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PRELIMINARY ESTIMATION OF AGE- AND SEX-SPECIFIC NATURAL MORTALITY OF BIGEYE TUNA IN THE EASTERN PACIFIC OCEAN BY APPLYING A COHORT ANALYSIS WITH AUXILIARY INFORMATION TO TAGGING DATA

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SUMMARY

Cohort analysis is used to analyze release and recapture tagging data to estimate age- and sex-specific natural mortality for bigeye tuna in the eastern Pacific Ocean. The model allows simultaneously fitting to 1) tagging data, 2) estimates of natural mortality from previous analyses, and to 3) data on proportion female at age (sex ratio). The estimates of natural mortality are consistent with the values assumed in the current stock assessment. However, the estimates are highly uncertain, and dependent on the assumed reporting rate for the archival tags recaptured by the longline fishery. The apparent restricted movement of bigeye tuna inhibits mixing of the tagged fish over the whole eastern Pacific, and limits the recaptures of large tagged bigeye in the longline fishery. Therefore, a more comprehensive tagging program is needed with a wider spatial distribution of releases, releases of older bigeye tuna, improved reporting rates for conventional tags from the longline fisheries, and estimates of reporting rates.

1. INTRODUCTION

Along with growth and the steepness of the stock-recruitment relationship, natural mortality (M) is one of the most important parameters used in fisheries stock assessment models. The natural mortality value directly influences the production function of the stock, which determines the status of the stock in terms of both biomass and fishing mortality (Maunder 2003). Unfortunately, natural mortality is one of the most difficult parameters to estimate for fish populations (Vetter 1988). One of the main methods to estimate natural mortality is analysis of tagging data (*e.g.* Hampton 2000).

We develop a cohort analysis approach to analyze tag release and recapture data that also includes auxiliary information, such as previous estimates of natural mortality and proportion female data, to estimate age- and sex-specific natural mortality. We apply this method to bigeye tuna in the eastern Pacific Ocean (EPO), and determine the impact of the new estimates on management quantities estimated by a stock assessment model. We also investigate the estimation of natural mortality within the stock assessment model, and compare the results with those estimated from the tagging data.

2. METHOD

Cohort analysis is used to analyze tag release and recapture data to estimate age-specific natural mortality. The estimation method is based on the assertion that, if mortality due to fishing (the recoveries) is known, then the remaining mortality is due to natural causes, and this can be estimated by assuming that, at some age, all individuals will be dead. The method works because the number of releases must equal the number of individuals that die from natural causes plus the recoveries (assuming no emigration, and adjusting for tag shedding, reporting rates, and tag-induced mortality). Age-specific natural mortality can be estimated if releases are made at each age and the age of the individuals is known.

A tag cohort, defined in the application as all the fish released at the same age and with the same type of tag type, is modeled assuming that the recoveries are removed at the middle of the time period (quarter in the application) and releases are at the start of the time period.

$$N_{a+1} = \left(N_a e^{-0.5M_a - 0.5\eta} - \sum_g \frac{C_{g,a}}{\lambda_g} \right) e^{-0.5M_a - 0.5\eta}$$

where M_a is the natural mortality at age a, $C_{g,a}$ is the catch (recoveries) at age a in fishery g, λ_g is the reporting rate for fishery g, and η is the continuous tag-related mortality or tag loss.

To avoid computational problems, the cohort is modeled in reverse time:

$$N_a = \frac{\dfrac{N_{a+1}}{e^{-0.5M_a - 0.5\eta}} + \sum_g \dfrac{C_{g,a}}{\lambda_g}}{e^{-0.5M_a - 0.5\eta}}$$

The above model assumes that the exploitation rate on the oldest age for which recoveries are observed is one (*i.e.* the numbers of tagged fish at that age equal the number of recoveries modified by half a time period's natural mortality and tag loss). This assumption can be relaxed by dividing the recoveries for the maximum age for which recoveries are observed, for that cohort, by a terminal mortality. The age for which this is applied may differ among the cohorts modeled.

The parameters of the model are estimated by fitting the model predicted numbers for a cohort at the age at release to the actual releases adjusted by the initial tag loss and tag-related mortality τ. The standard deviation of the negative log-likelihood is assumed to be proportional to the square root of the number of releases:.

$$-\ln\left[L(\theta \mid R)\right] = \sum_i \ln\left[\sigma_R \sqrt{R_i}\right] + \frac{\left(N_{i,a} - R_i(1-\tau)\right)^2}{2\left(\sigma_R \sqrt{R_i}\right)^2}$$

2.1. Parameterizing natural mortality

There may not be enough information in the tagging data, or releases may not include all age groups, so it is not possible to estimate a natural mortality parameter for each age. Therefore, a functional form for the natural mortality may be required. Natural mortality may also differ between males and females. The natural mortality is parameterized based on "broken stick" models. The natural mortality has a linear decline from M_0 at age zero to M_c at age c, and is constant at that level until the age at maturity. The natural mortality for these ages is the same for males and females. At the age when individuals start becoming mature (a_{matLB}), natural mortality increases to $M_{A,s}$ at the age when most individuals are mature (a_{matUB}) (the maximum age in the model), which can differ between males and females.

$$M_{m,a} = \begin{cases} M_0 - \dfrac{M_0 - M_c}{c} a & a < c \\ M_c & c \le a \le a_{matLB} \\ M_c - \dfrac{M_{A,m} - M_c}{a_{matUB} - a_{matLB}} \left(a - a_{matLB} \right) & a_{matLB} < a \le a_{matUB} \\ M_{A,m} & a_{matUB} < a \end{cases}$$

$$M_{f,a} = \begin{cases} M_{m,a} & a \le a_{matLB} \\ M_c - \dfrac{M_{A,f} - M_c}{a_{matUB} - a_{matLB}} \left(a - a_{matLB} \right) & a_{matLB} < a \le a_{matUB} \\ M_{A,f} & a_{matUB} < a \end{cases}$$

The combined-sex natural mortality, which is needed if the released fish are not sexed, is calculated as

$$M_a = \frac{N_{a,f} M_{a,f} + N_{a,m} M_{a,m}}{N_{a,f} + N_{a,m}}$$

where

$$N_{f,0} = p_{f,0}$$
$$N_{m,0} = 1 - p_{f,0}$$
$$N_{s,a+1} = N_{s,a} \, \mathrm{e}^{-M_{s,a}}$$

where $p_{f,0}$ is the proportion female at age zero.

2.2. Fitting to auxiliary data

Estimates of natural mortality by age from other studies are fitted in the model using a normal-distribution-based likelihood function.

$$-\ln\left[L\left(\theta \mid M^{obs} \right) \right] = \sum_i \ln\left[\sigma_{M,i} \right] + \frac{\left(M_i^{obs} - M_a \right)^2}{2\sigma_{M,i}^2}$$

where M_i^{obs} is the value of natural mortality at age *a* for auxiliary data *i*.

The model is fitted to the proportion-female data using a binomial distribution

$$-\ln\left[L\left(\theta \mid n \right) \right] = -\sum_i n_{f,i} \ln\left[p_i \right] + n_{m,i} \ln\left[1 - p_i \right]$$

$$p_i = \frac{N_{f,a}}{N_{f,a} + N_{m,a}}$$

where p_i is the proportion female at age *a* in sample *i*.

2.3. Application

The method was applied to tagging data for bigeye tuna in the EPO, which include both archival tags and conventional tags. The model was conducted on a quarterly time step. Recoveries were aggregated into two fisheries, surface (purse seine and pole-and-line) and longline. Immediate and continuous tag loss/mortality were assumed negligible for archival tags, immediate tag loss was set equal to 3% for conventional tags (Maunder *et al.* 2007), and continuous tag loss for conventional tags was set equal to $0.1y^{-1}$ (0.025 qtr^{-1}, Maunder *et al.* 2007). A separate standard deviation is estimated for the archival and conventional tag release likelihood functions.

