

Natural mortality rates in tropical tunas: size really does matter

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Abstract: Important size-related variability in natural mortality rates has been revealed in populations of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) in the western tropical Pacific Ocean using a new, size-structured tagging model. The tagging data were classified into release groups by size at release, and a growth model was used to predict size at each time at liberty interval. Natural and fishing mortality rates were categorized by broad size-classes and estimated by maximum likelihood. The method incorporates a correction for incomplete mixing of new releases. For each population, the natural mortality rate declined by about an order of magnitude over the initial size-classes. For skipjack and yellowfin tuna, there was also evidence of elevated natural mortality for some of the larger size-classes. Size- or age-related variability in natural mortality is likely to have important implications for tropical tuna stock assessment in the western Pacific.

Résumé : On a observé que le taux de mortalité naturelle variait fortement en fonction de la taille chez des populations de bonite à ventre rayé (*Katsuwonus pelamis*), d'albacore (*Thunnus albacares*), et de thon obèse (*Thunnus obesus*), de l'ouest du Pacifique tropical, à l'aide d'un nouveau modèle des données de marquage structuré selon la taille. Les données de marquage ont été classées en groupes de lâchers en fonction de la taille au lâcher, et un modèle de croissance a été utilisé pour prédire la taille à chaque intervalle de temps en liberté. Les taux de mortalité naturelle et par pêche ont été répartis en catégories selon des grandes classes de taille et estimés par la technique de la probabilité maximale. La méthode comporte une correction pour le mélange incomplet des poissons nouvellement libérés. Pour chaque population, le taux de mortalité naturelle diminuait d'environ un ordre de grandeur par rapport aux classes de taille initiales. Dans le cas de la bonite à ventre rayé et de l'albacore, on a relevé des signes de mortalité naturelle élevée chez certaines classes de poissons de grande taille. La variabilité de la mortalité naturelle liée à la taille ou à l'âge aura vraisemblablement des effets importants pour l'évaluation des stocks de thons tropicaux dans l'ouest du Pacifique.

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Introduction

The natural mortality rate (M) is the aggregate of several processes, including predation, starvation, and senescence, that can rarely be observed in natural fish populations. Consequently, it is difficult to estimate accurately and is frequently a major source of uncertainty in fish stock assessments (Vetter 1987).

It has been long recognized (e.g., Beverton and Holt 1957; Ricker 1975) that the biological processes producing natural mortality are likely to vary substantially over the life span of a fish. Most early studies of variability in M were based on catch-curve analyses of lightly exploited populations, which showed increases in total mortality with age over the exploited phase (for details, see Beverton and Holt 1957). Although the details may vary considerably among species, there seems to be general agreement that M is likely to be high during early juvenile stages, low during the onset of adulthood, and increasing with senescence to produce an overall U-shaped function (Vetter 1987). Despite the com-

elling logic of this theory, there is little evidence that estimates of size- or age-dependent M are routinely used in many fisheries stock assessments. For example, none of the approximately 400 M estimates reported in FishBase 97 (Froese and Pauly 1997) are size or age specific. However, given the difficulties in estimating even an average value of M , this is not altogether surprising.

In this paper, I present analyses of tagging data to derive size-specific estimates of M and fishing mortality rate (F) for three species of tuna in the western tropical Pacific Ocean: skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*). The method of analysis is new and is potentially applicable to other fish species for which suitable tagging data and information on growth are available. The results show that M for the small juvenile size-classes is up to an order of magnitude higher than for mid-sized fish. For skipjack and yellowfin tuna, there was also evidence of elevated M for some of the larger size-classes. Such size-related variability in M is likely to have important effects on stock assessments for these species.

Materials and methods

Western Pacific tuna fishery

The western Pacific tuna fishery, which extends from the Philip-

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lines to about 160°W longitude (Fig. 1), provides about 50% of the world's current tuna production. Since 1990, total annual catches have been about 1 500 000 t, comprising mainly skipjack (67%), yellowfin (25%), and bigeye tuna (6%) (Lawson 1998). The three species are caught by purse seiners operating in the equatorial band (60% of the total catch). Skipjack tuna are also caught by pole-and-line vessels (8%) and yellowfin and bigeye tuna by longliners (7%) in the same area. Small-scale fisheries in Indonesia and the Philippines catch mainly juvenile tuna and contribute about 25% of the total regional catch.

The diverse character of the western Pacific tuna fishery results in significant exploitation of the three species over much of their size range. Skipjack, yellowfin, and bigeye tuna as small as 20 cm fork length (FL) are captured by the small-scale fisheries in the Philippines. Purse seiners capture skipjack tuna over their entire adult size range (about 40–80 cm FL), yellowfin tuna as juveniles and younger adults (about 40–120 cm FL), and bigeye tuna mainly as juveniles (about 40–100 cm FL). Longliners capture yellowfin and bigeye tuna over their entire adult size range (about 100–180 cm FL). Assessment of the impacts of these components of the fishery on the stocks and on each other requires information on *M* and its variability over the exploited size ranges.

