A simple model for age-structured natural mortality based on changes in sex ratios

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Abstract

Natural mortality is critical to the estimation of MSY and other management parameters yet we have great difficulty obtaining objective estimates of it. Here we describe a simple biological model to describe natural mortality at age. The model is based upon the common observations in tunas that there is a reduction in the proportion of females in catches as size increases. To illustrate the approach we apply the model to biological data for bigeye tuna (*Thunnus obesus*). We assess the sensitivity of the estimates of natural mortality to alternative model assumptions and estimates of the sex ratios in bigeye. To determine the impacts of this uncertainty on management quantities, we complete a stock assessment for a number of alternative mortality schedules, comparing estimates of sustainable yields and current stock status. We discuss some important assumptions of the model and discuss potential improvements to the model and biological research that may reduce uncertainty.

1 Introduction

Natural mortality (M) is an extremely difficult parameter to estimate and yet critical to estimation of important management quantities (e.g., MSY). The purpose of this document is to provide a detailed description how natural mortality at age is determined for the assessment of tuna in the eastern tropical Pacific Ocean (EPO). We construct a very simple model, which incorporates a range of biological data and requires a number of strong assumptions, that is used to provide estimates of age-specific natural mortality that are used in the assessment of tuna in the EPO. This approach has been used in the derivation of mortality estimates for both yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obsesus*). Similar approaches have been used in previous assessments (Maunder and Watters 2001; Watters and Maunder 2001). We then describe an application of the approach to data for bigeye tuna (*Thunnus obesus*), testing the sensitivity of the estimates of mortality and management parameters to model assumptions and the biological input.

Many researchers have observed 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). It would be useful to combine these observations with biological theory for determining patterns in natural mortality based on life history parameters and behavioral observations (Roff 1984; Charnov 1993).

Before the change in sex ratio can be attributed to sex-specific natural mortality, other assumptions must be considered. Everett and Punsly (1994) analyzed sex ratios in catches from three gear types of yellowfin tuna in the EPO and found statistically significant differences in sex ratios attributed to a number of factors including fish size, and fishing gear. They speculated that there were three possible causes of the observed changes in sex ratios

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

Though they 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 was not supported by the data. Though Wild (1986) reported sexually-dimorphic growth rates in yellowfin tuna, there is no evidence that the size-at-age of females is any less than males over the ages for which there were sufficient observations (Wild 1986, Figure 4).

Though Everett and Punsly (1994) observed differences in sex ratios by gear type, the proportion of females declined at large sizes in the catches of both surface and longline fisheries. This provides some evidence that differential vulnerability to fishing mortality is unlikely but does not rule it out.

The final hypothesis, and the basis of our model here, is that the mortality of larger female tuna is higher than that of large male tuna (**Something from Pat**). Within this hypothesis 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? Either of these would lead to the same pattern in the sex ratios and is a common problem when interpreting sex ratio data (e.g., Harley (2002a)).

The trade-off between somatic growth and gonadal development, and the other energetic considerations associated with spawning are well understood (Ursin 1979; Woodhead 1979). If the spawning costs for female tuna are greater than those of male tuna, a well documented occurrence in other fishes (Wootten 1984), this would provide a mechanism for the increase in female mortality.

It is not clear exactly how natural mortality in tropical tuna will increase as tropical tunas have the capacity to spawn all year round given suitable environmental conditions (Schaefer 1986). It may well have a cumulative effect, but we have not modelled this. Rather, we have 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.).

2 Methods

2.1 Data

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, and estimates of mean length-at-age (to convert length-based estimates to age-based). In addition to these data we also require some estimates of natural mortality. These will generally be associated with so much uncertainty to be of little use on their own. Here we include the estimates of natural mortality at age estimated from tagging data by Hampton (2000).

2.2 Model

Before providing equations, it is useful to describe the model in words. There are three parts to the model (Figure 1):

- Part 1: mortality is the same for males and females and declines linearly from some first age (min age) to some breakpoint (break age).
- Part 2: mortality is constant and the same for males and immature females from this breakpoint until females begin to mature.
- 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.

Notation used in model are provided in Table 1.

2.3 Mortality by age and sex

We estimate natural mortality by age and sex based on two estimated parameters and a number of assumptions. The first parameter, M^1, is the natural mortality rate of males and immature females in Parts 2 and 3 in Figure 1. The second, M^2, is the mortality rate of females that have been mature for l quarters and is used in Part 3. When $l = 0$, the increased natural mortality occurs as soon as the female becomes mature, otherwise, if $l > 0$, it is lagged. We define $M_{s,\text{min age}} = 2M^1$, and assume a linear decrease of δ each time step until the breakpoint where Part 2 begins, where $\delta = M^1/(\text{break age - min age})$.