Estimates of natural mortality for bigeye tuna in the western and central Pacific Ocean (Hampton 2000) where used as auxiliary data. A single standard deviation for the likelihood function was used for all estimates, and was estimated as a parameter in the model.

Proportion female data were taken from the purse-seine (Schaefer *et al.* 2005) and longline fisheries (Miyabe Naozumi, pers. com.). The sample size for the longline data was divided by 100 to make the sample sizes similar to those from the purse-seine fishery. Data for large fish only were used for the longline fisheries, because the proportion female for small fish in the longline fisheries is suspected to be biased low.

Age at release (and ages for the proportion female data and auxiliary M estimates) is calculated by taking the von Bertalanffy curve used in the assessment and assigning all lengths equal to the length at age and less than the length equal to the length at age + 1 to that age.

Initial analyses suggest that there is little information in the data about the tag reporting rates. Therefore, we run the analysis fixing archival tag reporting rate for the purse-seine and the longline at several different levels (0.6, 0.7, 0.8 and 0.4, 0.6, 0.8, respectively). We also present results from an analysis that estimates all the reporting rates, and an analysis that sets the purse-seine archival tag reporting rate and the longline archival tag reporting rate to a single estimated parameter. The estimates of natural mortality are then used in the bigeye tuna assessment model developed by Aires-da-Silva and Maunder (2009) to determine 1) how consistent the estimates of natural mortality are with the assumed population dynamics and other data used in the stock assessment and 2) how they influence the estimates of management quantities. We also investigate estimating the natural mortality inside the stock assessment model and then evaluate the estimates of natural mortality with the tagging model.

3. RESULTS

The model with all the reporting rates estimated fits the release, natural mortality, and proportion female data reasonably well (Figures 1 and 2). The estimates of natural mortality appear reasonable, but are very uncertain (Figure 3); the coefficient of variation for these estimates ranges from 0.60 to 0.84 for all but the youngest ages. The results are highly dependent on the reporting rates, for which there is little information available, particularly for the archival tags caught by the longline fishery (Figures 4 to 6).

The estimates of natural mortality generally increase as the assumed reporting rates increase (Table 1). The total negative log-likelihood is similar for all reporting rates investigated. The negative log-likelihood for the sex ratio data is the same for all reporting rates investigated. The biggest change in the negative log-likelihood is due to the fit to Hampton’s estimates of natural mortality for low archival tag reporting rates for the purse-seine fisheries.

At high assumed levels of the archival (Figure 4) or conventional (Figure 6) reporting rates for the purse-seine fishery, the longline archival reporting rates are estimated to be one, and the estimates of natural mortality for mature individuals decline as the reporting rates are increased. At high reporting rates, the natural mortality of mature individuals can be less than that for age 5. Since the reporting rate has to be equal to one or less, this suggests that the reporting rate for conventional and archival tags in the purse-seine fishery should be no more than 0.7 and 0.85, respectively.

Both the natural mortality assumed in the stock assessment model and that estimated in the stock assessment model provide slightly worse fits to the tag recovery data and moderately worse fits to Hampton’s natural mortality estimates (Table 1).

When the natural mortality from the tagging analysis is used in the stock assessment model, the negative log-likelihood is moderately better than the current assessment, but not as good as when the natural mortality is estimated within the stock assessment model (Table 1). The improved fit occurs in the two main data sets (indices of abundance based on catch per unit of effort (CPUE) and length composition data) and in the penalty on the temporal recruitment deviates. The fit to the data is better for the higher reporting rates, and consequently for the higher levels of natural mortality.

The estimates of management parameters from the stock assessment model are sensitive to the assumed value of the reporting rates (Table 1). The higher the reporting rates, the more optimistic the estimated stock status. Maximum sustainable yield (MSY), the current spawning biomass relative to the spawning biomass corresponding to MSY, and the *F* multiplier (the current effort as a ratio of the effort corresponding to MSY) all generally increase with the assumed value for the reporting rate. The estimates of *F* multiplier are highly dependent on the longline archival tag reporting rate (Figure 7).

4. DISCUSSION

The results of the tagging analysis suggest that the general trend in age- and sex-specific natural mortality used in the current stock assessment for bigeye in the EPO (Aires-da-Silva and Maunder 2009) is reasonable, except that the natural mortality for males may also increase as they mature. However, there is great uncertainty in the estimates, and they are highly dependent on the reporting rate for archival tags recaptured by the longline fishery.

Application of the cohort analysis approach requires reporting of every tagged individual that is recaptured, or reliable estimates of reporting rates. Reporting rate experiments for purse-seine vessels were considered unsuccessful due to tag shedding problems (Maunder *et al.* 2007). It was thought that improper placement of tags by inexperienced taggers caused high levels of tag loss while the fish were in the vessel wells. The reporting rate analysis used logistic regression with species (bigeye, yellowfin, and skipjack tuna), tag type (single- or double-tagged), and fish length as explanatory variables. The estimates of reporting rate for bigeye tuna ranged from 0.55 to 0.85. The reporting rate declined with length, and was higher for double-tagged fish (Figure 8). The estimates of conventional tag reporting rates for purse-seine fisheries from the cohort analysis are consistent with the tag reporting rates of Maunder *et al.* (2007), suggesting that the estimates of Maunder *et al.* (2007) may not be as biased as initially thought. Reporting rates of conventional tags from longline vessels in the EPO are considered to be poor, which is corroborated by the estimates from this study.

The cohort-analysis approach treats the fishing mortality of tagged fish at age as independent from the fishing mortality experienced by the stock as a whole. This accommodates any incomplete mixing of the tagged fish over the whole distribution of the stock. Comparison of the observed recoveries by fishery with the expected recoveries of archival tags based on estimates of fishing mortality rates from the assessment model show that there are more purse-seine recoveries and less longline recoveries than expected (Figure 9). The non-mixing is apparent in the archival tag movement trajectories compared to the spatial distribution of the catch by fishery (Schaefer and Fuller 2009; Figure 10). In particular, few tagged individuals move into the areas comprising the majority of the longline catch, although the movement illustrated in Figure 10 may be biased if the tagged fish caught in the longline fishery are not reported. The low recovery rate for the longline fishery could also be due to low reporting rates. Comparison of the archival tag recoveries in the longline fishery as a ratio of the archival tag recoveries in the purse-seine fishery with the catch in the longline fishery as a ratio of the catch in the purse-seine fishery suggests that the reporting rate for archival tags in the longline fishery is considerably less than in the purse-seine fishery. However, the ratio of observed recoveries to expected recoveries increases with age, and is probably related to the time at liberty, indicating that the low recovery rate in the longline fishery is due to the slow mixing rate (Figure 9).

Higher reporting rates correspond to higher levels of natural mortality. Some of the reporting rates also correspond to increased natural mortality for mature males. The negative log-likelihood for the stock assessment model is lower for higher natural mortality rates, suggesting that the higher natural mortality is more consistent with the assumed population dynamics of bigeye tuna in the EPO and the size composition data and the CPUE data. One interesting aspect of the higher natural mortality rates is that they increase the estimated recruitment for the period prior to the expansion of the purse-seine fishery on floating-objects (Figure 11). In the current assessment, the estimated recruitment increases around the time of the expansion of that fishery. It has been suggested that this is a consequence of a "new" component of the stock being fished. However, it may be due to the simultaneous decline in the longline catch and a misspecified natural mortality.

The method used to analyze the tagging data assumes that, at the time of the last recapture, all the tagged fish are dead, but this may not be true for the more recent tagging experiments. We excluded data from the more recent experiments to avoid this bias. If old fish are not selected by the fisheries or, as in this application, the fisheries that catch the old fish have low reporting rates, there may be fish not represented in the analysis.

