Abstract–Tag release and recapture data of bigeye (*Thunnus obesus*) and yellowfin tuna (*T. albacares*) from the Hawaii Tuna Tagging Project (HTTP) were analyzed with a bulk transfer model incorporating size-specific attrition to infer population dynamics and transfer rates between various fishery components. For both species, the transfer rate estimates from the offshore handline fishery areas to the longline fishery area were higher than the estimates of transfer from those same areas into the inshore fishery areas. Natural and fishing mortality rates were estimated over three size classes: yellowfin 20–45, 46–55, and ≥56 cm and bigeye 29–55, 56–70, and ≥71 cm. For both species, the estimates of natural mortality were highest in the smallest size class. For bigeye tuna, the estimates decreased with increasing size and for yellowfin tuna there was a slight increase in the largest size class. In the Cross Seamount fishery, the fishing mortality rate of bigeye tuna was similar for all three size classes and represented roughly 12% of the gross attrition rate (includes fishing and natural mortality and emigration rates). For yellowfin tuna, fishing mortality ranged between 7% and 30%, the highest being in the medium size class. For both species, the overall attrition rate from the entire fishery area was nearly the same. However, in the specific case of the Cross Seamount fishery, the attrition rate for yellowfin tuna was roughly twice that for bigeye. This result indicates that bigeye tuna are more resident at the Seamount than yellowfin tuna, and larger bigeye tunas tend to reside longer than smaller individuals. This may result in larger fish being more vulnerable to capture in the Seamount fishery. The relatively low level of exchange between the Seamount and the inshore and longline fisheries suggests that the fishing activity at the Seamount need not be of great management concern for either species. However, given that the current exploitation rates are considered moderate (10–30%), and that Seamount aggregations of yellowfin and bigeye tuna are highly vulnerable to low-cost gear types, it is recommended that further increases in fishing effort for these species be monitored at Cross Seamount.

Dynamics of bigeye (*Thunnus obesus*) and yellowfin (*T. albacares*) tuna in Hawaii's pelagic fisheries: analysis of tagging data with a bulk transfer model incorporating size-specific attrition

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Around the Hawaiian Islands, a variety of small and medium-scale fisheries target bigeye (*Thunnus obesus*) and yellowfin tuna (*T. albacares*) associated with offshore seamounts, weather monitoring buoys, an inshore network of fish aggregating devices (FADs), and natural aggregation sites (Itano and Holland, 2000). These fisheries, conducted from longline, troll, and handline (and to a lesser extent pole-and-line) vessels provide an important source of revenue for the state of Hawaii (Boggs and Ito, 1993; Ito and Machado[1]). The small-gear fleet (essentially trolling and the handline vessels) supports recreational and subsistence fisheries for both residents and the tourist industry (Pooley, 1993; Hamilton and Huffman, 1997).

An important sector of the small-scale commercial fisheries is the offshore handline fishery, which targets mixed species aggregations found in association with offshore NOAA weather-monitoring buoys and seamounts (Itano and Holland, 2000). Most of the catch and effort in this fishery, which currently lands roughly 500 t per year, concentrates on the Cross Seamount and takes mostly juvenile and subadult yellowfin and bigeye tunas. Concerns have been raised as to whether the seamount fishery intercepts too many juveniles

that might otherwise recruit to inshore fisheries or to the offshore longline fishery (Holland et al., 1999). There is also concern among the handline fishermen exploiting the seamount that further increases in fishing effort could overexploit offshore tuna resources and reduce the economic viability of their fishery. Moreover, yellowfin and bigeye tuna around Hawaii are part of the wider Pacific Ocean stock that are being exploited by the various coastal and high seas fisheries (Hampton and Fournier, 2001; Hampton and Fournier[2]) and therefore the overall health of the Pacific-wide stock is important for the viability of the local fisheries. In these concerns, the Hawaiian Cross Seamount fishery exemplifies resource

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[1] Ito, R. Y., and W. Machado. 1999. Annual report of the Hawaii-based longline fishery for 1998. Honolulu Laboratory Admin Report. H-99-06, 62 p. National Marine Fisheries Service, NOAA, SWFSC, 2570 Dole St., Honolulu, HI-96822-2396.

[2] Hampton, J., and D. Fournier. 2001. A preliminary stock assessment model for bigeye tuna in the Pacific Ocean. Working Paper submitted to the Fourteenth Meeting of the Standing Committee on Tuna and Billfish, 9–16 August 2001. Secretariat of Pacific Community, BP D5, 98848 Noumea Cedex, New Caledonia.
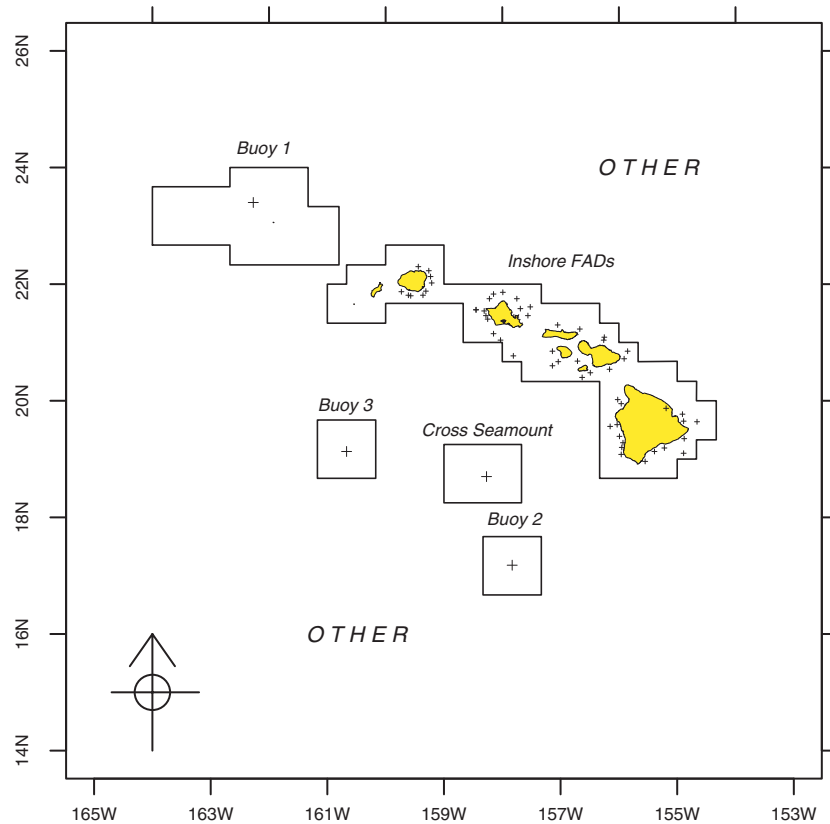
Figure 1

The study area around the Hawaiian archipelago showing the boundaries of the sites used in the model. Individual crosses indicate the geographic location of the FADs.

allocation and sustainability issues that are increasingly frequent in all oceans.

Conventional tagging of bigeye and yellowfin tuna was initiated in 1995 in order to advance understanding of the dynamics of tuna aggregations in the Hawaiian fishery and to provide management guidance. Although initially concentrating on the Cross Seamount, the Hawaii Tuna Tagging Project (HTTP) expanded its scope to tag fish throughout the archipelago and has tagged and released more than 17,000 bigeye and yellowfin tuna of roughly equal numbers during a five-and-half year period.

Previous analyses of the data suggested that recruitment (transfer) rates from the Cross Seamount to the inshore areas were low and concluded that fishing effort on the Cross Seamount was not having an adverse impact on other components (inshore trolling and handlining, offshore longlining) of the local tuna fisheries (Sibert et al., 2000). It was also suggested that bigeye tuna on the Cross Seamount had a higher mean residence time than yellowfin tuna (Holland et al., 1999; Sibert et al., 2000).