Tagging data

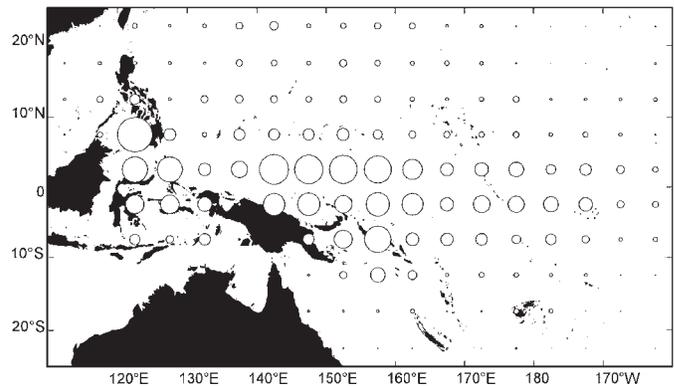
The data analyzed in this paper consisted of tag releases and returns of skipjack, yellowfin, and bigeye tuna tagged during the Secretariat of the Pacific Community's Regional Tuna Tagging Project (RTTP). Tuna were tagged during the period July 1989 to December 1992, with the tag releases and returns covering the main tuna fishing area of the western tropical Pacific (Fig. 2). Most of the tagging was carried out from a chartered pole-and-line vessel, supplemented in some countries by short-term charters on commercial pole-and-line vessels. Standard tuna tagging equipment and techniques (Hampton 1997) were used throughout. Most tuna were single tagged, with a sample double tagged to estimate tag-shedding rates (Hampton 1997). Tags and accompanying information (FL, date, location, fishing method, etc.) for recaptured tuna were reported by fleets throughout the fishery (for details, see Kaltongga 1998). The return of recovered tags was promoted by a widespread publicity campaign and attractive tag rewards. The tag-reporting rate was estimated independently by a tag-seeding experiment carried out on purse seiners (Hampton 1997).

In total, 98 401 skipjack, 40 075 yellowfin, and 8074 bigeye tuna were tagged during the RTTP. The percentage of tags returned was 12–13% for each species. Most skipjack tuna were recaptured within 3 years of release and most yellowfin tuna within 4 years of release, while small numbers of bigeye tuna were still being recaptured 7 years after release.

The data were screened to include only those records for which the tuna had been accurately measured at release (99% of releases). The release and recapture dates were also required for the analysis. The release dates were known for all releases and the recapture dates were known with an accuracy of calendar month or better for 91% of tag returns. For the returns with more uncertain recapture dates, the midpoint of the period during which recapture was considered most likely to have occurred was used. For some tag returns, an accurate FL measurement was taken soon after the fish had been recaptured. Where available, recapture FLs were also included in the data set for growth analysis. Details of the final, screened data set are provided in Table 1.

The size composition of RTTP tag releases was similar to those of purse-seine, pole-and-line, and other surface fisheries operating in the region (Fig. 3). In particular, the tag-release sample included considerable numbers of smaller tuna released during tagging cruises in the Philippines. Because pole-and-line gear is not effective in catching large yellowfin and bigeye tuna, relatively few tuna

Fig. 1. Average distribution of the catch of skipjack, yellowfin, and bigeye tuna, 1990–1997. The area of the circle in each 5° square is proportional to the catch; the largest circle size represents an average annual catch of 94 359 t.



>100 cm FL were tagged. However, these larger fish are represented in the recaptured sample (Fig. 4).

Analytical methods

Size-specific tagged population model

The size-specific tagged population model is a generalization of the size-aggregated model of tagged fish dynamics often referred to as the tag-attribution model (Kleiber et al. 1987; Hampton 1997). The size-aggregated model in its simplest form can be expressed as

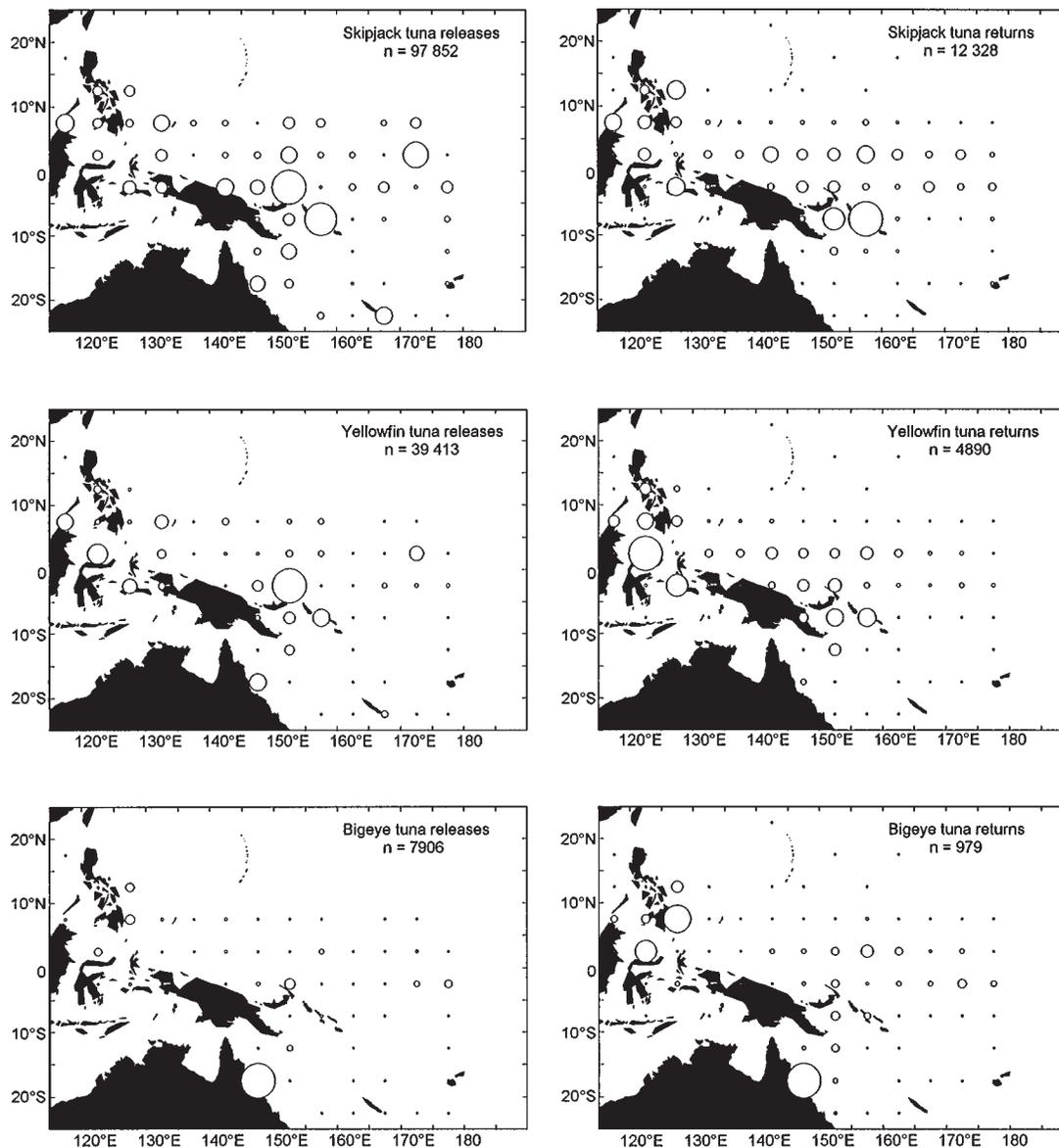
$$(1) \quad \hat{r}_{ij} = (1 - \alpha)R_i \exp[-(F + M + \lambda)(j - 1)\Delta t] \times \frac{F}{F + M + \lambda} [1 - \exp(-F - M - \lambda)\Delta t]$$