Other factors that may bias the estimates of natural mortality include tag loss and tag-induced mortality. Tag loss is included in the model, based on estimates from double-tagging experiments (Maunder *et al.* 2007). Initial tag loss has been shown to be low, and continuous tag loss moderate. No estimates of tag-related mortality are available. Initial tag-related mortality would reduce the effective number of releases, and continuous tag-related mortality would be confounded with natural mortality. Both cases would cause natural mortality to be overestimated.

The modeling approach will continue to be improved, by including tag return data as it arises, and with additional analyses. For example, incorporating data into the analysis by release group (*i.e.* year of release) will allow evaluation of residuals in more detail. This may help determine which release groups have been effectively removed from the stock, so that the exploitation rate of the last year is one. Finally, integrating the cohort analysis method with the stock assessment model would allow the length-frequency data to also provide information on natural mortality. This may provide information on the increase in natural mortality for mature males.

The natural mortality estimates are highly dependent on the recoveries of old bigeye tuna caught in the longline fishery. There is no information in the data on the reporting rates for the archival tags caught in the longline fishery, and therefore the estimates of natural mortality are highly uncertain. Our results suggest that a more comprehensive tagging program is needed, with a wider spatial distribution of releases, releases of older bigeye tuna, improved reporting rates of conventional tags from the longline fisheries, and estimates of reporting rates.

ACKNOWLEDGEMENTS

Miyabe Naozumi provided the proportion-female data for the Japanese longline fishery.

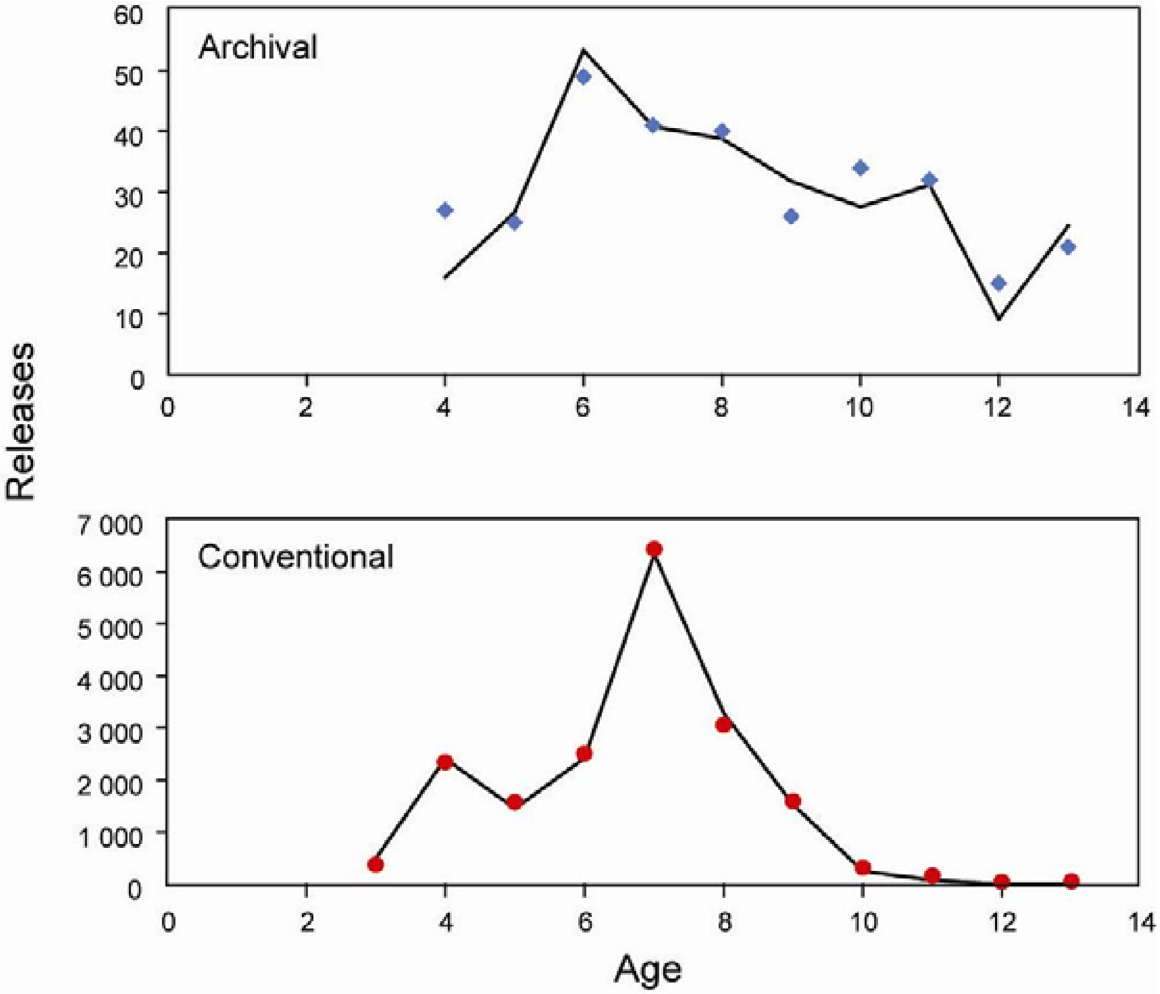

FIGURE 1. Fit of the model to the number of releases, by tag type.