For males, the full mortality schedule is:

$$M_{M,a} = \begin{cases} 2M^1 & \text{for } a = \text{min age} \\ M_{M,a-1} - \delta & \text{for } a = \text{min age} + 1, \ldots, \text{break age} \\ M^1 & \text{for } a = \text{break age+1}, \ldots, A \end{cases} \tag{1}$$

For females, the full mortality schedule is:

$$M_{F,a} = \begin{cases} 2M^1 & \text{for } a = \text{min age} \\ M_{F,a-1} - \delta & \text{for } a = \text{min age+1}, \ldots, \text{break age} \\ M^1(1 - \varphi_{a-l}) + M^2(\varphi_{a-l}) & \text{for } a = \text{break age+1}, \ldots, A \end{cases} \tag{2}$$

2.4 Population projection

We use the observed sex ratio of the youngest age class and estimates of mortality by age and sex to predict the composition of a cohort through time. From an initial recruitment, R, the population is projected as follows:

$$N_{s,a} = \begin{cases} R\phi_a^{\text{obs}}; R(1 - \phi_a^{\text{obs}}) & \text{for } a = \text{min age} \\ N_{s,a-1}\exp(-M_{s,a-1}) & \text{for } a = \text{min age} + 1, \ldots, A-1 \\ \frac{N_{s,a-1}\exp(-M_{s,a-1})}{(1-\exp(-M_{s,A}))} & \text{for } a = A \end{cases} \tag{3}$$

Provided that fishing mortality is not sex-specific (one of our assumptions), neither overall natural mortality or the sex ratios will be affected by fishing mortality.

2.5 Model predictions and fitting

We use this model to make predictions of quantities for which we have observations. Here we have two data sources, proportion of males at age and combined natural mortality at age.

The model prediction of the proportion of males at age is simply

$$\phi_a = \frac{N_{M,a}}{N_{M,a} + N_{F,a}}. \tag{4}$$

The sex-aggregated natural mortality at age is is the weighted average of male and female mortality at age and can be derived from ϕ_a,

$$M_{\bullet,a} = \phi_a M_{M,a} + (1 - \phi_a) M_{F,a}. \tag{5}$$

The overall objective function here is comprised of two components, the fit to each of the data sources. It could be possible to use maximum likelihood methods to fit to the observed data but we have used only least squares here. The component for the proportion of males is

$$\text{SSE}_{\text{males}} = \sum_a (\phi_a - \phi_a^{\text{obs}})^2, \tag{6}$$

and the component for the tagging estimates of mortality is

$$\text{SSE}_{\text{M}} = \sum_a (\log(M_{\bullet,a}/M_{\bullet,a}^{\text{obs}}))^2. \tag{7}$$

Explain why I choose LS for one and the logged deviates for the other.

We find the parameters M^1 and M^2 that minimize:

$$\mathcal{F} = \text{SSE}_{\text{males}} + \text{SSE}_{\text{M}}. \tag{8}$$

3 Application to bigeye tuna in the EPO

3.1 Biological data

There has been a large number of studies providing estimates of the proportion of males by size class for bigeye tuna. These data are summarized in Figure 2 (top). Our 'best estimate' of the proportion of males by age class are based on a logistic fit to a composite data set combining estimates by Kurt Schaefer for small fish (IATTC 2003) and Kume and Joseph (1966) for larger fish (Figure 2, bottom). For sensitivity we compared two other series based on fitting a logistic curve to data for the WCPO from Hampton et al. (1998) and for the Atlantic Ocean from Miyabe (2002).

The maturity ogive for females is based on a logistic fit to estimates by Kurt Schaefer (IATTC 2003) (Figure 3). These estimates are different to that used in previous assessments (Figure 3). It is not clear how the previous estimate was determined.

Hampton (2000) provided estimates of natural mortality for a number of size class of small bigeye tuna. These estimates are quite variable and uncertain and there are potential concerns due to potentially high initial tag-related mortality, particularly for small tuna.

As bigeye tuna have a relatively short life-span we run the model on a quarterly time step rather than an annual one.

3.2 Results

To determine our basecase we fitted the model assuming a range of lags for the period between maturity and increased mortality to see which gave the best fit to the data. While there was some evidence for yellowfin that a lag of six quarters may be appropriate, we have no *a priori* hypotheses about the lag for bigeye tuna. The best fit came with a lag of six quarters so this was used as the basecase (epolag6) (Table 2). We found that a $l = 6$ also provided the best fit when data on the proportion of males from the Atlantic (Miyabe 2002) was used.

Estimates of male and female mortality for the basecase are shown in Figure 4 and the fit to the observed proportion of males and combined natural mortality are shown in Figure 5.

The fit to the observed proportion of males is good and the fit to the mortality data passes through the cloud of highly variable estimates.

3.3 Sensitivity analyses

While $l = 6$ provided the best fit to the data, we were interested in how sensitive estimates of mortality were to the assumed lag. The parameter describing mortality for males and immature females was not sensitive to the values of l examined, but there was a positive relationship between l and the mortality for mature females (Table 2). The effect of this increase on combined natural mortality is shown in Figure 6 where longer lags are associated with later and steeper increases in combined mortality. The peak of mortality is also higher with the longer lags.

Another sensitivity analysis was performed to assess the sensitivity of combined mortality to the observed mortality of the youngest size class from Hampton (2000). We excluded this point from the basecase analysis as it was believed to be too high, potentially due to high initial mortality of small tagged fish (**REF**). When it was included (epolag6all), it shifted the entire curve up by about 25%. This is partly due to the constraint that $M_{\bullet,\text{min age}} = 2 * M^1$.

Finally, we compared the basecase to runs where different observed proportions of males were used; one series from the WCPO (wcpolag6) (Hampton et al. 1998) and one from the Atlantic Ocean (atlag6) (Miyabe 2002). We assumed that $l = 6$. There was considerable difference in female mortality with the basecase estimates in between those from the other data sets (Figure 7). There was no difference in natural mortality for males and only a slight difference in combined mortality.