However, those previous analyses were made while tagging was still in progress, using a small set of recapture data. Since that time, many more tag releases and recoveries have been made which permit a more complete view of movement and residence times. The work presented

here includes releases and recoveries up to June 2001. A size and site-specific tag attrition model was developed to analyze the data and provides information on transfer and exploitation rates that are important for management of the resource and for subsequent fishery assessments. The approach used in this research may prove useful in other areas where resource allocation issues need to be addressed.

Materials and analytical method

Data and tag attrition model

The analysis includes recaptures of tagged bigeye and yellowfin tuna released between August 1995 through November 2000 in the Hawaiian pelagic fishery in the geographic region 165°W to 153°W and 14°N to 26°N (Fig. 1). A total of 12,848 tag releases from within the area are examined here of which 7541 (59%) were bigeye and 5307 (41%) were yellowfin tuna. Releases were made primarily at the Cross Seamount which is located about 290 km south of Oahu at approximately 18°42′N, 158°16′W. Releases were also made at NOAA data buoys 51001, 51002, and 51003 (identified as buoy 1, buoy 2, and buoy 3 in this paper, see Fig. 1) and at inshore areas immediately surrounding the main Hawai-

Table 1

Summary of tag releases and recaptures by site and species with usable information. Geographic areas of the sites are given in Figure 1.

Site	Release	Recapture
Bigeye tuna		
Buoy 2	1493	317
Buoy 3	326	29
Cross Seamount	5371	653
Inshore areas	160	50
Other	0	48
Total	7350	1097
Yellowfin tuna		
Buoy 1	247	20
Buoy 2	260	40
Buoy 3	59	9
Cross Seamount	3423	635
Inshore areas	1239	254
Other	0	12
Total	5228	970
Grand total	12578	2067

ian Islands. Additional details on the tagging program and the fisheries are given in Itano and Holland (2000). As of June 2001, 1131 (14.9%) bigeye and 983 (18.5%) yellowfin tuna were recovered. A summary of releases and recaptures with usable information given in Table 1.

The method used to analyze the data is an extension of a tag attrition model commonly used in the analysis of tuna tagging data (e.g., Kleiber et al., 1987, Hampton, 1991a). We developed a site- and size-specific model to describe the dynamics of the tagged population in the study area by combining Sibert et al.'s (2000) site-specific model with Hampton's (2000) size-specific model. This size- and site-specific tag attrition model can be written as

$$\frac{dN_{ki}}{dt} = -\left(F_{i,L(l_k,\bar{t})} + M_{L(l_k,\bar{t})} + \lambda \sum_{j=1}^{n} T_{ij} \right) N_{ki}$$
$$+ \sum_{j=1}^{n} (T_{ji} N_{kj}), \tag{1.1}$$

where $T_{ii} = T_{jj} = 0$; and at $t=0$, $N_{ki} = \alpha N_{ki}^0$.

$$L(l_k,\bar{t}) = \left[\overline{L}_\infty - l_k \right] + \left[1 - e^{\left(-K(\bar{t}-t_0) \right)} \right] + l_k \tag{1.2}$$

$$\frac{dC_{ki}}{dt} = F_{i,L(l_k,\bar{t})} N_{ki} \text{ at } t = 0; \ C_{ki} = 0. \tag{1.3}$$

The subscripts i and j ($i, j=1,2..,n$) indicate release and recapture sites and k is the release cohort stratified over

three size classes (see below). Note "site" is used in this paper to refer to a release or recapture "compartment" from the modeling perspective. Equation (1.1) partitions the rate of attrition (loss of tags) into fishing mortality F, natural mortality M, tag shedding λ, and the transfer rates T_{ij} (emigration from site i to j). It may also include immigration of returnees that occurred in previous time step(s). Note that T_{ii} are not defined in the model and are set to zero. Tag shedding parameters λ and α were estimated by an independent tag-shedding analysis (see below). F and M are defined as functions of release size l_k and time-elapsed since release up to the middle of the current time interval $\bar{t}$. Because there is no direct way of observing the size of released cohorts as they grow in the model, we used a growth model to track their growth in the model. We assumed that individuals in tagged population grow according to the von Bertlanffy growth model (Eg. 1.2), which has the parameters t_0, K, and $\overline{L}_\infty$. The parameters of the growth model (K, and $\overline{L}_\infty$) may be estimated from the same data set by using the growth increment and time-at-liberty data (Hampton, 1991b). We attempted estimating the model parameters using our data set from various approaches (James, 1991; Kirkwood and Somers, 1984; Wang and Thomas, 1995). Regrettably none of the approaches provided satisfactory estimates of the growth parameters to cover the full size range of the fish that would be required for the attrition model. The usable growth data and the size range available in the data set were simply not sufficient for estimating the growth parameters. Instead we used the parameter estimates for bigeye and yellowfin tuna from the tropical Central Pacific estimated by (Hampton, 2000). The third part of the model (Eq. 1.3) describes the recapture rate of the tagged fish (C_{ki}), which is assumed to be proportional to the numbers available (N_{ki}) in the time period—the proportionality constant being the fishing mortality rate.

For the purposes of this model, a release cohort is defined as the number of releases of a given size class stratified by site. One-centimeter initial size classes were used resulting in 252 cohorts (29–133 cm fork length, [FL]) for bigeye and 247 cohorts (20–140 cm FL) for yellowfin tuna for all the sites. The recoveries from each cohort were stratified by the recovery sites over 10-day time-at-liberty intervals. Further stratification of releases by calendar date was not practical because of the small numbers of releases and subsequent recaptures in each 1 cm × date × site stratum. Instead, we assumed that all releases occurred at time zero. This assumption in tag releases inevitably led us to assume that fishing effort was constant during the recovery period (1995–2000). This is a common assumption (e.g. Hampton, 2000) and justified if the fishery operated at a more or less constant level during the recovery period. Although the crude catch and effort (fishing days) data that we have show seasonality in the catch rates, we felt it was reasonable to assume the fishing effort exerted on the fishery remained constant throughout the experiment

We assumed zero tagging-induced mortality and that nearly all (95%) recoveries were reported, at least from the local fisheries. Close communication and a high level of cooperation between the fishing and fish processing

community of Hawaii and the HTTP were maintained to ensure high levels of reporting. There were 191 releases of bigeye (2.5% of release) lacking size of fish or geographic position of released fish (or both), which are necessary information for the analysis. For yellowfin tuna this figure was 79 (1.5% of release). The number of tag returns with no usable information, i.e. accurate recapture fork length or recapture position (or both) were few (2.9% for bigeye and 1.1% for yellowfin tuna). We had to assume a value for α, because this parameter cannot be estimated accurately from tagging data. The components included in α were the proportions recoveries with no useful information, proportion of tags lost immediately following release (the so called type-I shedding, see below) and the nonreporting of recoveries. Using the proportions in these categories, we obtained values of α as 0.85 for bigeye and 0.87 for yellowfin tuna, which were fixed in the model fits.

In order to reduce the number of parameters, attrition was estimated over size classes instead of the one-centimeter release cohorts. First a vector indexed from the smallest to the largest possible size was used to assign the one-centimeter size classes of the cohort as it "grew" in the model over time. A second vector with the same number of elements indexed with the desired size-class numbers can then be mapped onto the previous vector to estimate attrition over size classes. The attrition rates were estimated over three size classes for each species. For yellowfin tuna the size classes were 20–45, 46–55, and ≥56 cm FL and for bigeye tuna the size classes were 29–55, 56–70, and ≥71 cm FL. There was no reason for selecting these size classes but these ranges produced strata with sufficient numbers of recaptures to give model stability and convergence.

The number of parameters to be estimated can be further reduced by only estimating transfer coefficients for empirically observed transfers. It is possible to estimate coefficients for all possible transfers. However, we found that estimated coefficients for nonobserved transfers are not well determined by the data. Therefore in the interest of parsimony and model stability, we estimated transfer coefficients for the observed transfers only and assumed transfer coefficients for unobserved transfers to be zero.