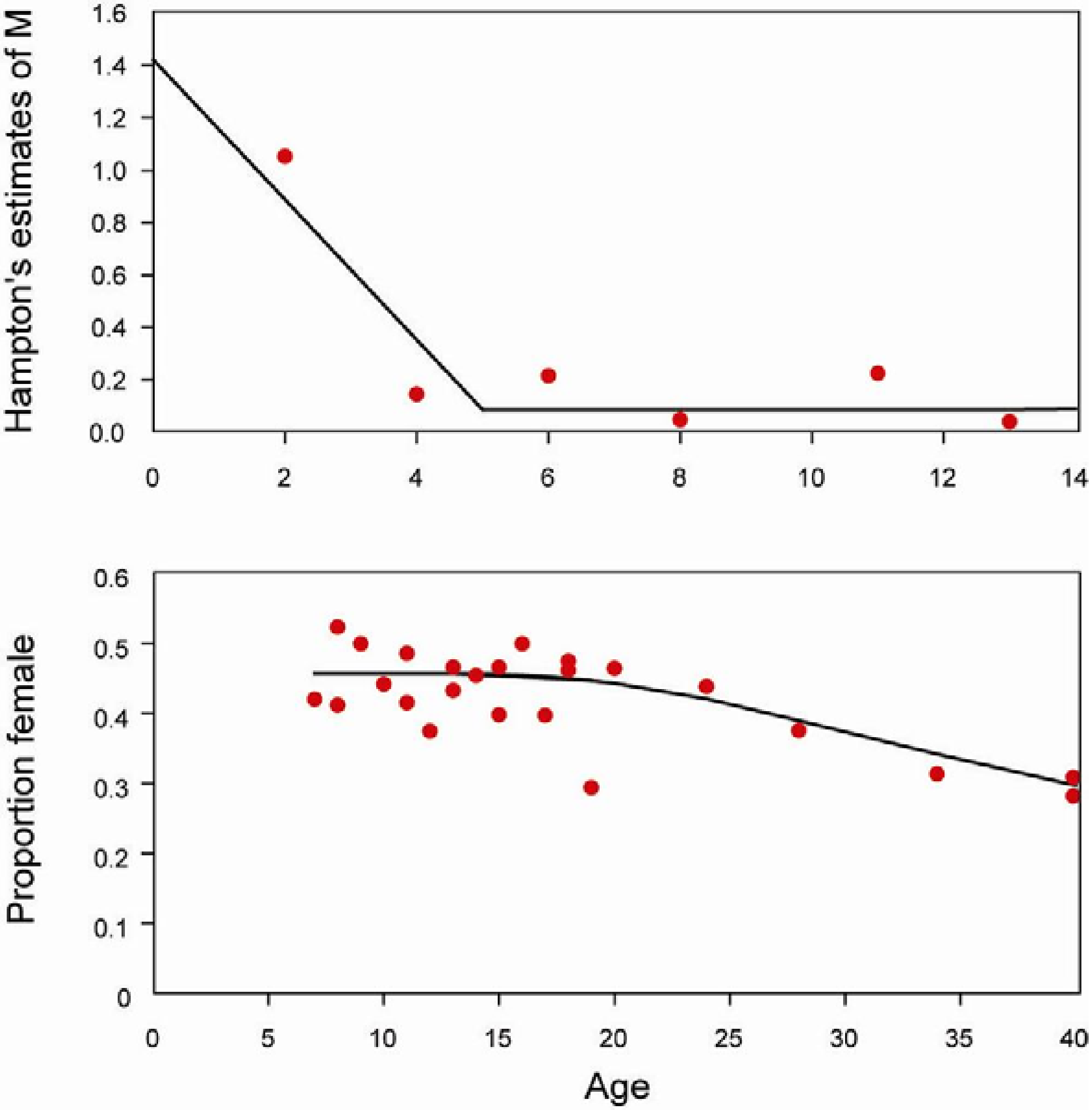

FIGURE 2. Fit to Hampton's (2000) estimates of natural mortality (top) and the proportion-female data (bottom).

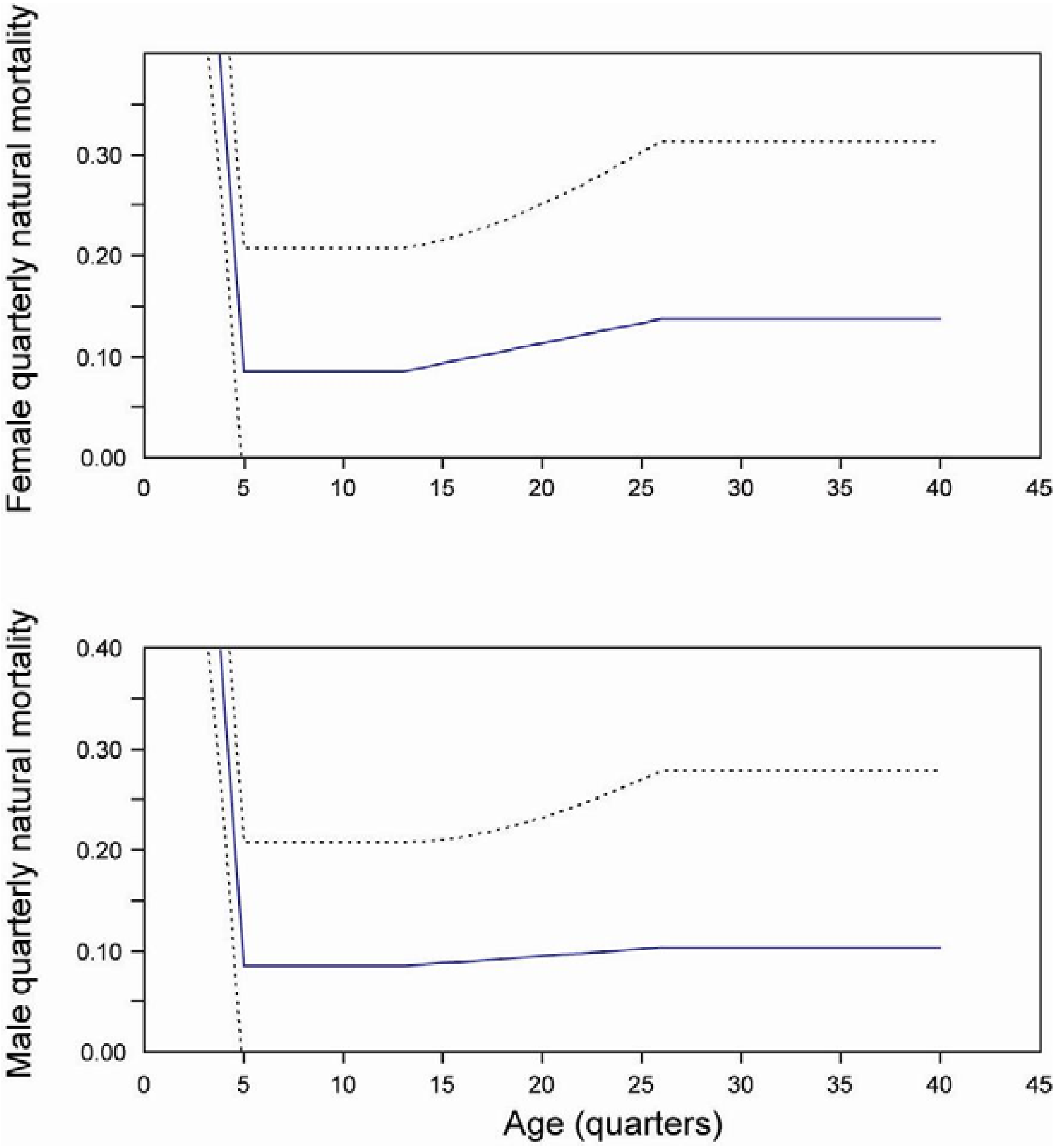

FIGURE 3. Estimates of female (top) and male (bottom) quarterly natural mortality, by age in quarters, with 95% confidence intervals. The range of the y-axis has been restricted to show the contrast in the natural mortality for old bigeye.

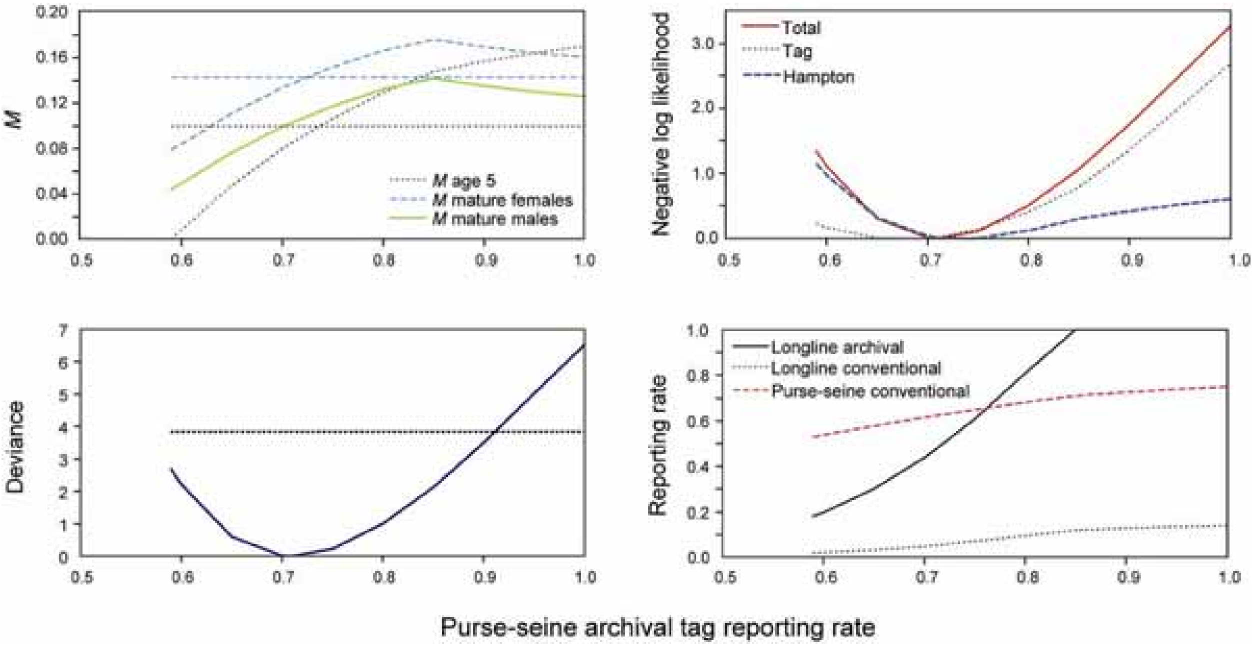

FIGURE 4. Estimates of natural mortality (top left), negative log-likelihood (top right), deviance (bottom left), and reporting rates (bottom right) for different fixed values of the archival tag reporting rates for the purse-seine fishery. The horizontal lines in the top left figure represent the natural mortality rate for intermediate-aged bigeye (dotted line) and the mature females (dashed line) assumed in the stock assessment. The horizontal line in the bottom left figure is the deviance corresponding to the 95% confidence interval.