where \hat{r}_{ij} is the predicted number of tag returns from tag-release group *i* in the *j*th time period after release, α represents the type 1 tag loss rate (from tag shedding and nonreporting), R_i is the number of tag releases of group *i*, λ represents the continuous type 2 tag loss rate (from tag shedding), and Δt is the time step relative to the units of the instantaneous rates (normally, $\Delta t = 1$). The *F* and *M* are assumed to be constant over time, fish size, and age.

To add size structure to eq. 1, we define a tag-release group as all releases at a given size. I used 1-cm initial size-classes, resulting in 60 release groups (21–80 cm) for skipjack tuna, 100 release groups (21–120 cm) for yellowfin tuna, and 103 release groups (21–140 cm, some lengths not represented) for bigeye tuna. The *F* and *M* were then stratified by broad size intervals, appropriate to the distribution of the tag-return data, as follows. Skipjack tuna: 21–30, 31–40, 41–50, 51–60, 61–70, >70 cm FL; yellowfin tuna: 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100, >100 cm FL; bigeye tuna: 21–40, 41–60, 61–80, 81–100, 101–120, >120 cm FL. The size-structured version of eq. 1 is then

$$(2) \quad \hat{r}_{ij} = (1 - \alpha)R_i \exp \left[-\sum_{k=1}^{j-1} (F_{s(l_i,k)} + M_{s(l_i,k)} + \lambda)\Delta t \right] \times \frac{F_{s(l_i,j)}}{F_{s(l_i,j)} + M_{s(l_i,j)} + \lambda} [1 - \exp(-F_{s(l_i,j)} - M_{s(l_i,j)} - \lambda)\Delta t]$$

Fig. 2. Geographical distribution of RTTP releases and returns of skipjack, yellowfin, and bigeye tuna. The area of the circle in each 5° square is proportional to the number of releases or returns.



Size-class s is specified as a function of the initial size of release group i (l_i) and the time after release j . It is necessary to use a model to predict s from l_i and j , as we need to specify s for every time interval after release, and this cannot be observed directly. For these predictions, I used a simple von Bertalanffy model of the form

$$(3) \quad \hat{L}_j = [\bar{L}_\infty - l_i][1 - \exp(-Kt_j)] + l_i$$

where \hat{L}_j is the predicted size at time t_j , the middle of the j th period after release, and \bar{L}_∞ and K are the von Bertalanffy growth parameters mean maximum length and growth coefficient. The \bar{L}_∞ and K were estimated by maximum likelihood from tag-return records in which accurate measurements of FL at recapture were available. The estimation model incorporated individual variation in L_∞ as well as observation error (model 3 in Hampton 1991a).

I assumed that α comprised instantaneous tag shedding and nonreporting of tags and used an estimate of 0.45 for the three species (Hampton 1997). Tagging mortality was assumed to be insignificant.

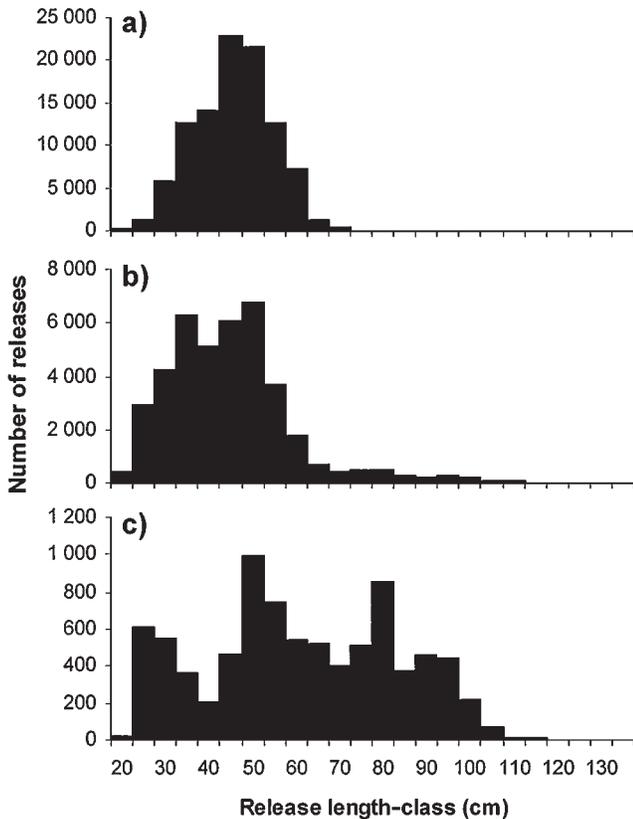
Table 1. Tag releases and returns of skipjack, yellowfin, and bigeye tuna used in the analysis of size-specific mortality rates.

	Skipjack tuna	Yellowfin tuna	Bigeye tuna
Tag releases	97 852	39 413	7906
Tag returns	12 328	4 890	979
Tag returns with accurate recapture FL measurement	4 242	1 629	307

Likewise, λ was assumed to consist only of type 2 tag shedding, and an estimate of 0.0023-month^{-1} (Hampton 1997) was used. These parameters were assumed to be independent of fish size.

