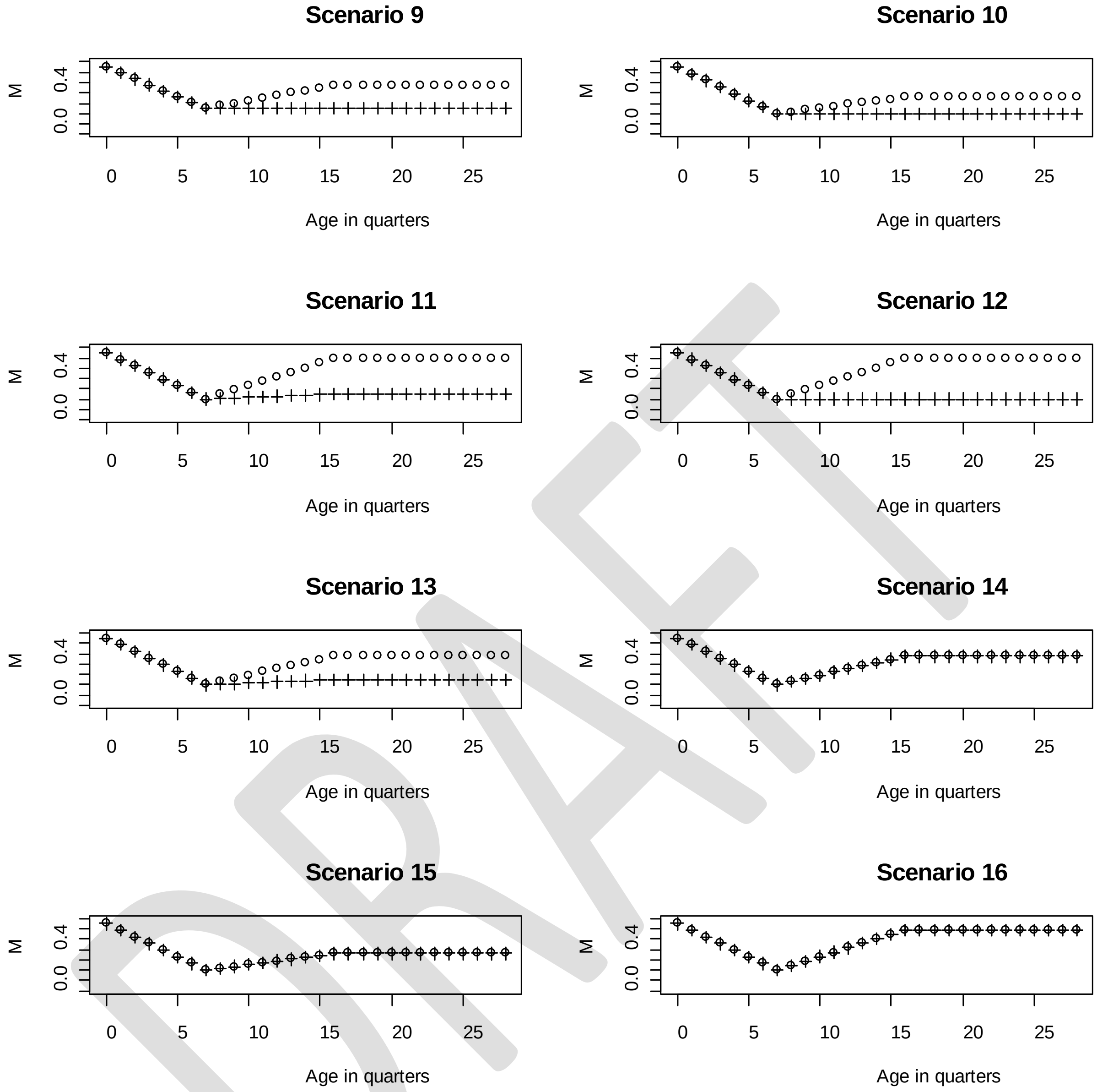

Figure 8b. Age and sex-specific M (q-1) scenarios used to investigate the influence of M on management quantities.