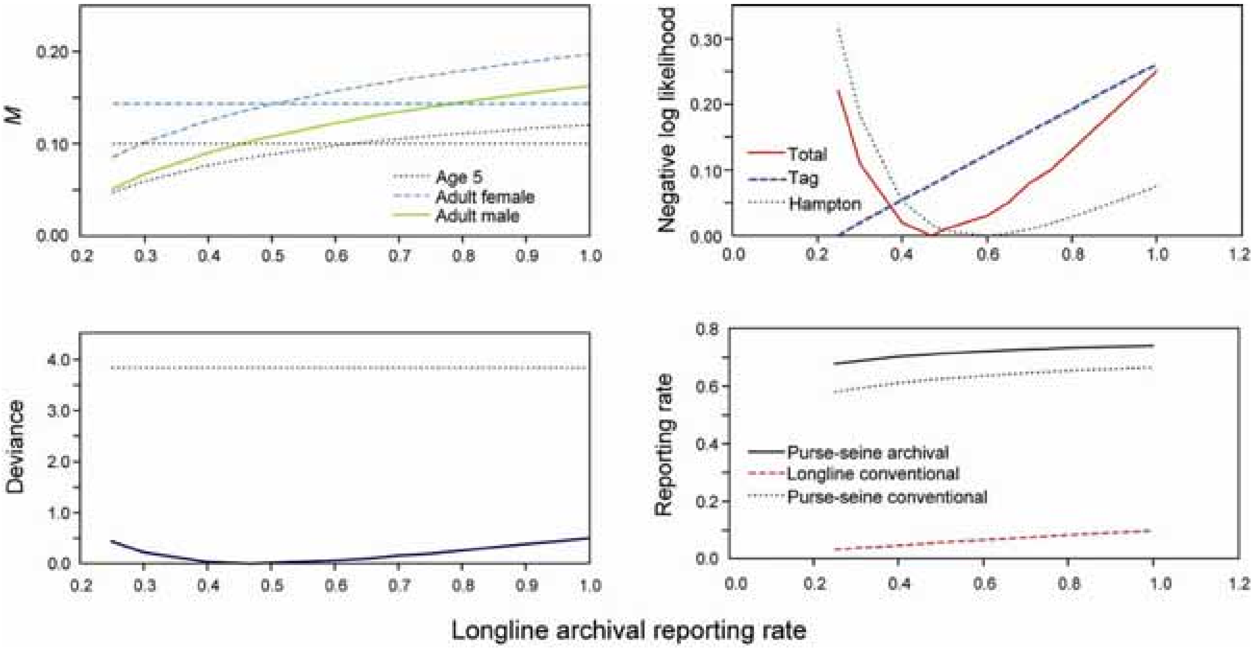

FIGURE 5. Estimates of natural mortality (top left), negative log-likelihood (top right), deviance (bottom left), and reporting rates (bottom right) for different fixed values of the archival tag reporting rates for the longline fishery. The horizontal lines in the top left figure represent the natural mortality rate for intermediate aged bigeye (dotted line) and the mature females (dashed line) assumed in the stock assessment. The horizontal line in the bottom left figure is the deviance corresponding to the 95% confidence interval.

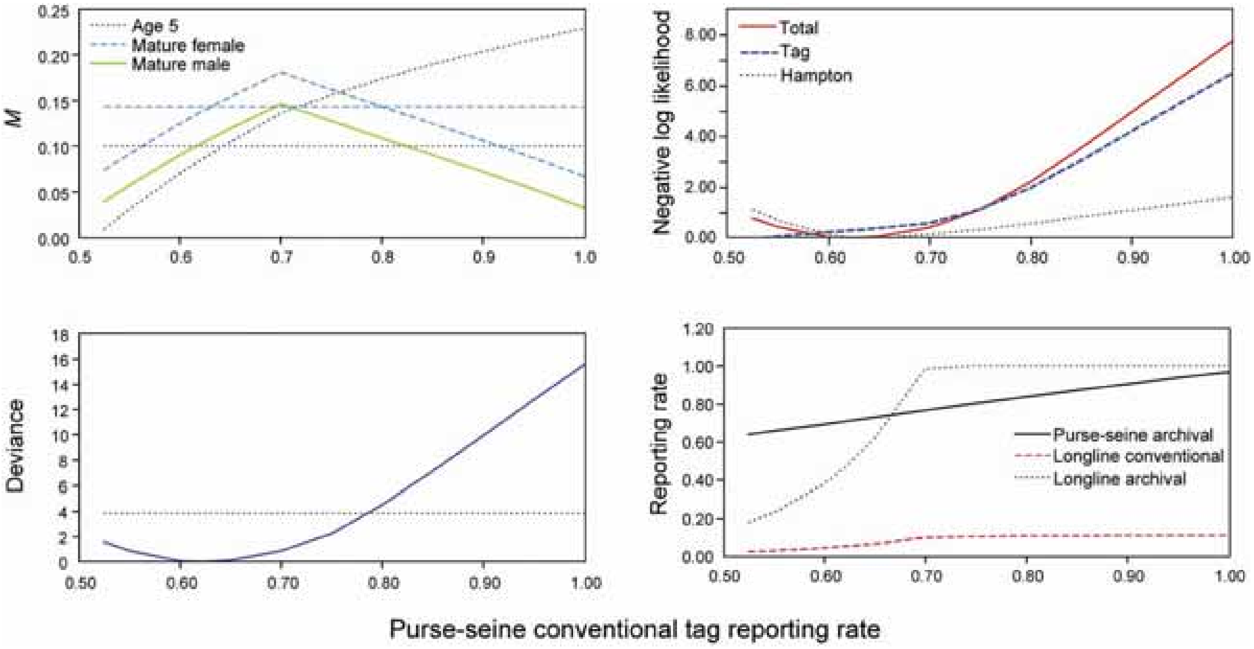

FIGURE 6. Estimates of natural mortality (top left), negative log-likelihood (top right), deviance (bottom left), and reporting rates (bottom right) for different fixed values of the conventional tag reporting rates for the purse-seine fishery. The horizontal lines in the top left figure represent the natural mortality rate for intermediate-aged bigeye (dotted line) and the mature females (dashed line) assumed in the stock assessment. The horizontal line in the bottom left figure is the deviance corresponding to the 95% confidence interval.