3.4 Determination of stock status and yields

To determine the sensitivity of the important management quantities to our analysis, we ran the stock assessment model for some of alternative scenarios described above. We also compared the estimates to a corrected version (revised maturity data) of the 2002 stock assessment.

With the exception of the sensitivity analysis that included all of the tagging estimates (epolag6all) from (Hampton 2000), all estimates of MSY were 10-15% lower than last years model. This is because natural mortality is generally lower in these runs and MSY is correlated with natural mortality (all other things being equal). This also affects the estimate of the estimated F-scalar, the basecase recommends a reduction in fishing mortality while the 2002 assessment determined fishing mortality to be optimal and epolag6all suggested that a 30% increase in fishing mortality is necessary.

Spawning biomass (biomass of mature females) and spawning biomass at MSY (Smsy) are much lower for analyses using the sex ratio data for the WCPO, this is because of the high mortality for mature females estimated from these data (Figure 7) and the much greater skewness of the sex ratios (Figure 3).

There were some qualitative agreements across runs, all suggest that the stock is above Bmsy and Smsy and that current catches are greater than MSY. This last point is likely related to both the high recruitment observed in the mid to late 1990s and the estimated overfishing in many of the model runs (related to the estimated F-scalar).

While the best fit came from the epolag6all model, none of the fits were significantly better or worse than another.

4 Discussion

Here we have described a simple model that integrates biological data with tagging data to provide estimates of age-specific natural mortality. This is similar to what was used in previous years (Maunder and Watters 2001; Watters and Maunder 2001) with the addition of the lag and a more statistical approach to estimating the mortality parameters.

The model is based on the assumption that increases in the proportion of males in larger size classes is solely due to increases in natural mortality of females. Furthermore, the increase is a function of maturity of females. Everett and Punsly (1994) discussed three equally plausible explanations for the pattern, i.e., differential growth, vulnerability, or mortality. To improve our understanding of each hypothesis it would be useful to further some of the preliminary analyses that they undertook.

A key reason for our inability to separate different hypotheses is that our approach is two-step rather than integrated (Maunder), i.e., we have one model for determining natural mortality and a second for the assessment of the stock. A better approach is that used in MULTIFAN-CL where natural mortality is estimated within the stock assessment model incorporating data from tagging, CPUE, and catch composition (Fournier et al. 1998). However, MULTIFAN-CL is a single-sex model but it still may be possible to integrate some aspects of our analysis into MULTIFAN-CL. A-SCALA (Maunder and Watters 2003)provides an even greater challenge as it is not presently structured to incorporate tagging data that is critical to estimation of natural mortality (Hampton and Fournier 2001). The development of sex-structured stock assessment models will provide a useful tool in the further (integrated) development of models for natural mortality.

We have shown that some of the important management quantities are quite sensitive to even slight changes in assumptions in the model of natural mortality. This is of some concern but is likely to remain until we are better able to understand these biological processes. Recent estimates of sex ratios, combined mortality, and maturity, are all for young bigeye with few samples of mature individuals. There is also a strong reliance on estimates of biological parameters collected decades ago. It will be important to further develop programs for the collection of these data.

It will also be prudent to review the extensive literature of life history characteristics to determine what alternative models and processes could be included. There is also likely to be benefits of a meta-analytical approach (Harley 2002b) whereby we examine if there are similar patterns observed in other populations or closely related species, e.g., Fromentin and Fonteneau (2001).

In future development of this model it would be useful to incorporate differential growth estimates if they are found and age- and sex-specific vulnerability to fishing gear could be included to allow examination of the trade-off between these alternatives. It will also be important to incorporate alternative functional forms for the natural mortality at age, e.g., quadratic mortality for females. It may well be possible to integrate this model for the estimation of natural mortality into the assessment. Rather than estimate age-specific natural mortality, we could estimate the 2-3 parameters estimated here. Also, the model fitting procedure used here is very primitive, i.e., least-squares, so it could be useful to examine different error structures within a maximum likelihood framework, but this is unlikely to be a priority until more data area available.

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Table 1: Summary of notation used in the model

Symbol	Description
s	sex: M-male and F-female
min age	first age in the model
break age	age separating Parts 1 and 2 in the model
a, A	age and age of plus-group
$M_{s,a}$	natural mortality by sex and age
M^1, M^2	estimated natural mortality parameters
ϕ_a	proportion of fish at age a that are male
$N_{s,a}$	number of individuals by sex and age
φ_a	proportion of females mature at age
l	lag between maturity and increased mortality for females
R	Recruitment assumed in model
obs	distinguishing observed values and model predictions

Table 2: Estimates of mortality parameters and values for the components of the objective function for different assumed lags between maturity and increased mortality in the analysis of the EPO data.

lag (l)	$\mathrm{SSE}_{\mathrm{M}}$	$\mathrm{SSE}_{\mathrm{males}}$	$\mathcal{F}$	M^1	M^2
0	2.475	0.388	2.863	0.094	0.159
2	2.467	0.223	2.689	0.094	0.172
4	2.464	0.091	2.555	0.094	0.191
6	2.464	0.017	2.481	0.094	0.218
8	2.464	0.027	2.491	0.094	0.257

Table 3: Sensitivity of a range of important management quantities to alternative assumptions about natural mortality. Average fishing mortality for 2000 and 2001 was used in the calculations. F is the value of the overall objective function (smaller is better). See text for a description of each model.