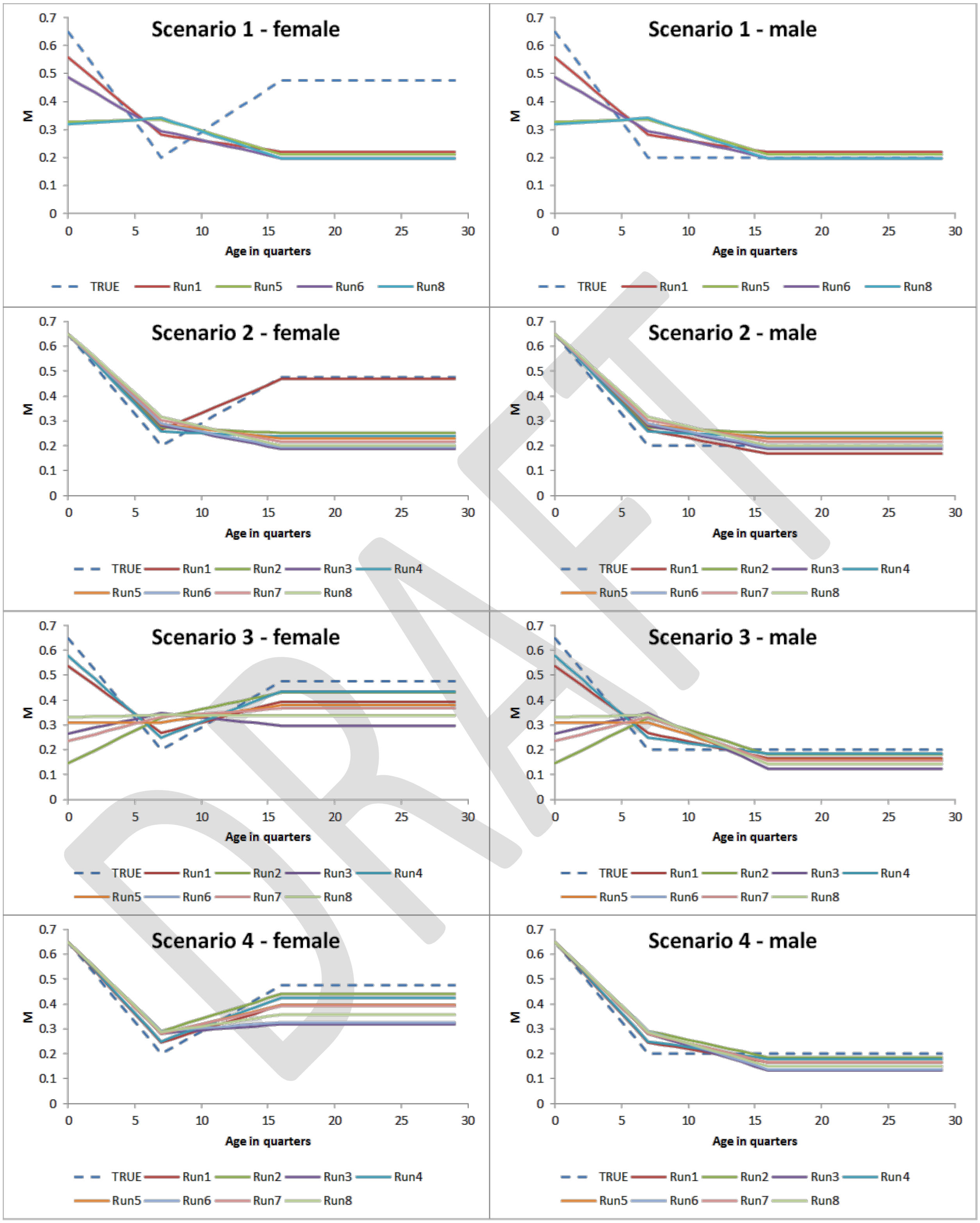

Figure 9. Estimates of M (q-1) from the simulated data.