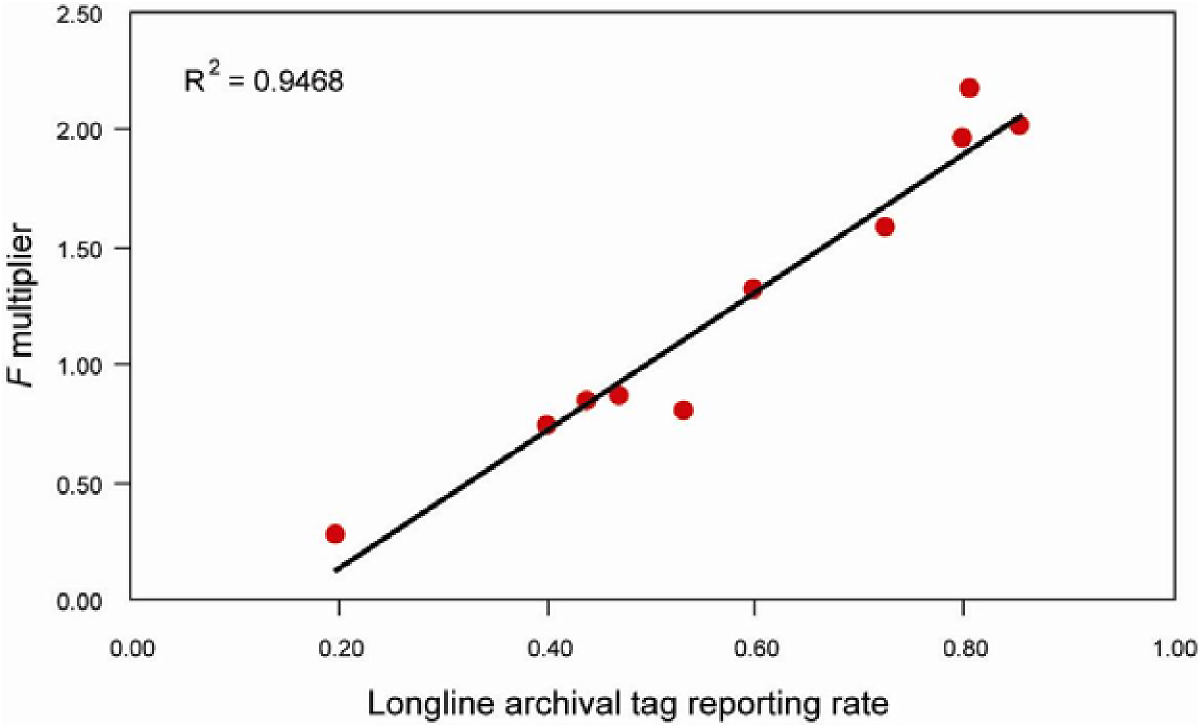

FIGURE 7. Correlation of the estimated *F* multiplier with the assumed value of the reporting rate of archival tags by the longline fishery.

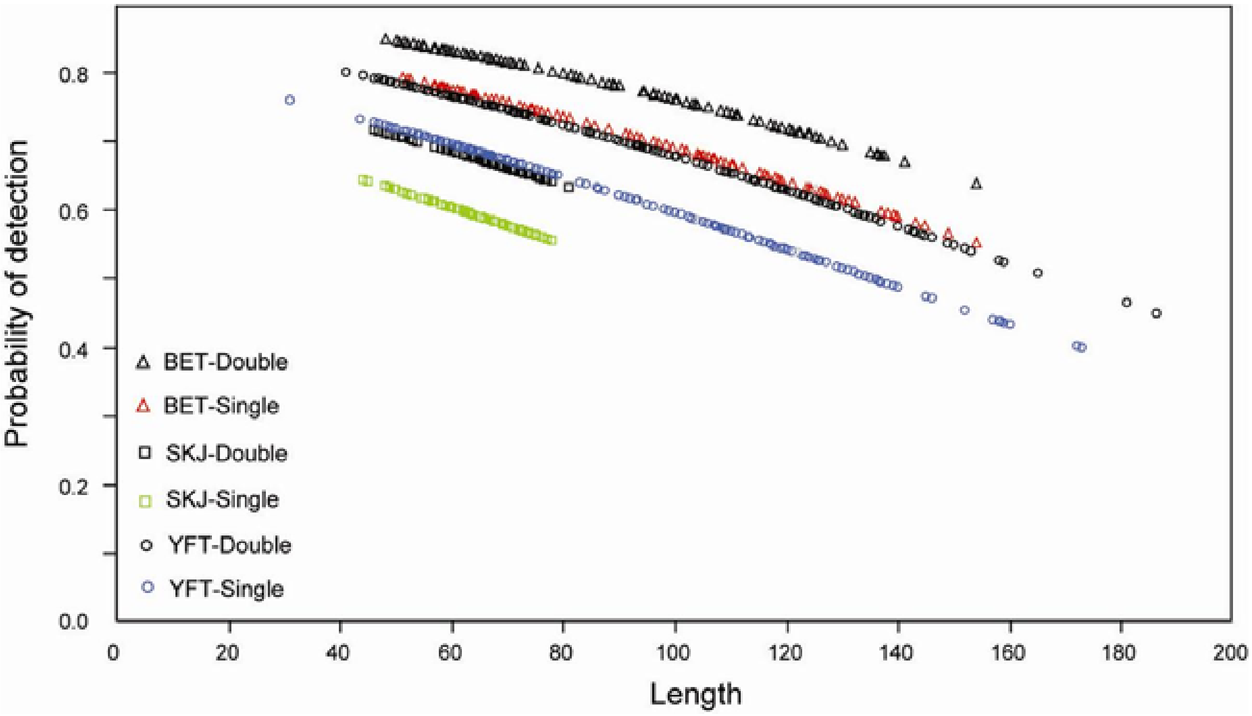

FIGURE 8. Estimates of reporting rate from a tag-seeding experiment, using logistic regression with species, tag type (single or double tagged), and length as explanatory variables. BET = bigeye tuna, SKJ = skipjack tuna, YFT = yellowfin tuna.