Attrition from cohorts was followed independently for 140 ten-day time periods (approximately 47 months). A semi-implicit finite difference approximation was used to obtain numerical solutions of Equation 1.1. The estimates of the parameters were the values, which maximized the Poisson likelihood function:

$$L = P(C_{kit} \mid \hat{C}_{kit}) = \prod_k \prod_i \prod_t \left[\frac{\hat{C}_{kit}^{C_{kit}} e^{-\hat{C}_{kit}}}{C_{kit}!} \right], \qquad (2)$$

where C_{kit} = the observed recoveries; and
$\hat{C}_{kit}$ = the predicted recoveries from the model.

The maximum likelihood estimates of the parameters were obtained by minimizing the negative log of the likelihood function (Eq. 2) with ADModel Builder nonlinear optimization package (Otter Research Ltd., 2000).

Tag shedding

Tag shedding was estimated independently from a double tagging experiment conducted simultaneously with the main experiment with identical methods and procedures. The first tag was inserted on the left side and the second tag on the right side. Of the total 200 fish (bigeye and yellowfin tuna) double tagged and released, 57 were recovered; 49 with two tags and eight with one tag. The model used to estimate tag shedding was a simple exponential decay model with constant type-II shedding rate (Kirkwood and Walker, 1984; Hampton, 1997). The probability of retaining a tag $Q(t)$ over time is given by

$$Q(t) = \alpha e^{-\lambda t} \quad \text{where } 0 < \alpha \leq 1, \qquad (3)$$

where α = the type-I retention proportion; and
λ = the constant type-II shedding rate.

Using the assumptions and method described in Adam and Kirkwood (2001), we obtained the maximum likelihood estimates of the parameters by comparing the observed and predicted returns using exact dates of recovery.

Site selection

One of the primary goals of conducting the HTTP was to estimate the transfer rates between various fishery components, such as the Cross Seamount and the inshore fishing areas, and the Cross Seamount and offshore longline fishery. For the type of "bulk transfer" model described here, a site can be any arbitrary area with reasonable numbers of releases or recoveries (or both). The sites used in our study were carefully selected to represent individual fishery components from a management perspective. A total of six such compartments were identified and are shown in Figure 1. There were no releases of bigeye tuna from buoy 1 and only two recoveries of bigeye tuna were made from buoy 1 from the releases made elsewhere. For these reasons, these two recoveries were assigned to "other" area. This protocol resulted in five sites for bigeye and six sites for yellowfin tuna (see Table 1).

The NOAA weather-monitoring buoys 1, 2, and 3, act as *de facto* fish aggregating devices that concentrate large schools of bigeye and yellowfin tuna, making them highly vulnerable to the handline fishery (Itano and Holland, 2000). From a management point of view, the fishery around these offshore FADs is essentially similar to the Cross Seamount fishery and is exploited by the same vessels. The primary method of fishing at these areas is handlining. The inshore fishing areas contain a network of some 50 moored FADs that, when combined, can be considered one of the most frequently visited inshore fishing areas used by a diverse small-boat fleet (Itano and Holland, 2000). Fishing methods around inshore FADs include surface trolling, live baiting, jigging, and handline. The "other" area specified in the model is essentially the longline fishing ground more than 50 nmi offshore from the inshore sites. From the model's perspective, this area,

Table 2

Bigeye tuna: Observed and predicted tag transfers from the full model $M_3F_{3,5}T_{13}$, $n = 31$. The rows are release sites and columns are recapture sites.

	Recapture sites					
Tag release sites	All	Buoy 2	Buoy 3	Cross Seamount	Inshore	Other
Observed						
All	1097	317	29	653	50	48
Buoy 2	321	294	5	18	3	1
Buoy 3	40	2	19	11	1	7
Cross Seamount	711	21	5	623	22	40
Inshore	25	0	0	1	24	0
Other	0	0	0	0	0	0
Predicted						
All	1115.8	332.0	29.7	652.7	50.9	50.5
Buoy 2	342.4	296.2	5.2	22.6	7.9	10.6
Buoy 3	36.8	0.7	18.5	12.6	2.0	3.1
Cross Seamount	715.3	34.3	5.9	604.7	34.1	36.1
Inshore	21.3	0.7	0.1	12.8	6.9	0.8
Other	0.0	0.0	0.0	0.0	0.0	0.0

which is the area other than the bounded compartments, would represent the entire Pacific-wide fishery.
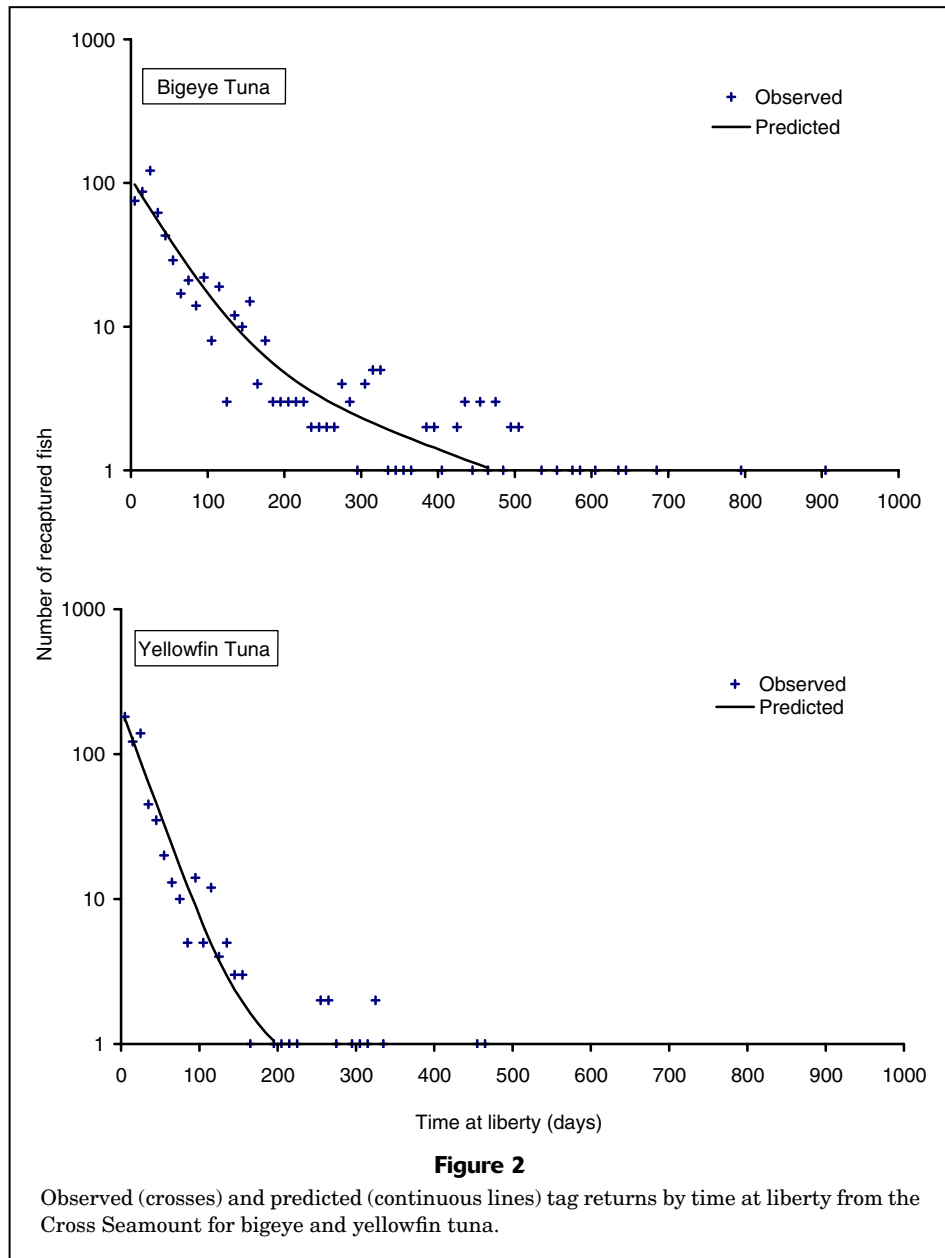
Results

The maximum likelihood method of estimating parameters allows one to statistically select among nested models those models that best fit the data on the basis of the likelihood ratio test (Brownlee, 1965; Hilborn and Mangel, 1997). The size-specific attrition model is a special case and is nested within the general model with constant mortality rates. By setting the size-specific attrition to be the same for all the sizes, the model reverts to the general case. Thus, with only a minor change, the model can be made to estimate attrition over a single size class or a single F for more than one site by describing alternative models of the data.