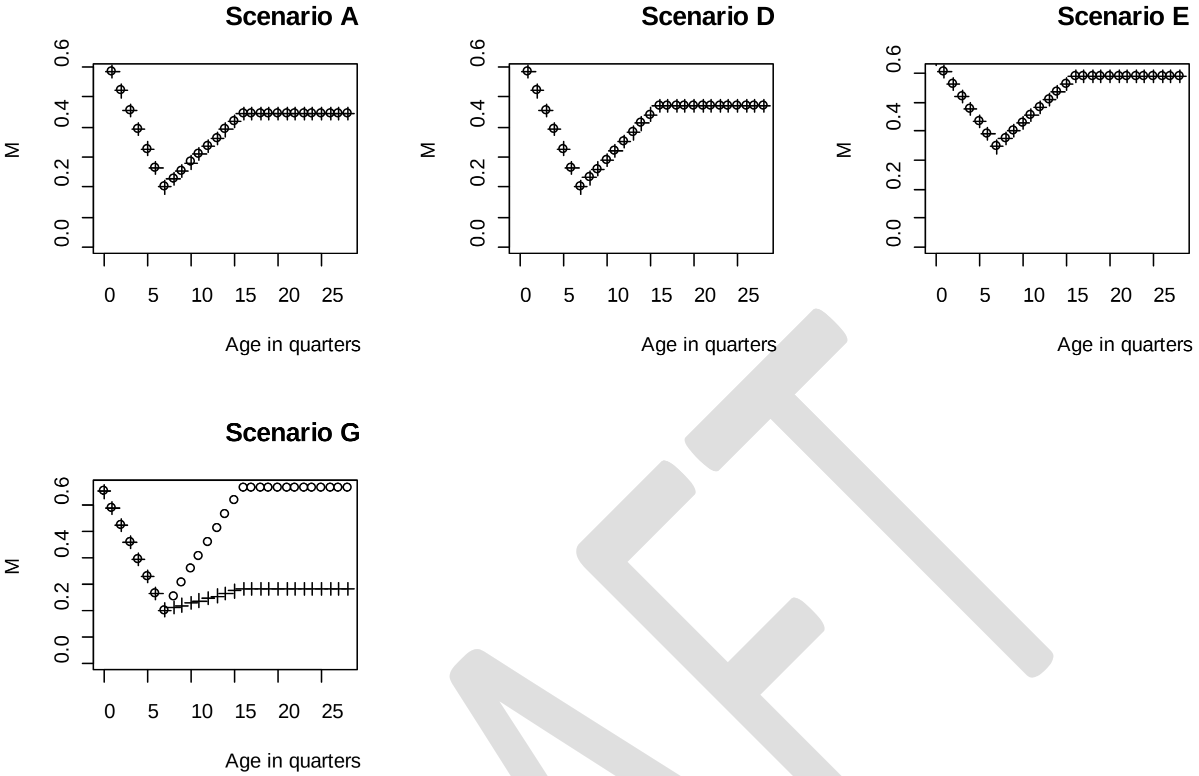

Figure 10. Age and sex specific M (q-1) estimated in the different scenarios relating to which parameters are estimated.

Table 1. Direct estimates of natural mortality (y-1) for yellowfin tuna in the Pacific Ocean from Hampton (1992).