I made the simplifying assumption that F_s and M_s did not vary over time, enabling the tag releases to be aggregated over time. Effectively, the data were treated as if all tag releases occurred at the same time. This is a common assumption with respect to M_s and

Fig. 3. Length–frequency distributions of RTTP releases of tagged (a) skipjack, (b) yellowfin, and (c) bigeye tuna. The length-class labels refer to the lower boundaries of the 5-cm length-classes.



may not be unreasonable for F_s if the recapture fishery operated at a fairly constant level over the course of the recapture period. The time series of commercial catch data during the recapture period show seasonal and some lower frequency variation, but there are no consistent trends that might indicate a serious failure of this assumption (Fig. 5).

Some constraints on the selection of time interval and size-classes are necessary. Accuracy may suffer if the time strata j are large relative to the time taken to grow through the size-classes. In cases where j cannot be made sufficiently small, e.g., because of recapture date resolution, subiterations (whereby j is broken up into n subperiods of length $\Delta t = 1/n$ for computing eq. 2) may be used to increase accuracy. For the tuna analyses, rerunning the models with up to five subiterations demonstrated that acceptable accuracy was obtained using a single monthly computational time step.

Incomplete mixing of new releases

New tag releases are not immediately mixed throughout the range of the fishery and may therefore experience a different level of fishing mortality than the mixed population in that size-class. Such anomalous returns soon after release may bias the estimates of M_s and F_s for the fully mixed population unless explicitly dealt with in the model. This involves estimating the additional fishing mortality parameters F'_{im} , where m indexes a number of initial, premixing periods (Hoenig et al. 1998; Bertignac et al. 1999). The number of such “nuisance” parameters to be estimated is potentially large (the number of premixing periods times the number of release groups). The most efficient procedure is to set $\hat{r}_{ij} = r_{ij}$ for each of the premixing periods and to solve the equivalent of eq. 1 for F'_{im} using the Newton–Raphson technique (for details, see

Fig. 4. Length–frequency distributions of RTTP returns of tagged (a) skipjack, (b) yellowfin, and (c) bigeye tuna. The length-class labels refer to the lower boundaries of the 5-cm length-classes.

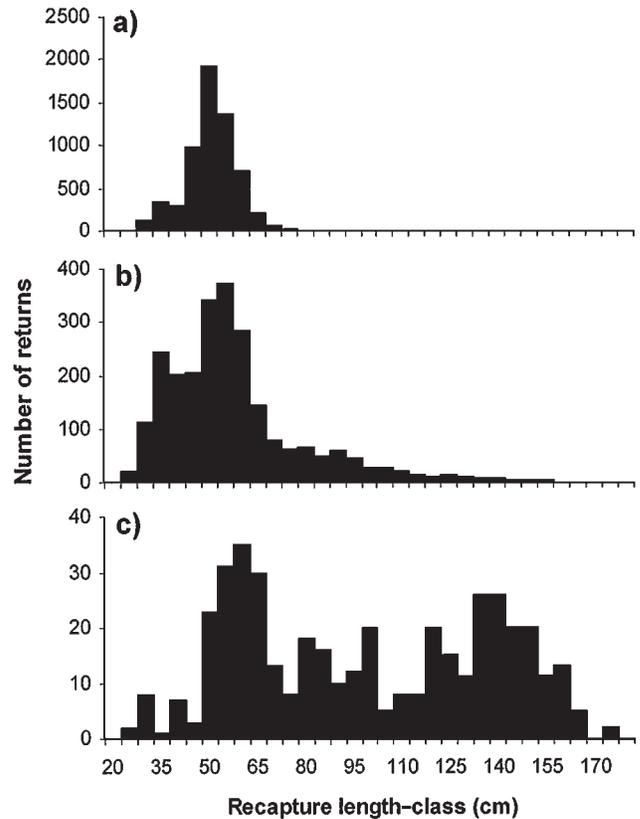
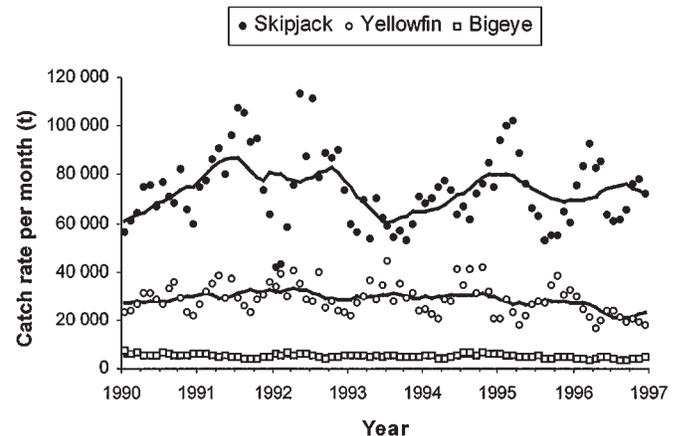


Fig. 5. Estimated monthly catches of skipjack, yellowfin, and bigeye tuna in the western and central Pacific Ocean. The lines are 12-month moving averages.