The parameters of the tag shedding model were estimated at $\alpha = 0.94 \pm 0.035$ and $\lambda = 0.000243 \pm 0.000452$ per day. Because the standard deviation of the estimate of λ was greater than the estimate, λ was assumed to be zero in the analysis. Estimates of α and the point estimate of λ were consistent with what has been estimated elsewhere with the same methods of tag release (Table 2, Adam and Kirkwood, 2001).

Several variants of the attrition model were evaluated including attrition estimated over a single size class and common fishing mortality rates among the offshore sites, (buoy 1, buoy 2, buoy 3, and Cross Seamount). The number of parameters to be estimated may be conveniently used to identify these structurally different models. For example, $M_3F_{3,5}T_{13}$ is the model in which M is estimated over three size classes, F over three size class and by five sites and with 13 transfer coefficients for the observed exchanges.

For both species, the model in which the attrition is partitioned over size classes demonstrated significant improvement ($P>0.999$ using a likelihood ratio test) over the reduced models: $M_3F_{3,5}T_{13}$ versus $M_1F_{1,5}T_{13}$ for bigeye tuna and $M_3F_{3,6}T_{17}$ versus $M_1F_{1,6}T_{17}$ for yellowfin tuna. Similarly, the models with site-specific fishing mortalities described the data significantly better ($P>0.999$) than models where a common fishing mortality was estimated for all offshore sites. The observed and predicted tag returns by time-at-liberty and by initial size classes of releases provide good descriptions of the data. The graphs for the Cross Seamount fishery are shown in Figures 2 and 3. Agreement between observed and predicted number of tags by site is reasonably good, particularly for sites where large numbers of recoveries were made (Tables 2 and 3).

The transfer coefficient estimates for movements between the various sites ranged from virtually zero to 0.05/day (Tables 4 and 5). For bigeye tuna, the transfer rate estimates from buoy 2, buoy 3, and the Cross Seamount to the longline fishery were higher than the transfer rates from those same sites to inshore areas (Tables 3 and 4). For yellowfin tuna, the pattern was similar except for the additional high transfer estimate from buoy 1 to the longline area. These differences between the transfer rates (from offshore sites to inshore site versus offshore sites to longline area) in both species were statistically significant (taken to mean that the 95% CI ranges did not overlap) showing the importance of emigration into the longline fishery compared with emigration into the inshore area. Yellowfin tuna transfer rate from inshore to the Cross Seamount was virtually zero but transfer from inshore to the longline area was very low (0.00703/day). There was no observed transfer of bigeye tuna to the longline fishery from the inshore areas and a very low transfer rate was estimated to the Cross Seamount (0.00375/day).

Figure 2

Observed (crosses) and predicted (continuous lines) tag returns by time at liberty from the Cross Seamount for bigeye and yellowfin tuna.
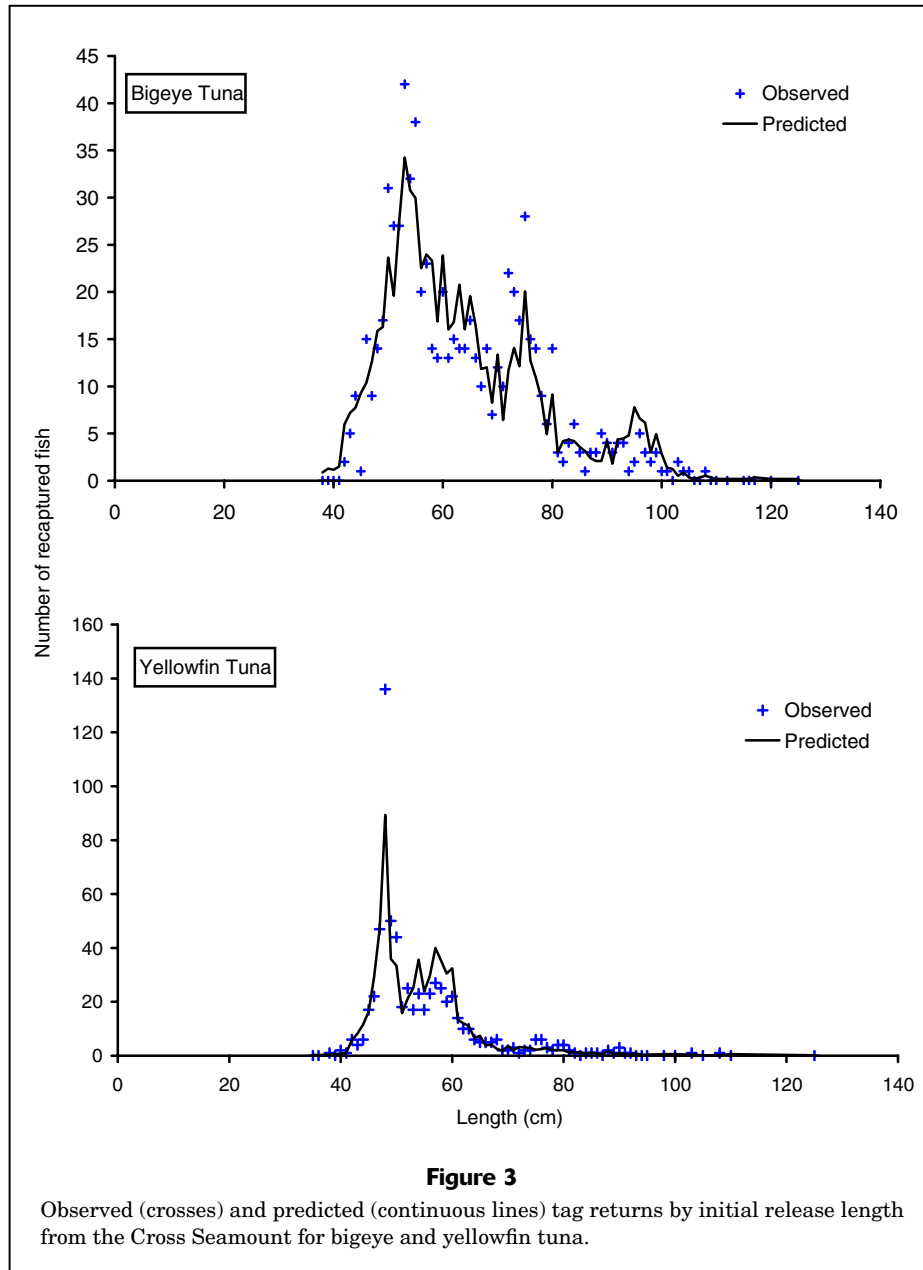
The estimates of natural mortality rate for both species were highest in the smallest size class. The estimates decreased gradually for both species, but for yellowfin tuna there was a slight increase in the largest size class, yielding a "U" shaped curve (Fig. 4). The estimates for bigeye tuna were 0.00576, 0.00372, and 0.00181/day (2.102, 1.356, and 0.660/yr) for 29–55, 56–70, and ≥71 cm, respectively, and for yellowfin tuna they were 0.01425, 0.00221, and 0.00361/day (5.203, 0.806, and 1.316/yr) for 20–45, 46–55, and ≥56 cm, respectively (Fig. 4 and Table 6). These estimates are within the range of the values estimated by Hampton (2000) from analyses conducted for fisheries in other regions of the Pacific.

Fishing mortality estimates are highly variable both within the three size classes and between the sites (Fig. 5).