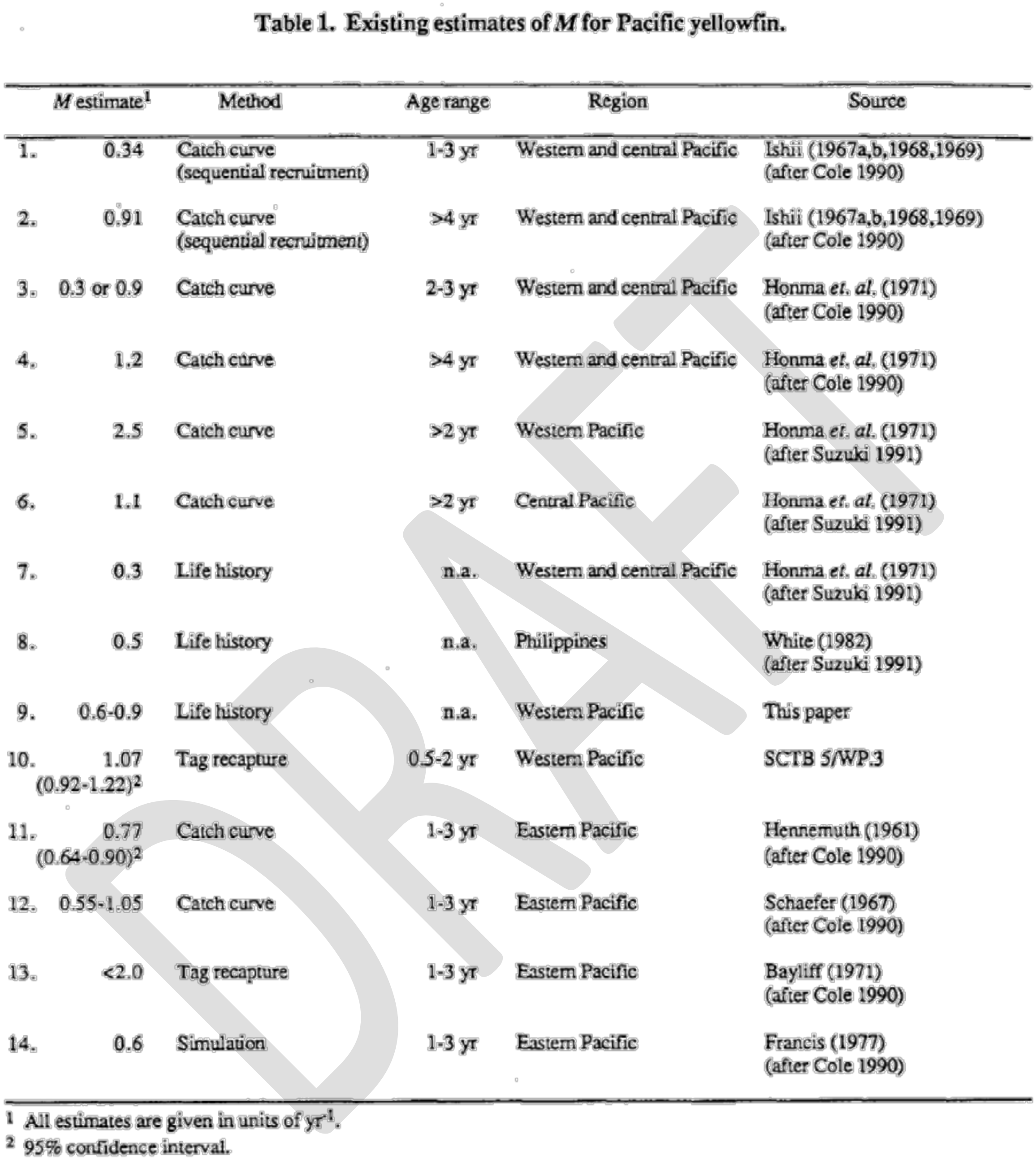

Table 1. Existing estimates of *M* for Pacific yellowfin.