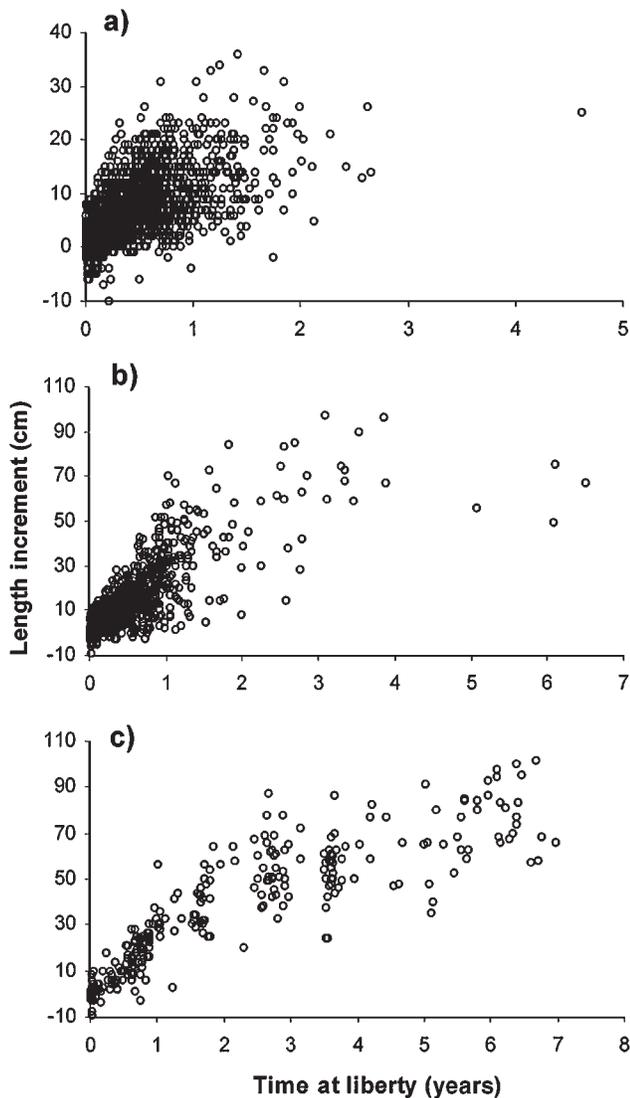


Press et al. 1988). As suggested by Hoenig et al. (1998), I used likelihood ratio tests to choose the optimal number of premixing periods for each data set. The number of premixing periods deemed to be optimal was the smallest number of periods for which the P value of the χ^2 test for adding a premixing period was >0.05 .

Parameter estimation

The F_s , M_s , and F'_{im} were estimated by minimizing the negative

Fig. 6. Length increment and time at liberty data for (a) skipjack, (b) yellowfin, and (c) bigeye tuna used to estimate growth models.



log of the multinomial likelihood function (omitting terms dependent only on the data):

$$(4) \quad -\sum_i \left[(R_i - \sum_j r_{ij}) \ln \left(1 - \frac{\sum_j \hat{r}_{ij}}{R_i} \right) + \sum_j \ln \left(\frac{\hat{r}_{ij}}{R_i} \right) \right]$$

where r_{ij} is the observed number of tag returns from tag-release group i in the j th time period after release. Approximate 95% confidence intervals for F_s and M_s were obtained using the percentile method (Efron 1982) applied to distributions of the parameters generated from 1000 bootstrap replicates. Growth parameter estimation was included in the bootstrapping. For the analysis of each replicate data set, estimates of tag-shedding and tag-reporting parameters were obtained by the parametric bootstrap (or Monte Carlo) approach described in Hampton (1997). The confidence intervals for the mortality parameters therefore incorporated estimated uncertainty in growth, tag-shedding, and tag-reporting rates.

Table 2. Growth parameter estimate mean maximum length (\bar{L}_∞) and growth coefficient (K) for skipjack, yellowfin, and bigeye tuna.

	\bar{L}_∞ (cm)	K (year ⁻¹)
Skipjack tuna	65.1 (0.58)	1.30 (0.065)
Yellowfin tuna	166.4 (13.5)	0.250 (0.031)
Bigeye tuna	181.7 (6.88)	0.251 (0.028)

Note: The standard deviations of the estimates obtained from 1000 bootstrap replicates are given in parentheses.

Table 3. Statistical tests to determine the appropriate number of premixing periods.

	No. mixing periods	df	χ^2	P
Skipjack tuna	1	60	2 248.2	<0.001
	2	120	353.4	<0.001
	3	180	161.3	<0.001
	4	240	133.0	<0.001
	5	300	77.8	0.060
Yellowfin tuna	1	100	635.7	<0.001
	2	200	160.8	<0.001
	3	300	94.4	0.640
	4	400	118.9	0.096
	5	500	95.8	0.599
Bigeye tuna	1	103	420.7	<0.001
	2	206	116.8	0.167
	3	309	76.5	0.977
	4	412	74.1	0.986
	5	515	75.8	0.980

Note: The df corresponds to the increase in the number of F'_{im} parameters to be estimated for successive increases in the number of premixing periods. The χ^2 statistic is twice the difference between the negative log-likelihood values for the current model and the model with one fewer premixing period. P is the probability that the improvement in fit of the current model is due to chance. For each species, the selected model, based on a critical value of $P = 0.05$, is boldfaced.

Results

Growth

Growth parameter estimates for the three species were required so that the tagged tuna populations would be assigned to length-classes at each time step of the analysis using eq. 3. Subsets of the tag-return data were analyzed for this purpose (Table 1). Plots of length increment against time at liberty (Fig. 6) show evidence of the asymptotic growth characteristic of von Bertalanffy and other commonly applied growth functions. The estimates of \bar{L}_∞ and K (Table 2) derived from these data imply growth rate estimates for the exploited size ranges that are consistent with the range of estimates obtained in other growth studies for these species in the Pacific Ocean (Miyabe 1994; Suzuki 1994; Wild and Hampton 1994).

Size-specific mortality

Likelihood ratio tests determined the optimal numbers of premixing periods to be four for skipjack tuna, two for yellow-

Fig. 7. Observed (circles) and predicted (line) (a) skipjack, (b) yellowfin, and (c) bigeye tuna tag returns by time at liberty.