	epolag6	atlag6	wcpolag6	epolag6all	2002 basecase
MSY	52166	50556	53009	66016	59920
B0	810968	813429	816323	723684	733474
S0	147301	203899	85817	113336	67129
Bmsy	203803	204387	204955	190728	190605
Smsy	26049	34368	15484	15764	10636
Bcur	260997	223588	273701	296659	239472
Scur	60982	62782	39145	61836	30777
Ccur	76110	76456	76096	76946	77926
Bmsy/B0	0.2513	0.2513	0.2511	0.2636	0.2599
Smsy/S0	0.1768	0.1686	0.1804	0.1391	0.1584
Ccur/MSY	1.459	1.5123	1.4355	1.1656	1.3005
Bcur/Bmsy	1.2806	1.0939	1.3354	1.5554	1.2564
Scur/Smsy	2.3411	1.8268	2.5281	3.9226	2.8937
Fscale	0.8018	0.6986	0.8394	1.3175	1.01
F	-239452.0	-239451.5	-239452.2	-239453.4	-239451.6

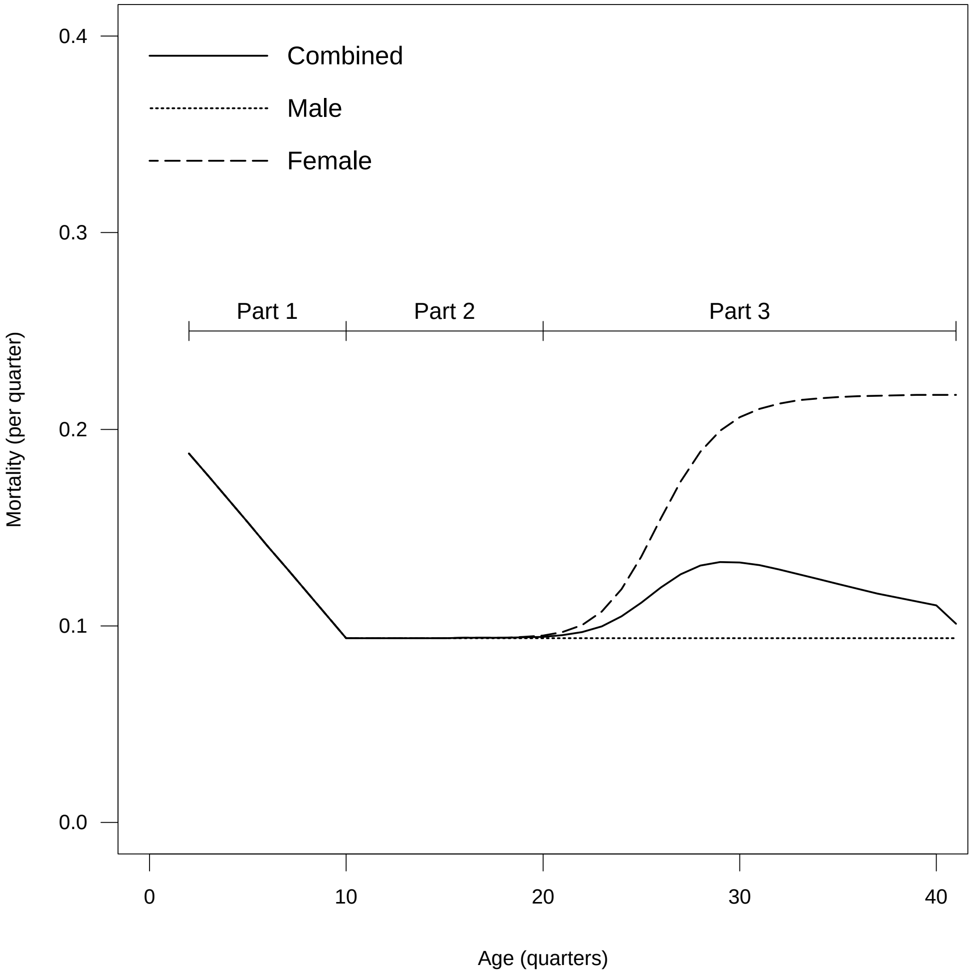


Figure 1: Schematic showing how male, female, and combined natural mortality varies in our three-part model.