	M estimate[1]	Method	Age range	Region	Source
1.	0.34	Catch curve (sequential recruitment)	1-3 yr	Western and central Pacific	Ishii (1967a,b,1968,1969) (after Cole 1990)
2.	0.91	Catch curve (sequential recruitment)	>4 yr	Western and central Pacific	Ishii (1967a,b,1968,1969) (after Cole 1990)
3.	0.3 or 0.9	Catch curve	2-3 yr	Western and central Pacific	Honma *et. al.* (1971) (after Cole 1990)
4.	1.2	Catch curve	>4 yr	Western and central Pacific	Honma *et. al.* (1971) (after Cole 1990)
5.	2.5	Catch curve	>2 yr	Western Pacific	Honma *et. al.* (1971) (after Suzuki 1991)
6.	1.1	Catch curve	>2 yr	Central Pacific	Honma *et. al.* (1971) (after Suzuki 1991)
7.	0.3	Life history	n.a.	Western and central Pacific	Honma *et. al.* (1971) (after Suzuki 1991)
8.	0.5	Life history	n.a.	Philippines	White (1982) (after Suzuki 1991)
9.	0.6-0.9	Life history	n.a.	Western Pacific	This paper
10.	1.07 (0.92-1.22)[2]	Tag recapture	0.5-2 yr	Western Pacific	SCTB 5/WP.3
11.	0.77 (0.64-0.90)[2]	Catch curve	1-3 yr	Eastern Pacific	Hennemuth (1961) (after Cole 1990)
12.	0.55-1.05	Catch curve	1-3 yr	Eastern Pacific	Schaefer (1967) (after Cole 1990)
13.	<2.0	Tag recapture	1-3 yr	Eastern Pacific	Bayliff (1971) (after Cole 1990)
14.	0.6	Simulation	1-3 yr	Eastern Pacific	Francis (1977) (after Cole 1990)

[1] All estimates are given in units of yr^{-1}.

[2] 95% confidence interval.

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Table 2. Age (and sex) specific values of M (q-1) used in the yellowfin stock assessments conducted by the four tuna RFMOs.

Age (quarters)	EPO Female	EPO Male	ICCAT	WCPO	IO Fixed	IO Estimated	IO Estimated age specific
0	0.7	0.7	0.2				
1	0.6	0.6	0.2	0.5	0.2	0.2866	0.1677
2	0.5	0.5	0.2	0.44	0.176	0.2522	0.1681
3	0.44	0.44	0.2	0.38	0.152	0.2178	0.14
4	0.38	0.38	0.2	0.32	0.128	0.1834	0.1333
5	0.32	0.32	0.2	0.26	0.104	0.149	0.1256
6	0.26	0.26	0.2	0.2	0.08	0.1146	0.1285
7	0.2	0.2	0.2	0.2	0.08	0.1146	0.1396
8	0.200465	0.2	0.15	0.2	0.08	0.1146	0.1484
9	0.21371	0.2	0.15	0.2001	0.08	0.1146	0.1504
10	0.260308	0.2	0.15	0.2006	0.08	0.1146	0.1482
11	0.324727	0.2	0.15	0.2028	0.084	0.1204	0.1443
12	0.380456	0.2	0.15	0.2108	0.0957	0.1371	0.148
13	0.418454	0.2	0.15	0.229	0.106	0.152	0.1513
14	0.441603	0.2	0.15	0.292	0.114	0.1634	0.1551
15	0.455123	0.2	0.15	0.3056	0.1188	0.1702	0.1947
16	0.463001	0.2	0.15	0.3244	0.1197	0.1715	0.2539
17	0.46768	0.2	0.15	0.3056	0.1168	0.1674	0.245
18	0.470541	0.2	0.15	0.2819	0.1111	0.1592	0.22
19	0.472349	0.2	0.15	0.2609	0.1038	0.1488	0.2027

20	0.47353	0.2	0.15	0.2443	0.0967	0.1386	0.1883
21	0.474324	0.2	0.15	0.2317	0.0907	0.13	0.1793
22	0.474873	0.2	0.15	0.2224	0.0863	0.1237	0.1793
23	0.47526	0.2	0.15	0.2158	0.0834	0.1196	0.1793
24	0.475539	0.2	0.15	0.211	0.0818	0.1172	0.1793
25	0.475743	0.2	0.15	0.2077	0.0808	0.1159	0.1793
26	0.475894	0.2	0.15	0.2053	0.0804	0.1152	0.1793
27	0.476007	0.2	0.15	0.2037	0.0802	0.1149	0.1793
28	0.476092	0.2	0.15	0.2025	0.0801	0.1148	0.1793
29	0.476156	0.2	0.15				

Table 3. Estimates of M (q−1) for yellowfin tuna from several methods based on maximum age and life history parameters. The equations are for annual estimates and they are divided by 4 to convert to quarterly. Mean annual surface temperature (assumed to be 25◦) from the EPO is used for Pauly's (1980) equation. The Quinn and Deriso (1999) natural logarithm version of Pauly's equation is used.