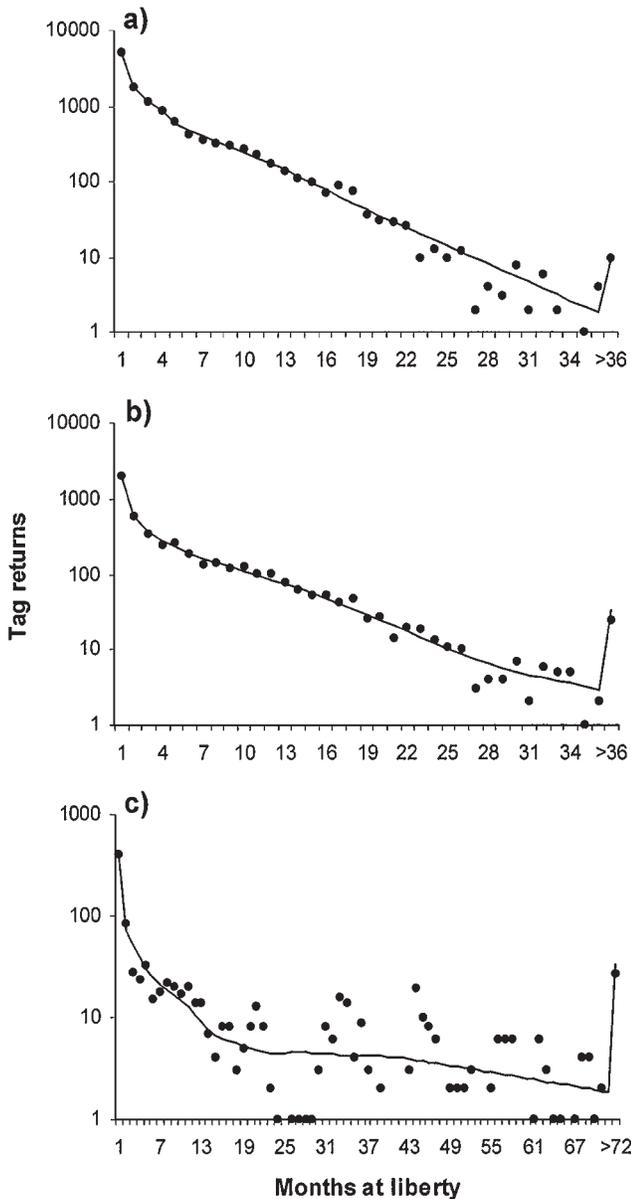
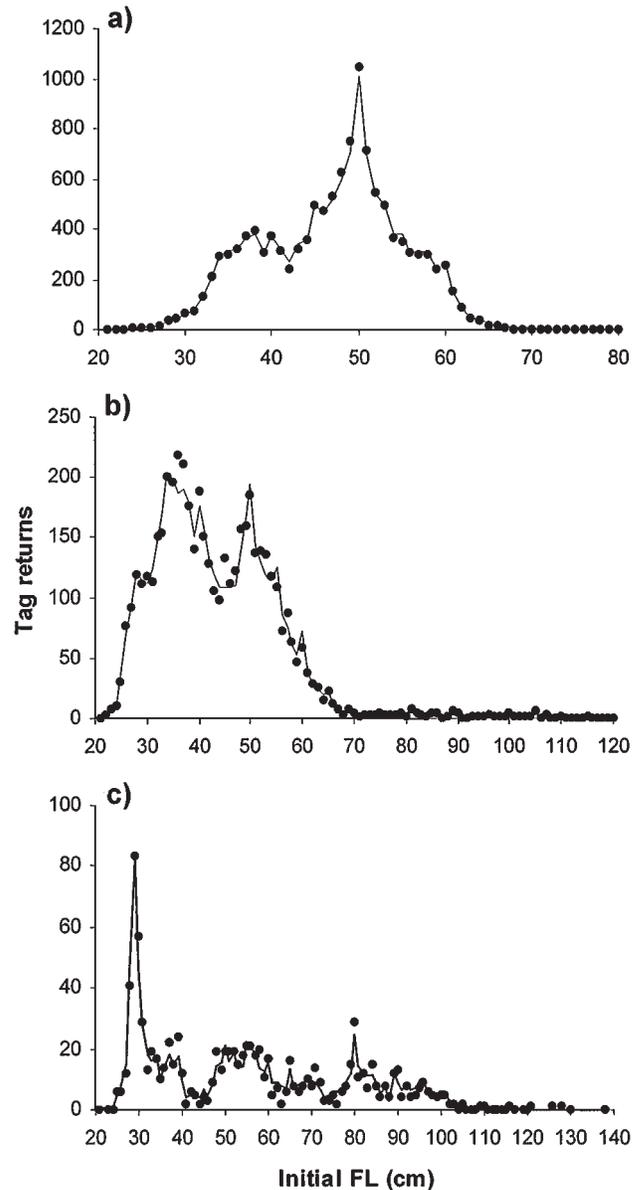


Fig. 8. Observed (circles) and predicted (line) (a) skipjack, (b) yellowfin, and (c) bigeye tuna tag returns by initial size of release groups.



fin tuna, and one for bigeye tuna (Table 3). The results presented below incorporate these premixing periods.

For each species, the parameter estimation was stable, and the negative log likelihoods converged rapidly to their minima. Scatter plots of parameter estimates for the 1000 bootstrap replicates did not reveal any serious cases of high parameter correlation. Likewise, plots of observed and predicted tag returns aggregated by time at liberty (Fig. 7) and by size at release (Fig. 8) indicated that the models provided reasonably good descriptions of the data, particularly for skipjack and yellowfin tuna where the numbers of returns were large. In each case, reduced models assuming constant M (but size-dependent F) produced significant degradation of the fits (likelihood ratio test, $P < 0.001$).

Skipjack tuna M estimates show a classical U-shaped relationship with size (Fig. 9a), with the median estimates of M

for the smallest (21–30 cm) and largest (>70 cm) size-classes approximately an order of magnitude higher than those for the 41–50, 51–60, and 61–70 cm size-classes. The estimates for these midsizes of skipjack tuna (which comprise the bulk of the exploited size range) are 1.6, 1.2, and 2.0-year⁻¹, respectively, which are similar to the size-aggregated estimate (about 1.9-year⁻¹) obtained from a previous skipjack tuna tagging experiment in the western tropical Pacific (Kleiber et al. 1987). The F for the mixed population tends to decline with increasing size (Fig. 9b). There are large 95% confidence intervals on F for the two smallest size-classes because most of the recaptures for these size-classes occur during the premixing periods.