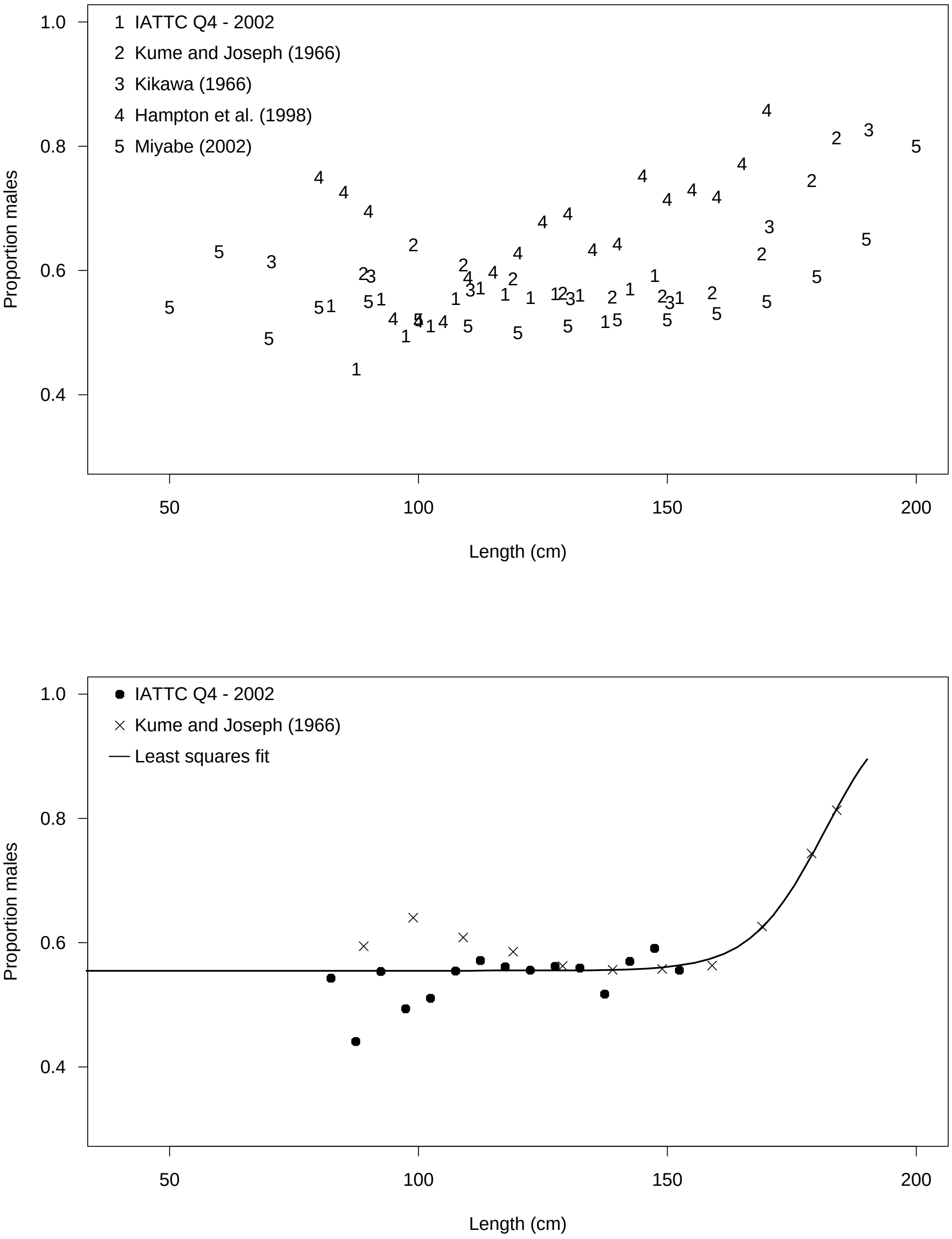


Figure 2: (Top) Data from five studies of the proportion of bigeye tuna in the catch by size-class. (Bottom) Data for the two studies, with the fit of a logistic curve, used as the basecase estimates in the analysis.