Reference	Equation	Quantity	M (q-1) estimate
Rule of thumb	3/amax	amax = 9	0.0825
Hoenig (1983)	Exp(1.46-1.01ln[amax])	amax = 9	0.1175
Jensen (1996) K vonB	1.60K	K = 0.09	0.035
Jensen (1996) K Richards	1.60K	K = 0.69	0.275
Jensen (1996) amat	1.65/amat	amat = 1.3 male amat = 2.0 female	0.3175 male 0.2075 female
Pauly (1980) K von B	Exp(-0.0152-0.279ln[Linf]+0.6543ln[K]+0.4634ln[T])	Linf = 484.55, K = 0.09,T = 25	0.04
Pauly (1980) K Richards	Exp(-0.0152-0.279ln[Linf]+0.6543ln[K]+0.4634ln[T])	Linf = 185.01, K = 0.69,T = 25	0.2
Gunderson (1997)	1.79GSI	GSI = NA	NA

Table 4. Management quantities, M estimates, and negative log-likelihood values for the different scenarios relating to which M parameters are estimated. Scenarios B, C, F, H, and I had convergence problems.

	Aires da Silva and Maunder (2012)	Broken stick M	A	D	E	G
Management quantities						
Msy	262642	263006	307108	326370	9.00E+17	284078
Bmsy	356682	352865	362940	380523	7.00E+17	343565
Smsy	3334	3072	2937	2993	2.00E+15	2506
Bmsy/Bzero	0.31	0.31	0.34	0.34	0.32	0.33
Smsy/Szero	0.26	0.25	0.17	0.17	0.06	0.23
Crecent/msy	0.79	0.78	0.67	0.63	2.30E-13	0.73
Brecent/Bmsy	1.00	1.04	1.44	1.51	2.59	1.31
Srecent/Smsy	1.00	1.07	1.97	2.16	12.63	1.57
Fmultiplier	1.15	1.21	2.22	2.54	2.00E+13	1.83
Negative log likelihoods						
Survey	-148.93	-149.06	-152.37	-154.29	-147.15	-151.26
Length	8443.82	8450.42	8412.02	8401.87	8392.98	8452.89
Recruitment	-5.41	-5.11	-4.30	-4.31	-2.38	-4.70
Total	8289.5	8296.27	8255.37	8243.29	8243.47	8296.94
M estimates						
F0	NA	0.65	0.65	0.65	0.65	0.65
M0	NA	0.65	0.65	0.65	0.65	0.65

F7	NA	0.20	0.20	0.20	0.35	0.20
M7	NA	0.20	0.20	0.20	0.35	0.20
F16	NA	0.47	0.45	0.47	0.59	0.67
M16	NA	0.47	0.45	0.47	0.59	0.28

Table 5. Parameters use in the broken stick model to represent M (q-1).

Parameter	Age	Rational	Female	Male Offset (value)
1	0	The smallest age should have the highest M	0.65	0 (0.65)
2	7	The age where predation is assumed to be nominal	0.2	0 (0.2)
3	16	The age when most of the individuals are mature	0.474692203	-0.804349394 (0.2)

Table 6. Scenarios used to investigate the ability of the assessment model to estimate M (q-1)

Scenario	M0	a1	a2	Ma1	Mf	Moffset
A	0.65	7	16	0.2	est	est
B	0.65	7	16	est	est	est
C	est	7	16	est	est	est
D	0.65	7	16	0.2	est	0
E	0.65	7	16	est	est	0
F	est	7	16	est	est	0
G	0.65	7	16	0.2	est	-0.86
H	0.65	7	16	est	est	-0.86
I	est	7	16	est	est	-0.86