Yellowfin tuna M estimates decline sharply with increasing size, but there is a significant increase in M for the 81–

Fig. 9. Estimates of skipjack tuna (a) natural mortality rates and (b) fishing mortality rates by size-class. The circles represent the medians of 1000 bootstrap replicates; the ranges are the 2.5–97.5 percentiles.

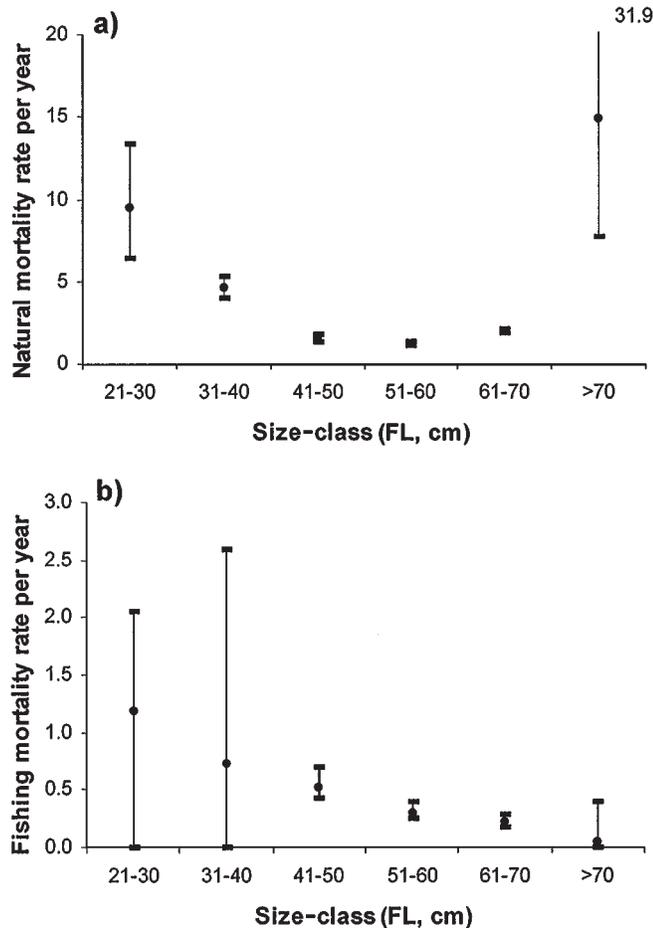
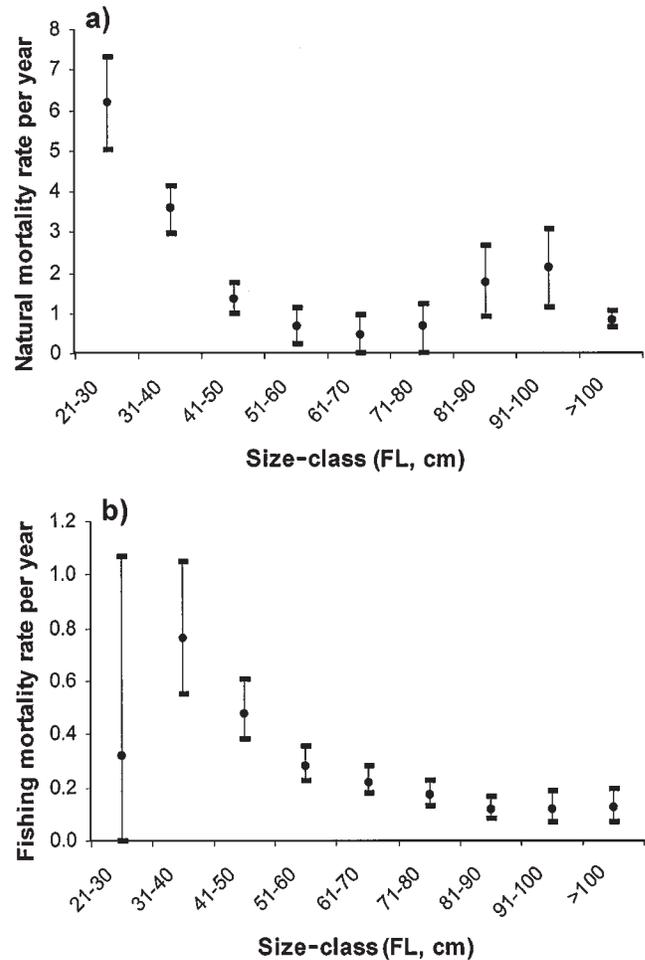


Fig. 10. Estimates of yellowfin tuna (a) natural mortality rates and (b) fishing mortality rates by size-class. The circles represent the medians of 1000 bootstrap replicates; the ranges are the 2.5–97.5 percentiles.



90 and 91–100 cm size-classes (Fig. 10a). As with skipjack tuna, the decline with increasing size is by an order of magnitude, with the lowest M estimates for the midsized fish, in this case the 51–60, 61–70, and 71–80 cm size-classes. These estimates (0.68 , 0.44 , and 0.69-year^{-1}) are somewhat lower than the value of 0.8-year^{-1} , which seems to be most commonly used in yellowfin tuna assessment (Wild 1994), although several estimates in the $0.4\text{--}0.6\text{-year}^{-1}$ range have been reported (e.g., Schaefer 1967; Francis 1977). Apart from a relatively low estimate of F for the smallest size-class (the 95% confidence interval of which is large because of few tag returns in the postmixing periods), F declines with increasing size (Fig. 10b).