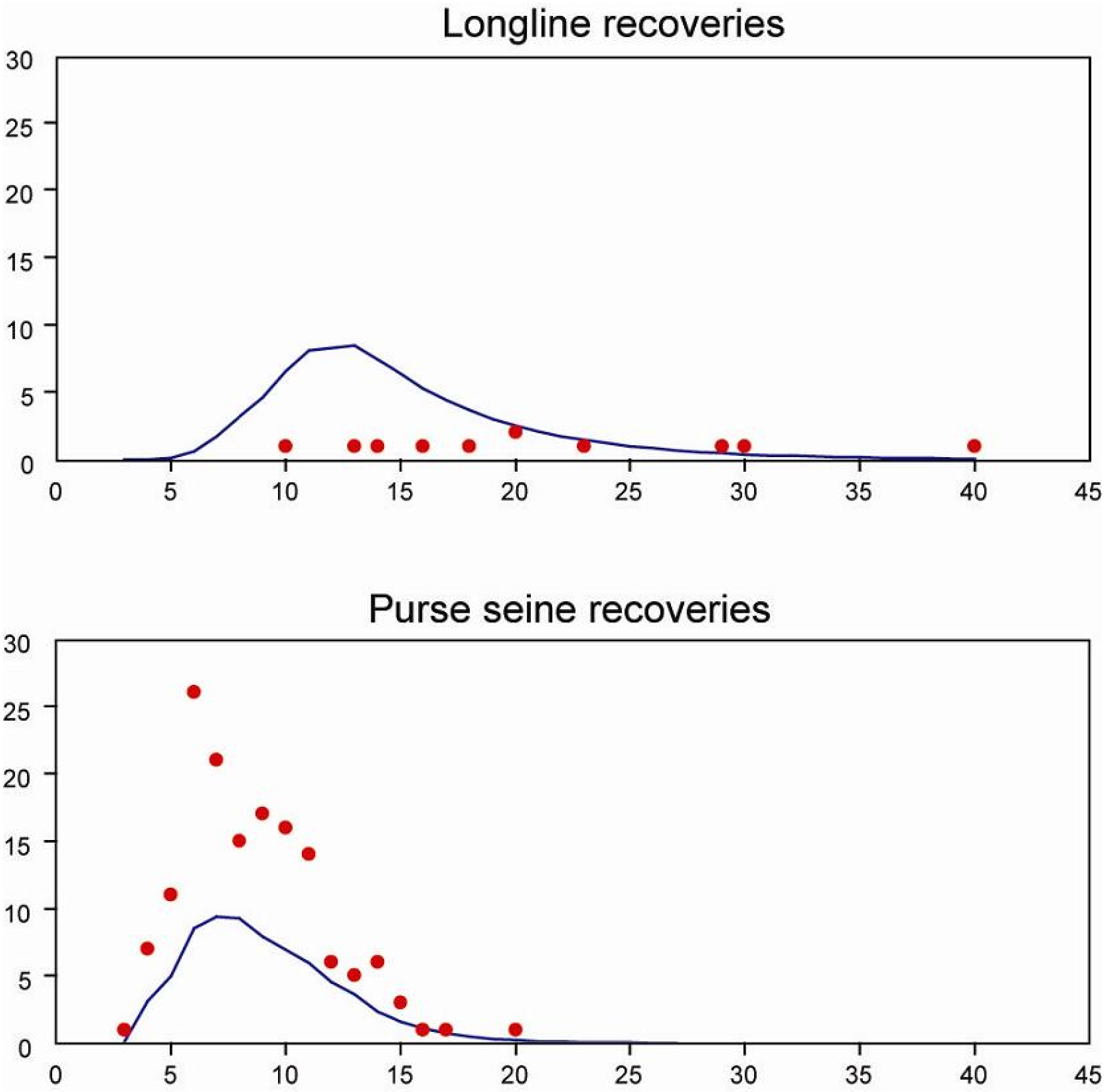

FIGURE 9. Comparison of observed and expected recoveries of archival tags from the longline fishery (top) and the purse-seine fishery (bottom). The expected recoveries are calculated by modeling the releases at age over time and applying the average (2000-2005) fishing mortality at age estimated by putting the estimates of natural mortality from the tagging model (all reporting rates estimated) into the stock assessment.

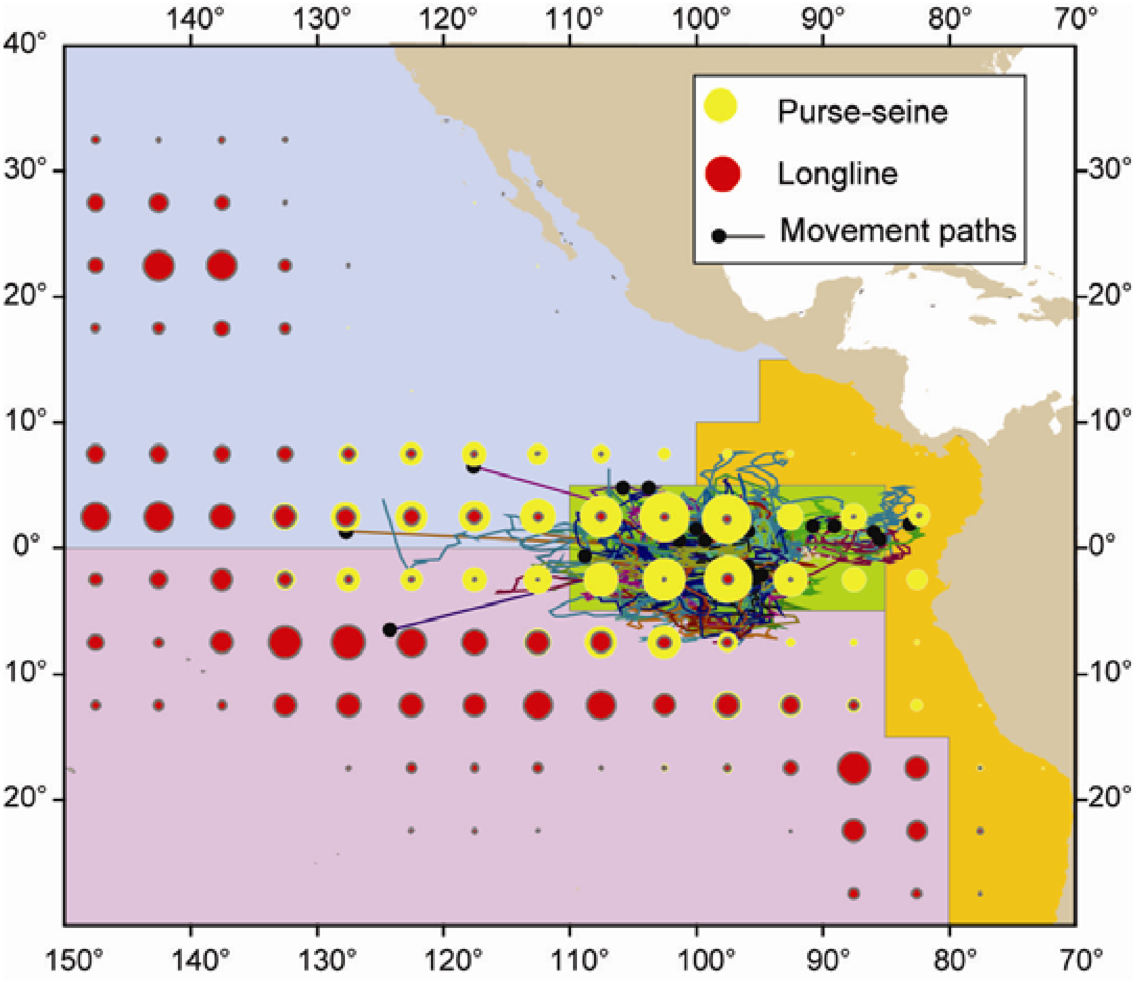

FIGURE 10. Comparison of archival tag movement tracks with spatial distribution of longline (red) and purse seine (yellow) catch. The catch is the average over 2000-2006, and includes all data available in the IATTC databases. The archival tag movement paths are based on data from 2000-2006 (Schaefer and Fuller 2009).

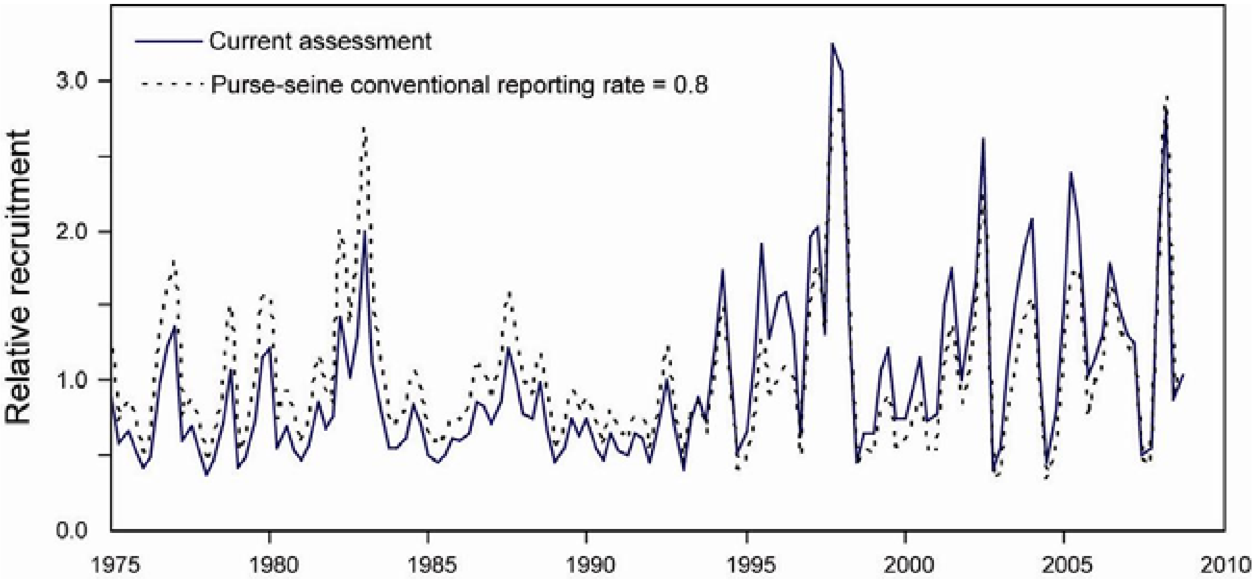

FIGURE 11. Estimates of relative recruitment from the current assessment (Aires-da-Silva and Maunder 2009) and from an assessment using estimates of natural mortality based on the cohort analysis with the purse-seine archival tag reporting rate set at 0.8.