For the Cross Seamount, F was nearly the same for bigeye tuna over the three size classes (≈0.0026/day) Yellowfin tuna F, estimated for Cross Seamount, was higher for the medium size than for the smaller and large size class (i.e. 0.0027, 0.0115, and 0.0067/day).

The total attrition rate by size k and by site i can be calculated from $Z_{ik} = M_k + F_{ik} + \lambda + \Sigma T_{ij}$, from which the averages for the size class or site may be obtained. Alternatively these could be estimated from a model in which Z is kept constant over the size classes. Although there were large variations in the estimates for different sites, the estimates were not appreciably different for each of the three size classes at any particular site. At the Cross Seamount, the gross attrition rate for yellowfin of 0.038/day was roughly twice that for bigeye tuna (0.022/day). However, the

Figure 3

Observed (crosses) and predicted (continuous lines) tag returns by initial release length from the Cross Seamount for bigeye and yellowfin tuna.

average gross attrition for the entire geographic range of the model area was not very different for the two species (0.033/day for bigeye and 0.034/day for yellowfin tuna). Similar results were obtained in a preliminary analysis of the early recaptures (Holland et al., 1999). In other words, there are consistent indications that yellowfin and bigeye tuna behave differently at Cross Seamount.

The attrition rate measures the rate of loss from the system. A more intuitive measure may be calculated from "half-life" ($\ln(2)/Z_{ik}$) which is a proxy for population residence (Holland et al., 1999). Essentially, half-life is the time required to reduce an existing size of the population by half. The half-life of about 18 days for yellowfin tuna at Cross Seamount was roughly one half that of bigeye tuna

(31 days). Although the half-life across the size classes for yellowfin tuna was similar, the half-life for the large size classes of bigeye tuna were significantly longer than those for the smallest size class (Table 6).

Table 7 shows the ratios of the attrition components to the total gross attrition for both species on the Cross Seamount. Roughly 70% of the total loss is due to emigration. Fishing mortality accounted for about 12% for each of the three size classes of bigeye tuna whereas yellowfin tuna F estimates were 7%, 30%, and 20%, respectively. The contribution of natural mortality to overall attrition in the smaller size classes was substantial. This was 24% for bigeye and 35% for yellowfin tuna. In the larger size classes, the contributions were in the range 6–16%.

Table 3

Yellowfin tuna: Observed and predicted tag transfers from the full model $M_3F_{3,6}T_{17}$, $n = 38$. The rows are tag release sites and columns are recapture sites.

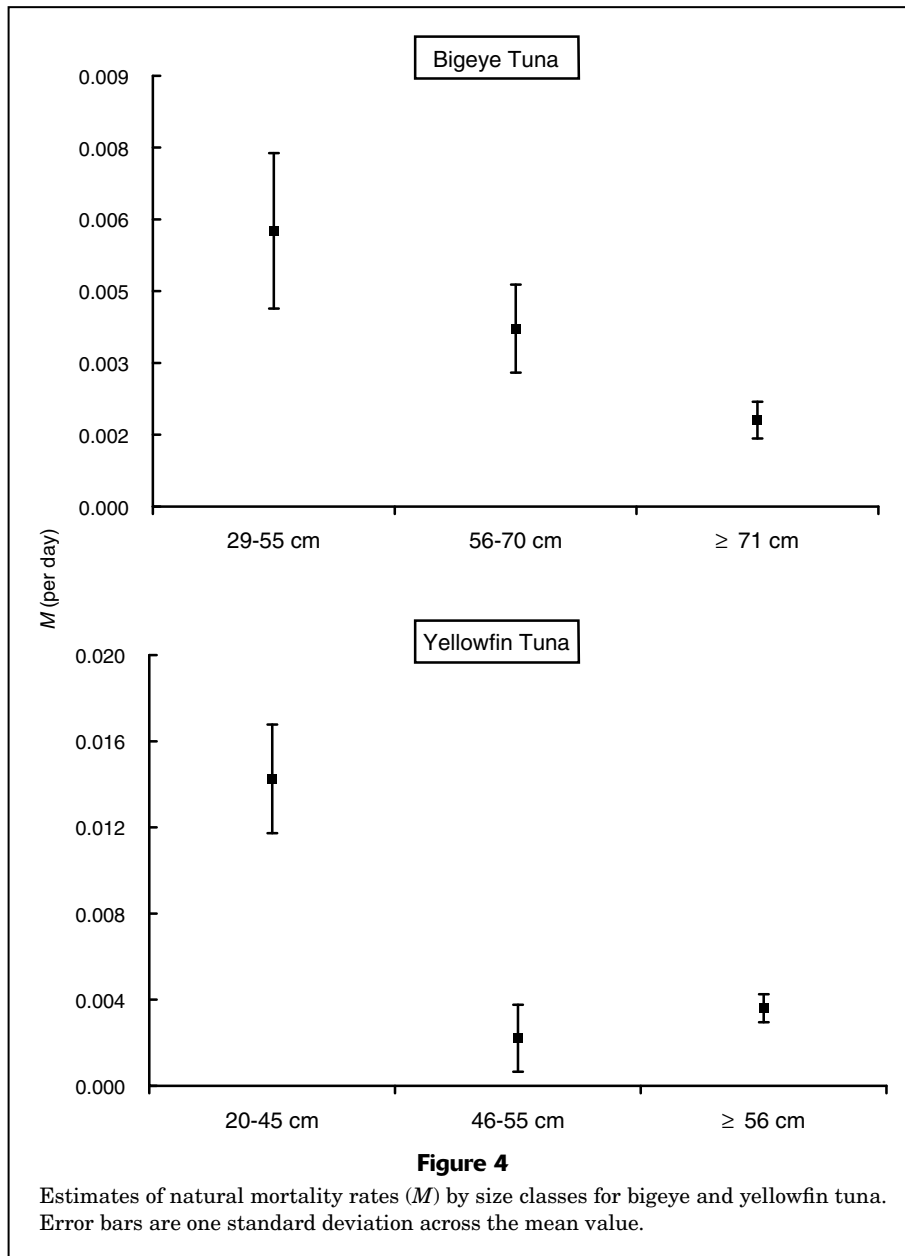| Tag release sites	All	Buoy 1	Buoy 2	Buoy 3	Cross Seamount	Inshore	Other
Observed							
All	970	20	40	9	635	254	12
Buoy 1	36	19	0	0	5	9	13
Buoy 2	47	0	32	1	7	6	1
Buoy 3	13	0	2	8	2	1	0
Cross Seamount	667	0	5	0	618	38	6
Inshore	207	1	1	0	3	200	2
Other	0	0	0	0	0	0	0
Predicted							
All	978.9	20.2	40.6	8.7	634.5	258.8	16.1
Buoy 1	33.5	18.6	0.5	0.0	5.0	8.1	1.3
Buoy 2	46.4	0.1	17.4	4.0	16.9	7.7	0.4
Buoy 3	7.8	0.0	0.6	1.1	3.9	2.0	0.1
Cross Seamount	677.1	0.4	20.7	3.2	606.5	34.3	11.9
Inshore	214.1	1.0	1.4	0.4	2.3	206.6	2.4
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 4

Bigeye tuna: Estimated transfer coefficients (per day) from the full model $M_3F_{3,5}T_{13}$, $n = 31$. Elements with asterisks indicate transfers that were not observed. The diagonal elements (dashed) were not defined in the model.

Tag release sites	Buoy 2	Buoy 3	Cross Seamount	Inshore	Other
Buoy 2	—	0.00245	0.00113	0.00752	0.02707
Buoy 3	0.00000	—	0.01111	0.01073	0.03927
Cross Seamount	0.00045	0.00026	—	0.00464	0.01057
Inshore	**	**	0.00375	—	**
Other	**	**	**	**	—

Table 5

Yellowfin tuna: Estimated transfer coefficients (per day) from the full model $M_3F_{3,6}T_{17}$, $n = 38$. Elements with asterisks indicate transfers that were not observed. The diagonal elements (dashed) were not defined in the model.