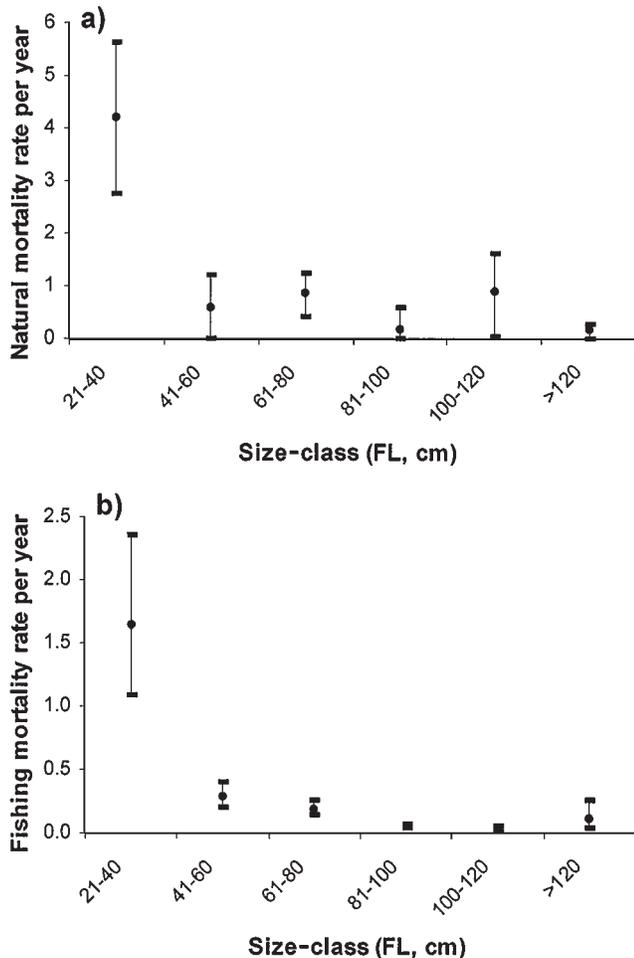
Bigeye tuna M estimates are considerably lower than those for skipjack and yellowfin tuna (Fig. 11a). Again, there is an order of magnitude decline in M from the smallest (21–40 cm) to the larger size-classes, but there is no evidence of an increase in M at larger size. The M varies between 0.15 and 0.90-year^{-1} for size-classes >40 cm, which compares with the range of $0.4\text{--}0.8\text{-year}^{-1}$ most often used in bigeye tuna stock assessment (Anonymous 1998). The F estimates are highest for the smallest size-class and decline with increasing size (Fig. 11b).

Discussion

The method described for deriving size-specific estimates of M and F from tagging data is new and is potentially applicable to other fish species. The data requirements are tagging data (size at release and times of release and recapture), independent estimates of nuisance parameters such as tag-shedding and tag-reporting rates, and a means of predicting length increment as a function of initial size and time period. In some cases, as for the applications in this paper, growth estimates may be obtained using a model fitted to length increment and time at liberty data available from the same tagging data set. However, a growth model derived from other data could also be used. If such a model provided estimates of length at age (which are generally not available from growth models fitted to tagging data), it would be a simple matter to adapt the existing model to estimate M and F by age-class rather than by size-class.

An alternative model structure to that used in this study would be to parameterize a specific functional form for the relationship between M and size or age. This type of approach was adopted by Chen and Watanabe (1989), who

Fig. 11. Estimates of bigeye tuna (a) natural mortality rates and (b) fishing mortality rates by size-class. The circles represent the medians of 1000 bootstrap replicates; the ranges are the 2.5–97.5 percentiles.



modeled M as an inverse function of growth rate. This approach may work in some cases, although a flexible functional relationship would be required to estimate, for example, the variation in yellowfin tuna M with size detected in this study.

I made the simplifying assumption that F for the fully mixed tagged population did not vary over time. This assumption may be justified if, as was the case here, the fisheries did not undergo significant changes during the period over which recaptures occurred. In cases where such an assumption cannot be made, it would be necessary to parameterize F as a function of fishing effort or catch (e.g., Kleiber et al. 1987; Hampton 1991b; Sibert et al. 1999) and to estimate the catchability coefficient (in the case of effort) or mean population size (in the case of catch) instead of F . This would be a straightforward adaptation of the present model.

The analyses of skipjack, yellowfin, and bigeye tuna tagging data revealed important size-related variation in M . For the three species, M for the smallest size-class was an order of magnitude higher than those for midsized fish. The transition from high to low M was around 40 cm FL, approximately the size at which the three species recruit to the

western Pacific purse-seine fishery. However, other fisheries, notably the domestic tuna fisheries in the Philippines and Indonesia, catch significant quantities of tuna < 40 cm FL (around 25% of the total western Pacific tuna catch by weight). The question of the impact of these catches of small tuna on other western Pacific tuna fisheries is frequently raised in fishery management meetings. Estimates of the impact can be derived using yield per recruit or some other form of size- or age-structured model. Estimates of M are frequently critical to such assessments, and in this case, the higher M estimates for the small tuna would considerably dampen the estimated impacts of small tuna catches on fisheries targeting larger tuna.

For skipjack and yellowfin tuna, there was evidence of elevated M for some of the larger size-classes as well. In the case of skipjack tuna, high M for the >70 cm size-class possibly indicates the onset of senescence, as this is near the maximum size for this species. For yellowfin tuna, there was an increase in M over the 80–100 cm size range. The significance of this pattern is not fully understood, but it could be related to the onset of reproductive maturity and the associated high energetic demands of spawning, particularly for females (Schaefer 1996).

The size-related variation in M demonstrated in this study suggests that size- or age-dependent M should be a feature of future stock assessment models for these species. The length-based, age-structured model developed by Fournier et al. (1998) incorporates an option for estimating M by age-class from time series of commercial catch, effort, and size composition data. This model is currently being extended to include tagging data in the analysis. The information on M and its variability obtained from the analyses of tagging data presented here suggests that the extended length-based, age-structured model may be a useful tool for assessment of western Pacific tuna stocks.

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