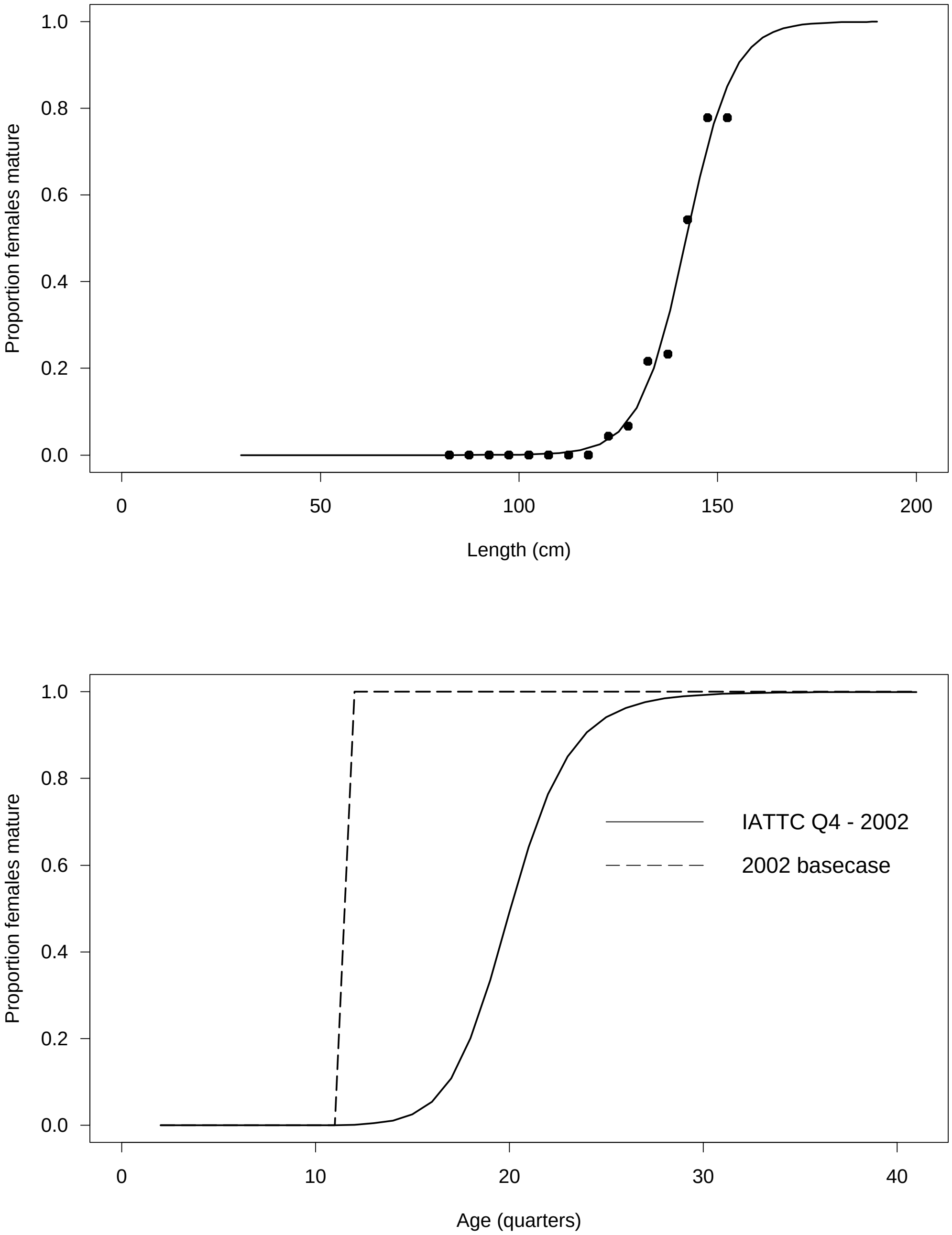


Figure 3: (Top) Observed (points) and predicted (line) proportion of female bigeye mature at size based on data presented in IATTC Quarterly Report, Q4 2002. (Bottom) Comparison between the new estimates and that used in previous assessments for the proportion of females mature by age-class.

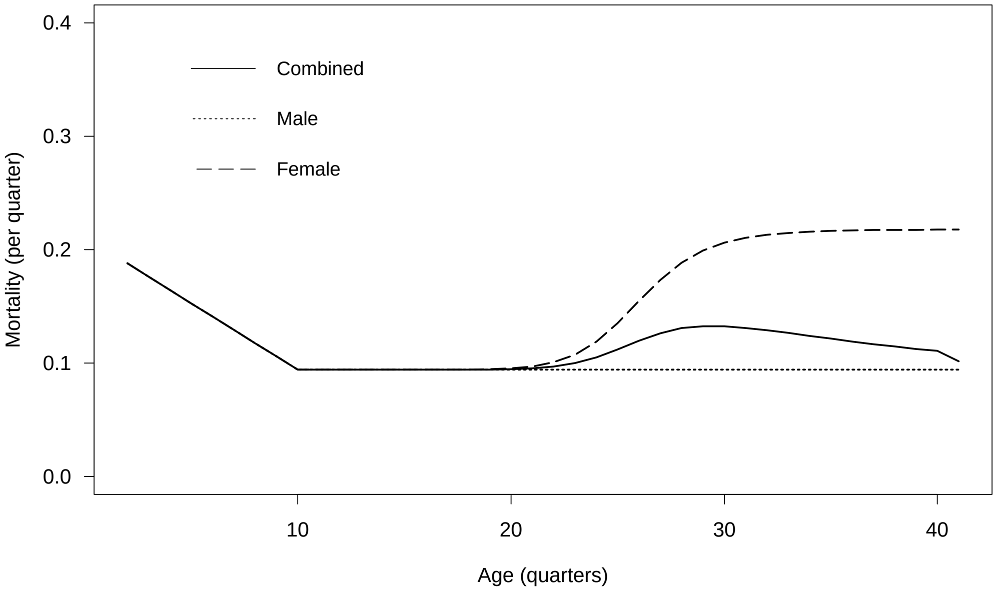
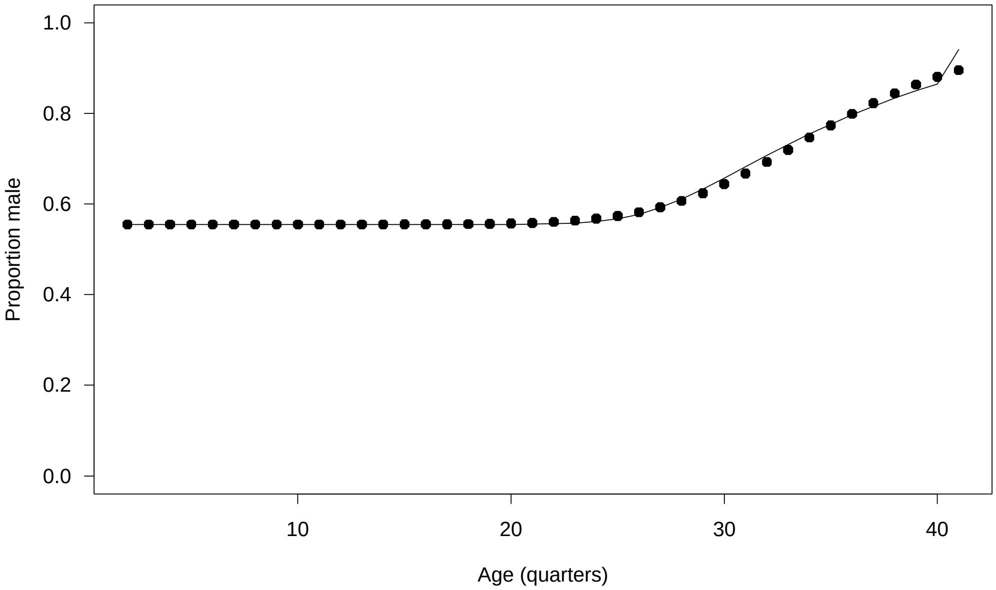


Figure 4: (Top) Estimates of male, female, and combined mortality by age class from the basecase model (i.e., $l = 6$). (Bottom) Maturity and sex ratio data used in the basecase analysis.