Tag release sites	Buoy 1	Buoy 2	Buoy 3	Cross Seamount	Inshore	Other
Buoy 1	—	**	**	0.00648	0.01055	0.04935
Buoy 2	**	—	0.04301	0.00217	0.00000	0.00024
Buoy 3	**	0.00036	—	0.00205	0.00101	**
Cross Seamount	**	0.00226	**	—	0.00136	0.02051
Inshore	0.00042	0.00069	**	0.00000	—	0.00703
Other	**	**	**	**	**	—

Figure 4

Estimates of natural mortality rates (*M*) by size classes for bigeye and yellowfin tuna. Error bars are one standard deviation across the mean value.

Discussion

The size- and site-specific attrition model described in this study is new and potentially applicable to other fish species where release and recapture data meet the model requirements. What is required are the size and geographic position of releases and recaptures. One difficulty encountered related to the quantity of release data that was available for analysis. Because releases were stratified over 1-cm size class cohorts to reliably track their growth over time, larger numbers of releases would be required to have reasonable numbers in the cohorts. Thus we assumed that all tags were released at some arbitrary time zero.

Attempts to estimate size-specific transfer rates were unsuccessful because of poor convergence of the numeri-cal estimation procedure. Size-specific transfer rates were poorly defined in the data sets because of the low number of recaptures in the relevant strata. It is, however, trivial to incorporate size-specific transfer rates in the model and use the same procedure to estimate the transfer rates by the size classes under consideration.

The growth of yellowfin and bigeye tuna in our model is assumed to follow the von Bertalanffy growth function for the entire lifetime of the cohort. However, Lehodey and Leroy,[3]

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[3] Lehodey, P., and B. Leroy. 1998. Age and growth of yellowfin tuna (*Thunnus alabcares*) from the western and central Pacific Ocean as indicated by daily growth increments and tagging data. Working paper 12. Eleventh Standing Committee on Tunas and Billfish, Secretariat of Pacific Community, BP D5, 98848 Noumea Cedex, New Caledonia.

Table 6

Estimates of size specific attrition components (per day) and residence times (half-life [days]) at the Cross Seamount with standard deviations of the estimates (in parentheses). Note: The different size classes for the two species; size classes. Also note that the size-independent transfer rates makes the emigration component constant for all the size classes. M is natural mortality rate; F is fishing mortality rate.

		Bigeye tuna		
Component	From	29–55 cm	56–70 cm	≥71 cm
M	All	0.0058 (0.0016)	0.0037 (0.0009)	0.0018 (0.0004)
F	Cross	0.0023 (0.0003)	0.0029 (0.0003)	0.0026 (0.0003)
Emigration rate	Cross	0.0159 (0.0017)	0.0159 (0.0017)	0.0159 (0.0017)
Residence time	Cross	28.9 (2.6)	30.7 (206)	34.0 (3.1)
		Yellowfin tuna		
	From	20–45 cm	46–55 cm	≥56 cm
M	All	0.0143 (0.0025)	0.0022 (0.0016)	0.0036 (0.0006)
F	Cross	0.0027 (0.0009)	0.0115 (0.0019)	0.0067 (0.0007)
Emigration rate	Cross	0.0241 (0.0019)	0.0241 (0.0019)	0.0241 (0.0019)
Residence time	Cross	16.9 (1.3)	18.3 (1.1)	20.1 (1.4)

Hampton and Fournier (2001) and Hampton and Fournier[2] have shown that growth of smaller-size fish does not conform to the von Bertalanffy function. They estimated a more linear and an increased growth rate for smaller sizes (<120 cm FL for yellowfin and <80 cm FL for bigeye tuna) than could be accounted from the von Bertalanffy function for the entire size range. Although this could, in principal, bias our size-based estimates of F and M, considering the growth variability and the large size ranges we have considered, we feel departure from von Bertalanffy growth is of little importance.

One of the primary objectives of the HTTP was to improve understanding of the dynamics of tuna aggregations at the Cross Seamount and to determine the importance of Cross Seamount associated fish to domestic longline and inshore fisheries. This discussion will therefore focus on the Cross Seamount fishery and its potential interaction with other fisheries. Previous analyses (using fewer data) have estimated gross attrition rates and residence times (Holland et al., 1999) and transfer and attrition rates (Sibert et al., 2000). Using the more recent and complete data set and including size specific attrition to improve the tag-attrition model, we have been able to extend the analysis to provide a more detailed picture of fishery dynamics and interactions.

The natural mortality rate is a critical parameter in stock assessment models, and size- (or age-) specific estimates would greatly improve stock assessment efforts. Unfortunately, natural mortality is not linked to a well-defined *in situ* process, and M is always estimated indirectly (e.g. Fournier et al., 1998). In tag attrition models, M is the "residual attrition" that cannot be accounted for by processes specified in the model. In our model, M would also include permanent emigration beyond the model area. Hampton
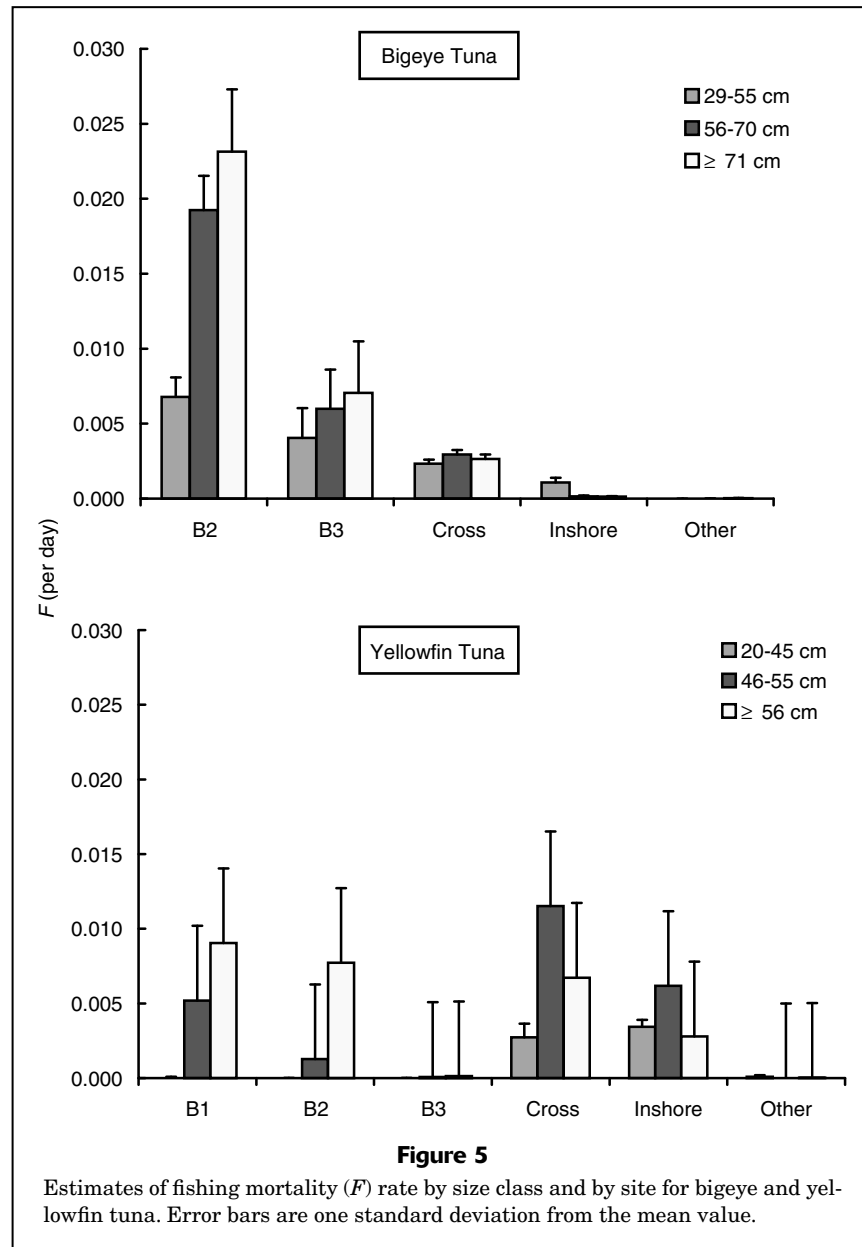
Table 7

Attrition component ratio (scaled by the total attrition) by size classes at Cross Seamount for bigeye and yellowfin tuna. E is the emigration rate.