TABLE 1. Negative log-likelihoods, parameter estimates, and estimates of management quantities. MLE is the analysis that estimates the reporting rates for both fishing methods and both tag types. SS3 estimates are the results based on estimating the natural mortality inside the stock assessment model. Share RR is the analysis that assumes the longline and purse-seine archival tag reporting rates are the same. Base case is based on the natural mortality rates used in the current stock assessment (Aires-da-Silva and Maunder 2009). sd is standard deviation.

	Purse seine			**Longline**			**MLE**	**SS3 estimates**	**Share RR**	**Base case**
	0.60	0.70	0.80	0.40	0.60	0.80				
Tagging model negative log-likelihood										
Total	3077.94	3076.84	3077.33	3076.85	3076.86	3076.96	3076.83	3085.07	3076.92	3084.29
Tag	79.68	79.52	79.92	79.51	79.58	79.65	79.54	80.81	79.63	80.75
Hampton M	-8.03	-8.97	-8.88	-8.95	-9.01	-8.98	-8.99	-3.02	-8.99	-2.96
Sex ratio	3006.29	3006.29	3006.29	3006.29	3006.29	3006.29	3006.29	3007.27	3006.29	3006.50
Reporting rates										
LL archival	0.20	0.44	0.81	0.40	0.60	0.80	0.47	0.85	0.73	0.53
PS archival	0.60	0.70	0.80	0.70	0.72	0.73	0.71	0.71	0.73	0.73
LL conventional	0.02	0.05	0.09	0.05	0.07	0.08	0.05	0.11	0.08	0.09
PS conventional	0.54	0.61	0.68	0.61	0.64	0.65	0.62	0.60	0.65	0.60
M estimates										
M_0	1.42	1.42	1.40	1.43	1.41	1.40	1.42	0.25	1.41	0.25
M_c	0.01	0.08	0.13	0.08	0.10	0.11	0.09	0.10	0.11	0.10
M_A female	0.08	0.13	0.17	0.12	0.16	0.18	0.14	0.22	0.17	0.14
M_A male	0.05	0.10	0.13	0.09	0.12	0.14	0.10	0.16	0.14	0.10
Ages for broken stick										
C_{age}	5	5	5	5	5	5	5	4	5	NA
AmatLB	13	13	13	13	13	13	13	14	13	NA
AmatUB	26	26	26	26	26	26	26	26	26	NA
Initial sex ratio										
initialSR	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46
Likelihood standard deviation scaling parameters										
Archival sd	0.96	1.02	1.09	1.01	1.03	1.05	1.02	1.15	1.04	1.14
Conventional sd	4.60	4.31	4.20	4.32	4.26	4.23	4.29	4.31	4.24	4.34
M sd	0.16	0.14	0.14	0.14	0.14	0.14	0.14	0.37	0.14	0.37
Stock assessment model negative log-likelihood										
CPUE	-238.94	-269.46	-273.50	-267.92	-272.26	-272.91	-270.35	-258.54	-272.76	-269.06
Length composition	1622.03	1627.52	1624.87	1631.12	1620.48	1614.12	1627.08	1581.73	1615.52	1648.30
Age composition	321.66	315.14	307.87	315.28	312.37	309.79	314.34	21.18	310.75	307.64
Recruitment	11.73	-31.87	-37.63	-29.47	-37.01	-37.75	-33.51	-31.52	-37.79	-29.99
Total	1716.48	1641.32	1621.61	1649.01	1623.59	1613.26	1637.80	1312.86	1615.96	1656.89
Stock assessment management quantities										
MSY	88,052	82,612	131,300	80,010	99,310	124,193	84,849	128,054	113,271	83,615
B_{MSY}	595,578	269,328	263,524	276,026	262,242	281,326	262,990	376,361	271,875	289,475
S_{MSY}	185,393	58,882	35,735	62,716	48,343	44,607	55,323	67,666	45,949	60,631
B_{MSY}/B_0	0.28	0.23	0.21	0.24	0.22	0.22	0.23	0.24	0.22	0.25
S_{MSY}/S_0	0.27	0.17	0.11	0.18	0.15	0.13	0.16	0.17	0.14	0.19
C_{recent}/MSY	1.13	1.20	0.76	1.24	1.00	0.80	1.17	0.78	0.88	1.19
B_{recent}/B_{MSY}	0.20	1.08	2.28	0.93	1.63	2.15	1.2	2.05	1.98	0.99
S_{recent}/S_{MSY}	0.12	0.96	2.86	0.79	1.68	2.47	1.09	2.13	2.18	0.89
F multiplier	0.28	0.84	2.17	0.74	1.32	1.96	0.87	2.01	1.58	0.81

TABLE 2. Estimates of longline archival tag reporting rates relative to purse-seine archival tag reporting rates, based on catch ratios.

Number of quarters for mixing	LL/PS catch ratio		Tag recapture LL/PS ratio	Relative reporting rate LL/PS	
	Ratio weighted based	Weight ratio based		Ratio weighted based	Weight ratio based
0.00	1.28	1.58	0.35	0.27	0.22
1.00	1.51	1.99	0.89	0.59	0.45
2.00	1.91	2.51	1.17	0.61	0.46
3.00	2.43	3.19	1.75	0.72	0.55
4.00	3.06	4.06	1.67	0.55	0.41

REFERENCES

Aires-da-Silva A. and M.N. Maunder. 2009. Status of bigeye tuna in the eastern Pacific Ocean in 2008 and outlook for the future. Inter-Amer. Trop. Tuna Comm., Stock Assess. Rep. 10..

Hampton, J. (2000). Natural mortality rates in tropical tunas: size really does matter. Can. J. Fish. Aquat. Sci. 57: 1002–1010

Maunder, M.N. (2003) Is it time to discard the Schaefer model from the stock assessment scientist's toolbox? Fisheries Research, 61: 145-149.

Maunder, M.N., Schaefer, K., Fuller, D., and Altamirano Nieto, E. (2007) Estimating tag reporting and tag shedding for tunas in the EPO. In: Report of the Inter-American Tropical Tuna Commission Workshop on Using Tagging Data for Fisheries Stock Assessment and Management, compiled by Maunder, M.N. http://www.iattc.org/PDFFiles2/Tagging-WS-Oct-2007-Report-ENG.pdf

Schaefer, K.M. and D.W. Fuller. 2009. Horizontal movements of bigeye tuna (Thunnus obesus) in the eastern Pacific Ocean, as determined from conventional and archival tagging experiments initiated during 2000-2005. Inter-Amer. Trop. Tuna Comm., Bull., in press.

Schaefer, K.M., Fuller, D.W., and Miyabe, N. (2005). Reproductive biology of bigeye tuna (*Thunnus obesus*) in the eastern and central Pacific Ocean. Inter-American Tropical tuna Commission Bulletin 23(1):1-31.

Vetter, E.F. (1988). Estimation of natural mortality in fish stocks: a review. Fishery Bulletin 86(1): 25-43.