Table 7. Scenarios used to investigate the influence of M (q-1) on management quantities

Scenario	M0	a1	a2	Ma1	Mf	Mm
1 (base)	0.65	7	16	0.2	0.474692	0.2
2	0.4875	7	16	0.2	0.474692	0.2
3	0.8125	7	16	0.2	0.474692	0.2
4	0.65	5	16	0.2	0.474692	0.2
5	0.65	9	16	0.2	0.474692	0.2
6	0.65	7	12	0.2	0.474692	0.2
7	0.65	7	20	0.2	0.474692	0.2
8	0.65	7	16	0.15	0.474692	0.2
9	0.65	7	16	0.25	0.474692	0.25
10	0.65	7	16	0.2	0.36	0.2
11	0.65	7	16	0.2	0.59	0.25
12	0.65	7	16	0.2	0.59	0.2
13	0.65	7	16	0.2	0.47	0.25
14	0.65	7	16	0.2	0.47	0.47
15	0.65	7	16	0.2	0.36	0.36
16	0.65	7	16	0.2	0.59	0.59

Table 8. Management quantities and negative log likelihood values for the scenarios used to evaluate the sensitivity of management quantities to M.

	1 (base)	2	3	4	5	6	7	8
Management quantities								
msy	263006	261563	262799	263005	266059	265228	261792	262720
Bmsy	352865	354251	353424	356394	354529	345392	358630	374742
Smsy	3072	3307	2904	3036	2767	2642	3352	3760
Bmsy/Bzero	0.31	0.32	0.31	0.31	0.31	0.31	0.31	0.31
Smsy/Szero	0.25	0.27	0.24	0.28	0.21	0.27	0.24	0.28
Crecent/msy	0.78	0.79	0.78	0.78	0.78	0.78	0.79	0.79
Brecent/Bmsy	1.04	0.97	1.07	0.99	1.12	1.1	1	0.87
Srecent/Smsy	1.07	0.95	1.14	0.98	1.29	1.18	1	0.81
Fmultiplier	1.21	1.04	1.28	1.09	1.45	1.34	1.14	0.94
Negative log likelihoods								
Survey	-149.06	-144.23	-147.09	-149.27	-149.00	-149.60	-148.68	-148.01
Length	8450.42	8485.20	8454.61	8501.05	8420.06	8482.19	8441.26	8437.51
Recruitment	-5.11	-5.38	-4.71	-5.20	-4.87	-5.13	-5.06	-5.40
Total	8296.27	8335.61	8302.82	8346.6	8266.21	8327.48	8287.54	8284.12

	9	10	11	12	13	14	15	16
Management quantities								
msy	287360	261392	273786	264759	269449	328890	279372	418320
Bmsy	344966	361537	343390	347458	346037	382797	350161	461123
Smsy	2346	3489	2671	2789	2928	3001	3169	3220
Bmsy/Bzero	0.32	0.31	0.32	0.31	0.32	0.34	0.33	0.35
Smsy/Szero	0.19	0.23	0.24	0.27	0.22	0.17	0.18	0.17
Crecent/msy	0.72	0.79	0.75	0.78	0.77	0.63	0.74	0.49
Brecent/Bmsy	1.34	0.97	1.21	1.09	1.15	1.52	1.25	1.76
Srecent/Smsy	1.78	0.97	1.37	1.15	1.28	2.19	1.53	2.85
Fmultiplier	2.02	1.1	1.58	1.3	1.45	2.58	1.68	3.96
Negative log liklleihoods								
Survey	-152.18	-148.43	-151.39	-149.43	-150.81	-154.39	-152.74	-154.23
Length	8447.82	8440.20	8447.21	8464.68	8433.76	8401.59	8410.23	8410.07
Recruitment	-4.56	-5.05	-4.95	-5.15	-4.95	-4.28	-4.70	-3.93
Total	8291.1	8286.73	8290.88	8310.11	8278.02	8242.93	8252.81	8251.92