Size class (cm)	M/Z	F/Z	E/Z
Bigeye tuna			
29–55	0.24	0.10	0.66
56–70	0.16	0.13	0.71
≥71	0.09	0.13	0.78
Yellowfin tuna			
20–45	0.35	0.07	0.59
46–55	0.06	0.30	0.64
≥56	0.10	0.20	0.70

(2000) estimated natural mortality rates from tagging data for a large number of size classes from a "single fishery" model. We have shown here that the attrition component can also be partitioned into size classes in a bulk transfer model. The relatively low number of recoveries from most of the sites did not allow us to estimate attrition over a larger number of size classes. However, our estimates of M are consistent with Hampton's (2000) estimates for both species within the size ranges considered.

The relatively low transfer rate estimates for both species from the Cross Seamount to the inshore areas supports earlier findings (Sibert et al., 2000). However, the relatively high transfer rates estimated for both species from the Cross Seamount and the offshore buoys to the longline fishery (and by inference to the Pacific-wide fishery)

Figure 5
Estimates of fishing mortality (F) rate by size class and by site for bigeye and yellowfin tuna. Error bars are one standard deviation from the mean value.

suggests that fish associated with these structures contribute substantially to the longline catch. Furthermore, the longline fishery considered in our model is an open compartment with no boundaries. Any recoveries outside the bounded compartments will be considered as an emigrant from inshore and offshore fisheries' perspective. In the likely scenario of higher underreporting of recoveries from non-Hawaii-based fisheries, our estimate of transfer rates from inshore and offshore sites to the longline fishery will be lower.

At first glance the higher transfer rates to the longline fishery could be explained by the fact that these offshore locations are contained within the geographical areas of operation of the longline fishery. However, analysis of the time-at-liberty of fish released at Cross Seamount indicates

that they first become vulnerable within the inshore FAD areas before recruiting to the longline fishery. For instance, bigeye tuna released at Cross Seamount were caught after 238 ±156 (median 254) days in the inshore fisheries but in the longline fishery they were caught after 542 ±297 (median 509) days. For yellowfin tuna however, there was little difference; 154 ±134 (median 88) days in the inshore fisheries and 157 ±112 (median 89) days in the longline fishery. These interspecific differences could be due in part to the different vulnerability of the two species to the gears used in the inshore and longline fisheries. Inshore fisheries generally target surface swimming fish, thereby favoring the exploitation of smaller-size yellowfin tuna, whereas the longline gear targets deep swimming adults. Implicit in these results are size-specific vulnerabilities in the inshore

and longline fishery. Similar to the inshore fisheries, the Seamount fishery targets surface swimming fish favoring small- to medium-size classes.

Because of the way in which cohorts were aggregated to maximize the number released per cohort, time varying fishing effort could not be used to reparameterize F with a catchability coefficient (e.g. Hampton, 2000). Instead, F was estimated as a constant proportion of the numbers available at a given time period. This was considered reasonable because there was no reason to believe that the fishery underwent notable change during the period of the tagging experiment. Under this assumption, F is similar to a catchability coefficient. Because both species are targeted with the same suite of gears (Itano and Holland, 2000), the differences in F would reflect their vulnerability to the gears. Higher overall F (vulnerability) at the Cross Seamount for yellowfin compared to bigeye tuna indicates that yellowfin tuna are more vulnerable there.

The gross attrition rate for any given spatial component Z_i in our model includes size-dependent M and F and size-independent T (emigration rate). At the Cross Seamount, the actual estimates of all three components were generally lower for bigeye than for yellowfin tuna, thereby making the estimated residence times for bigeye tuna roughly twice as high as those for yellowfin tuna (Table 6). Our estimate of residence time for bigeye tuna agree closely with earlier estimates (Holland et al., 1999; Sibert et al., 2000). More recently Musyl et al. (2003) found similar results from archival tagging data based on geolocation and vertical movement patterns. They estimated bigeye tuna residence time of 25 ±12 days at the Cross Seamount area—a value consistent with the estimates derived here using conventional tagging data.

Putting aside M, we do know why yellowfin tuna emigration rate from the Cross Seamount is higher while they appear to be more vulnerable in the fishery than bigeye tuna. Their higher vulnerability could in part be explained by their shallower swimming depths that bring them into more frequent contact with handline and troll gear. However, bigeye tuna contribute greatest to the commercial catches by weight from the Seamount (Itano and Holland, 2000). Sibert et al. (2000) suggested that this apparent discrepancy could be due to a much higher biomass of bigeye tuna on the Seamount compared to biomass of yellowfin tuna, coupled with longer residence times.

The apparent longer residence times for bigeye tuna at the Seamount could be due to longer periods of continuous residence or a greater tendency to revisit over time (or to both factors). It is possible that bigeye tuna may gain a trophic advantage by extended association with seamounts (Fonteneau, 1991; Brill and Lutcavage, 2001). Behavior of bigeye tuna associated with Cross Seamount, inferred from archival tag data (Musyl et al., 2003), indicates that their vertical movements are akin to the characteristic open water behavior. That is, they move within the surface mixed layer at night but remain deep during the day except for brief upward excursions (Holland et al., 1990; Dagorn and Josse, 2000). However, Musyl et al. (2003) note the irregular and sometimes more extended day-night transitions of the putative Cross Seamount associated bigeye tuna. This modified behavior at Cross Seamount, during day and night, could indicate that bigeye tuna are exploiting a food source that may not be available to or not preferred by sympatric yellowfin tuna. Unfortunately, similar vertical movement observations for yellowfin tuna at Cross Seamount are not currently available. Preliminary investigation on the food habits of bigeye and yellowfin tuna at Cross Seamount and offshore weather buoys suggest feeding ecology is very different between the two species even at immature sizes (Grubbs et al.[4]). They suggest that separation in vertical distribution may be maintained during feeding. Bigeye tuna may target the deep-scattering-layer prey while yellowfin tuna feed primarily on mixed-layer prey.

Estimates of horizontal movement patterns of bigeye tuna equipped with archival tags suggest that almost all bigeye tuna released from the Seamount stayed within close proximity of the seamount and around the Main Hawaiian Island chain (Sibert et al., 2003). The relatively high transfer rates between the Cross Seamount and the NOAA weather buoys and the similar magnitude of transfer rates between Cross Seamount and inshore areas suggests that the apparently lower emigration rate of bigeye tuna is due to returnees contributing to the recapture attrition curve. Given the estimated F at the Seamount for the two species in this study, the number of bigeye tuna residing at Cross Seamount has to be at least an order of magnitude greater than that for yellowfin tuna to match the catch observed in fishery statistics.