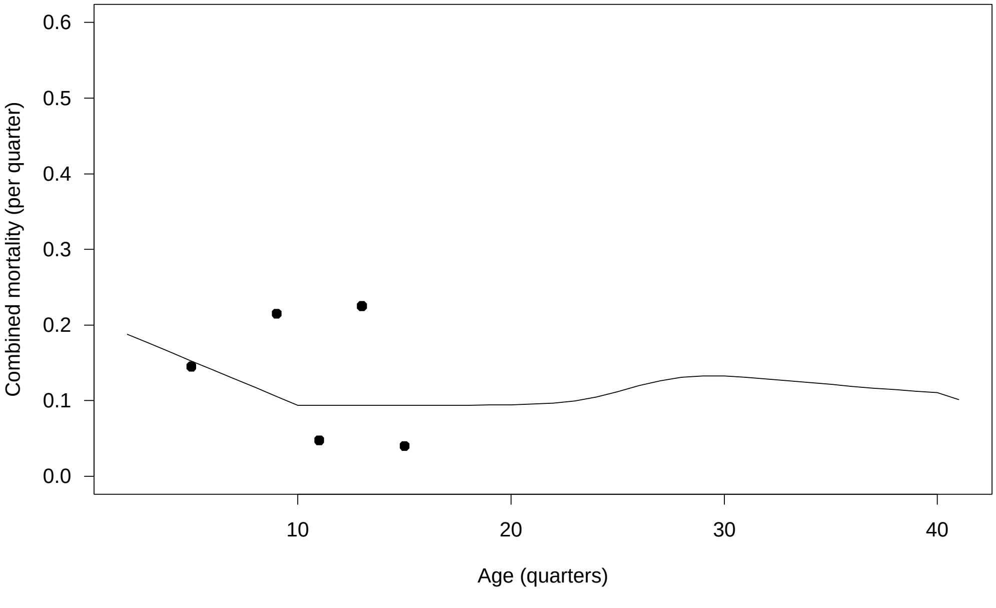
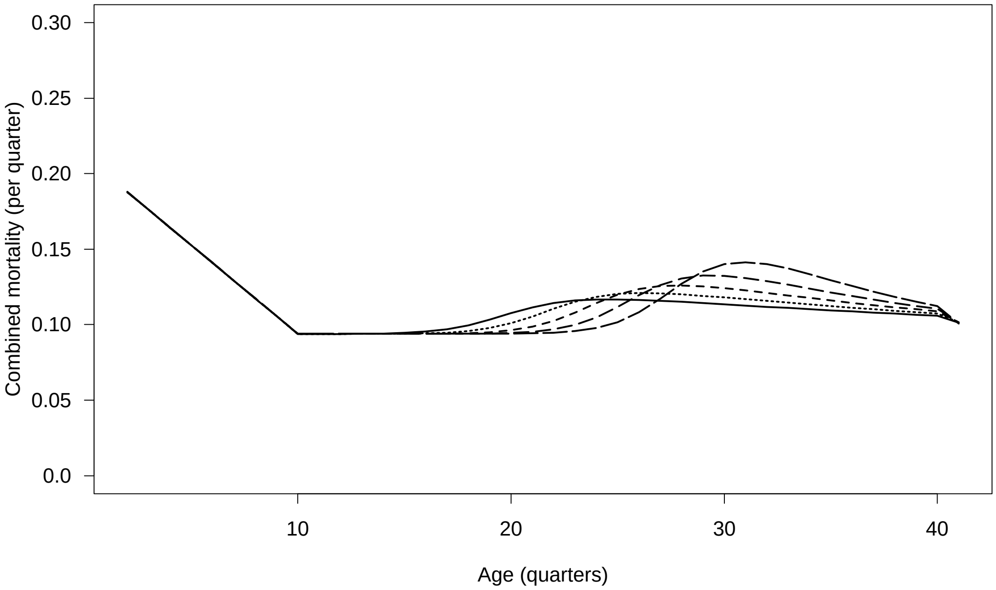


Figure 5: (Top) Observed (points) and predicted proportion of males by age-class from the basecase analysis. (Bottom) Observed (points) and predicted combined mortality by age-class from the basecase analysis