The overall picture emerging from the analysis is similar to the earlier findings of Sibert et al. (2000). At any given time the resident population (or standing stock) of yellowfin on the Cross Seamount is considerably smaller than the bigeye tuna population. However, during their brief stopovers on the Cross Seamount, yellowfin tuna are highly vulnerable to the offshore handline-troll fishery that occurs there. They associate with the Cross Seamount but leave quite rapidly, and most of them never return. In contrast, the longer apparent residency, or persistence, of bigeye tuna at the Cross Seamount may be due to longer periods of association and a tendency to return to the Seamount over time. Even though they tend to leave the Seamount (perhaps permanently when they grow to larger sizes), they appear to remain in the Hawaii area, at least for two to three years. Some of them become vulnerable in the inshore area but, if not captured, they are later caught by the longline fishery. This situation is very similar to the aggregation of bigeye tuna in the Coral Sea in northwestern Australia (Hampton and Gunn, 1998) where bigeye tuna appear to have a lower attrition rate than yellowfin tuna. Hampton and Gunn (1998) argued that although both species gradually disperse from the Coral Sea area, large numbers of bigeye tuna remain resident in the area for some

[4] Grubbs, R. D., K. Holland, and D. Itano. 2001. Food habits and trophic dynamics of structure-associated aggregations of yellowfin and bigeye tuna (*Thunnus albacares*, and *T. obesus*) in the Hawaiian Islands. Project description, rationale and preliminary results. Presented at the Fourteenth Standing Committee on Billfish and Tunas; Yellowfin Research Group, 9–16 August 2001. Secretariat of Pacific Community, BP D5, 98848 Noumea Cedex, New Caledonia.

time and become vulnerable in the fishery. More recently, archival tagging on drifting FADs in the eastern Pacific Ocean have shown that bigeye tuna remain resident in the general area of release for at least about an year (Schaefer and Fuller, 2002). In our study virtually all (99.4%) of bigeye tuna recoveries were made within the model area. These observations suggest some degree of regional fidelity in the exploited phase (medium size) of bigeye tuna and a low level of mixing with the central western Pacific region for these immature size classes. However, it appears that larger size bigeye tuna are not resident in Hawaiian waters because spawning condition adults do not recruit to the local longline or handline fisheries. It is likely that as these fish mature they move to warmer waters to the south of Hawaii where bigeye tuna spawning is known to occur (Nikaido et al., 1991).

The extent of catch interaction between the Cross Seamount fishery and the domestic inshore and longline fisheries does not appear to be of great management concern at current levels of exploitation. However, given that current exploitation rates are considered moderate (10–30%) and the seamount aggregations are highly vulnerable to low cost gear types, it was recommended that further increases in fishing effort for yellowfin and bigeye tuna be monitored at Cross Seamount. This note of caution is reinforced by the increased concern over recent bigeye and yellowfin tuna stock assessments from the western and central Pacific (Hampton and Fournier, [2001]; Hampton and Fournier[2]). These assessments suggest declining adult biomass, declining recruitment, and greatly increased fishing mortality on juveniles in the equatorial region, which is probably the main source of recruitment to the Cross Seamount and Hawaii-based fisheries.

Additional strategic tagging experiments involving the release of tuna should represent the full geographic and size range landed in the fisheries to adequately refine our estimates of fishery interaction and transfer rates. Comparative studies of yellowfin and bigeye tuna using electronic tags would also help to understand differences in how the two species partition their habitat. However, the current size-based estimates of natural and fishing mortality rates, together with transfer rates and other ancillary information, still remain useful to conduct a yield-per-recruit analysis to investigate various scenarios arising from an increase or decrease in fishing effort and its effects on the fishery components. The results of this analysis will also be useful in refining stock assessment models that are currently being developed for the species.

Acknowledgments

Literature cited

Adam, M. S., and G. P. Kirkwood.
 2001. Estimating tag-shedding rates for skipjack tuna, *Katsuwonus pelamis*, off the Maldives. Fish. Bull. 99: 193–196.
Boggs, C. H., and R. Y. Ito.
 1993. Hawaii's pelagic fisheries. Mar. Fish. Rev. 55(2): 69–82.
Brownlee, K. A.
 1965. Statistical theory and methodology, 590 p. John Wiley & Sons, New York, NY.
Brill, R. W., and M. E. Lutcavage.
 2001. Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. Am. Fish. Soc. Symp. 25:179–198.
Dagorn, L., P. Bach, and E. Josse.
 2000. Movement patterns of large bigeye tuna (*Thunnus albacares*) in the open ocean determined using ultrasonic telemetry. Mar Biol. 136:361–371.
Fonteneau, A.
 1991. Seamounts and tuna in the Tropical Eastern Pacific. Aquat. Living Res. 4:13–25.
Fournier, D., J. Hampton, and J. R. Sibert.
 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to south Pacific albacore, *Thunnus alalunga*. Can. J. Fish. Aquat. Sci. 55:2105–2116.
Hamilton, M. S., and S. W. Huffman.
 1997. Cost-earnings study of Hawaii's small boat fishery, 1995–1996, 104 p. University of Hawaii, Joint Institute for Marine and Atmospheric Research, Honolulu, HI.
Hampton, J.
 1991a. Estimation of southern bluefin tuna *Thunnus maccoyii* natural mortality and movement rates from tagging experiments. Fish. Bull. 89:591–610.
 1991b. Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertallanffy models incorporating individual variation. Fish. Bull. 89:577–590.
 1997. Estimation tag reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean. Fish. Bull. 95:68–79.
 2000. Natural mortality rates in tropical tunas: size really does matter. Can. J. Fish. Aquat. Sci. 57:1002–1010.
Hampton, J., and D. Fournier.
 2001. A spatially-disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Mar. and Freshwater Res. 52:937–963.
Hampton, J., and J. Gunn.
 1998. Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) tagged in the north-western Coral Sea. Mar. Freshwater Res. 49:475–89
Hilborn, R., and M. Mangel.
 1997. The ecological detective: confronting models with data. Monographs in population biology series, no. 28, 136 p. Princeton Univ. Press, Princeton, NJ.
Holland, K., R. W. Brill, and R. K. C. Chang.
 1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull. 88:493–507.
Holland, K. N., P. Kleiber, and S. M. Kajiura.
 1999. Different residence times of yellowfin tuna, *Thunnus*

albacares, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. Fish. Bull. 97:392–395.

Itano, D., and K. Holland.
    2000. Movement and vulnerability of bigeye (*Thunnus obesus*) and yellowfin tuna (*T. albacares*) in relation to FADs and natural aggregation points. Aquat. Living Resour. 13: 213–223.

Kirkwood, G. P., and M. H. Walker.
    1984. A new method for estimating tag shedding rates, with application to data for Australian Salmon, *Arripis trutta esper,* Whitely. Aust. J. Mar. Freshwater Res. 35:601–606.

Kirkwood, G. P., and I. F. Somers.
    1984. Growth of two species of tiger prawn, *Panaeus esculentus* and *P. semisculatus*, in the western Gulf of Carpentria. Aust. J. Mar. Freshwater Res. 35:703–712.

James, I. R.
    1991. Estimation of von Bertalanffy growth curve parameters from recapture data. Biometrics 47:1519–1530.

Kleiber, P., A. W. Argue, and R. E. Kearney.
    1987. Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44:1122–1134.

Musyl, M. K., R. W. Brill, C. H. Boggs, D. S. Curran, T K. Kazama, and M. P. Seki.
    2003. Vertical movements of bigeye (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main

Hawaiian Islands from archival tagging data. Fish. Oceanogr. 12(2):1–18.

Nikaido, H., N. Miyabe, and S. Ueyanagi.
    1991. Spawning time and frequency of bigeye tuna, *Thunnus obesus*. Nat. Res. Inst. Far. Seas Fish. Bull. 28:47–73.

Otter Research Ltd.
    2000. AD model builder documentation. Otter Research Ltd. [URL: http://otter-rsch.com/admodel.htm>], accessed November 2002.

Pooley, S. G.
    1993. Economics and Hawaii's marine fisheries. Mar. Fish. Rev. 55(2):93–101.

Schaefer, K. M., and D.W. Fuller.
    2002. Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. Fish. Bull. 100(4): 765–788.

Sibert, J. R., K. Holland, and D. Itano.
    2000. Exchange rates of yellowfin and bigeye tunas and fishery interaction between Cross seamount and near-shore FADs in Hawaii. Aquat. Living Resour. 13:225–232.

Sibert, J. R., M. K. Musyl, and R. W. Brill.
    2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalaman filter analysis of archival tagging data. Fish. Oceanogr. 12(3):1–11.

Wang, Y.-G., and M. R. Thomas.
    1995. Accounting for individual variability in the von Bertalanffy growth model. Can. J. Fish. Aquat. Sci. 52:1368–1375.