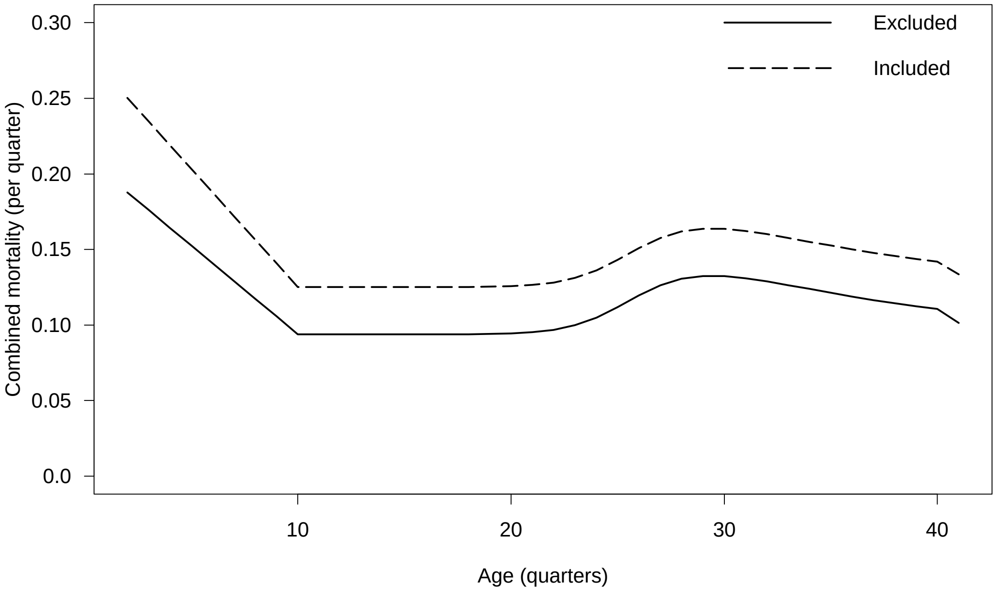


Figure 6: (Top) Estimates of combined natural mortality for the basecase data set with different values for the lag parameter. Lines with the earliest and latest peaks represent lags of zero and eight quarters respectively. (Bottom) Estimates of combined mortality for the basecase model with the first observation from the tagging study included or excluded (basecase).

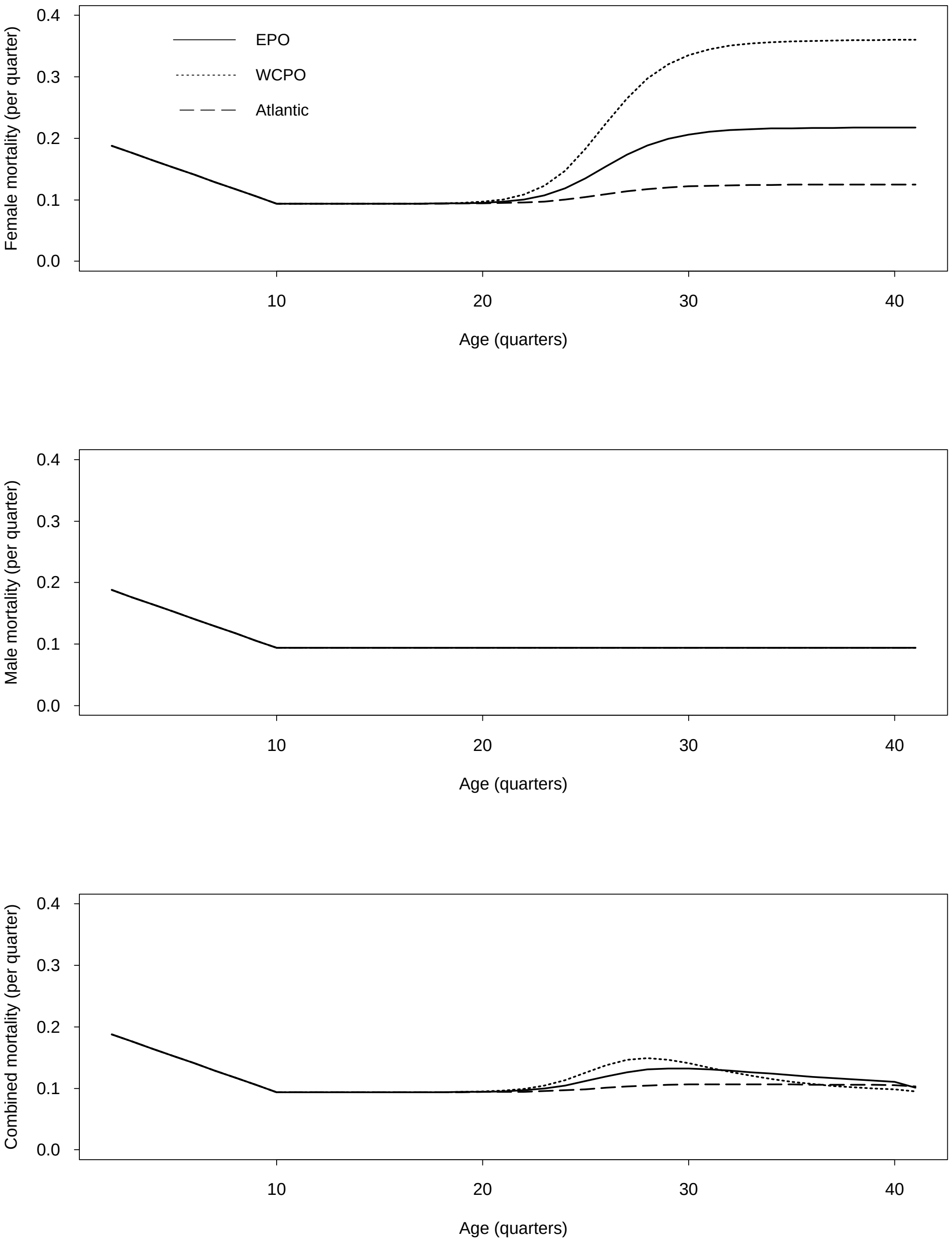


Figure 7: Comparison of estimates of female (top), male (middle), and combined (bottom) mortality based on three alternative data sets for the proportion of males in the population by age class. The EPO results represent the basecase configuration.