Abstract.—North Pacific albacore tagging data from a tag-release program conducted from 1971 to 1989 were analyzed to obtain estimates of exploitation rates and related parameters. The major albacore fishing fleets in the North Pacific, the U.S. baitboat, Japan baitboat, troll and longline fleets were used in the analysis. Another category of fleet (“other”) that combined remaining miscellaneous recapture sources was also used. Tag-attrition models incorporating variable availability of tagged albacore to the various fleets, seasonal catchability, and multiyear effects on catchability were developed and applied. The incorporation of all three effects was found to improve model fit significantly. If exploitation of the tagged population is representative of the North Pacific albacore population as a whole and if tag reporting rates were high, the results would suggest that the exploitation rate has been less than 10% per year since the early 1970s. However, a deficit of returns from the troll fleet in comparison with its catch suggested that the pattern of exploitation of the tagged population, by this fleet at least, was different from that for the untagged albacore population. After compensating for assumed depressed availability of tagged albacore to the troll fleet, annual exploitation rates were estimated to have declined from a high of 40% in the mid-1970s to <10% since the early 1980s.

Estimates of exploitation rates for north Pacific albacore, Thunnus alalunga, from tagging data

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Albacore tuna, Thunnus alalunga, occur in the tropical and subtropical waters of the Pacific Ocean, where they comprise separate stocks north and south of the equator (Murray, 1994). In the north Pacific, albacore spawn predominantly in the spring and summer over a wide area bounded approximately by 10°–30°N (Nishikawa et al., 1985). Juvenile albacore appear in the North Pacific Transition Zone (35°–45°N), where they are exploited by the surface fishery, comprising mainly Japanese and U.S. baitboat, troll, and until the early 1990s, Japanese and Taiwanese driftnet fleets (Fig. 1). Adult albacore are found at lower latitudes, where they are caught by the subsurface longline fishery, comprising Japanese, Korean, and Taiwanese fleets (Fig. 1). Longline catches have been fairly stable at 10,000–20,000 t annually. Total surface fishery catches (which have been dominated by Japanese baitboat catches) have declined from a peak of around 100,000 t in the mid-1970s to 20,000–50,000 t in recent years (Liu and Bartoo, 1995).

Since 1971, 23,780 albacore have been tagged in the North Pacific in a program conducted jointly by the U.S. National Marine Fisheries Service (NMFS) and the American Fisheremen’s Research Foundation. The tag recoveries have been used in studies of albacore movements (Laurs and Lynn, 1977), growth (Laurs and Wetherall, 1981), and fishery interaction (Kleiber and Baker, 1987). However, to date no formal analysis of the data has been undertaken to estimate exploitation rates and related parameters. In this paper, we develop tag-attrition models (Kleiber et al., 1987), incorporating different structural assumptions concerning availability and catchability of the tagged population. The models are fitted to the albacore tagging data to obtain estimates of the instantaneous rate of natural mortality and fleet-specific catchability coefficients. These estimates are used to construct time series of estimated exploitation rates. The relative merits of the alternative models and applicability of the estimates to the north Pacific albacore population in general are discussed.

Materials and methods

Tagging data

Albacore tagging occurred from 1971 to 1996, mainly during April–Sep-
September, with 97% of the 23,780 releases occurring prior to 1987 (Fig. 2). Tagging was carried out aboard U.S. troll vessels and baitboats by NMFS technicians and commercial fishermen trained in tagging. Tagging methods are described by Laurs et al. (1976) and Laurs and Wetherall (1981). Only albacore judged to be in very good condition were selected for tagging; therefore mortality due to tagging is believed to have been negligible. Tagged albacore were released over a wide area of the eastern and central North Pacific; the largest numbers of releases took place in coastal waters adjacent to North America at 30°–50°N (Fig. 3). Fewer albacore were tagged west of 180°, which is the main operational area of the Japanese baitboat fleet. The size distribution of tagged albacore is typical of surface fishery catches (Fig. 4).

As of 14 August 1997, 1302 tagged albacore (5.5% of the releases) had been recaptured and the tags returned to NMFS. Recaptures have been recorded from a wide range of national fleets and gear types, but the largest numbers of recaptures (68% of the total) were made by U.S. and Japanese baitboats and U.S. troll boats (Table 1). Recaptures occurred throughout the North Pacific, but most recaptures were concentrated in coastal waters adjacent to North America (mainly U.S. troll and baitboats) and west of 180° (Japanese baitboats) (Fig. 5).
Population dynamics model for tagged albacore

We used a tag-attrition model (e.g., Seber, 1973; Kleiber et al., 1987) to describe the dynamics of tagged albacore (hereafter referred to simply as “tags”). The model may be represented by

\[
\hat{r}_{ijf} = R_i (1 - \alpha) \beta \gamma \exp \left[ - \sum_{k=1}^{j-1} \sum_{f} (F_{ijk}) - (j-1)(M + \psi) \right]
\]

\[
\sum_{f} \frac{F_{ijf}}{F_{ijf} + M + \psi} \left[ 1 - \exp \left( - \sum_{f} F_{ijf} - M - \psi \right) \right]
\]

where \( \hat{r}_{ijf} \) = the estimated number of tags from release group \( i \) recaptured by fleet \( f \) in time period \( j \) and returned with complete information (recapture time and fleet);

\( R_i \) = the number of tags released in release group \( i \);

\( \alpha \) = the proportion of type-1 tag losses;

\( \beta \) = the proportion of recaptured tags that are returned;

\( \gamma \) = the proportion of returned tags having complete information;

\( F_{ijf} \) = the instantaneous rate of fishing mortality on release group \( i \) in time period \( j \) by fleet \( f \);

\( M \) = the instantaneous rate of natural mortality;

\( \psi \) = the instantaneous rate of type-2 tag loss;

\( i \) = an index for release group;

\( j \) = an index for time period;

\( k \) = an index for time periods prior to \( j \); and

\( f \) = an index for fleet.

Data stratification

In order to allow seasonal variability in tag returns to be modeled, tag releases and returns were grouped by the quarter (Jan–Mar, Apr–Jun, Jul–Sep, and Oct–Dec) and year of release and recapture. This resulted in 48 release groups (Table 2). Small numbers of releases in 1994 and 1995, from which no recaptures have so far been reported, were not included in the analysis. We defined five fleets: 1) U.S. baitboat; 2) Japanese baitboat; 3) U.S. and Canadian troll (referred to as the troll fleet); 4) Japanese, Korean, and Taiwanese longline (referred to as the longline fleet); and 5) others (consisting of recapture sources not otherwise defined). This definition was designed to group fleets having similar characteristics (fishing methods, seasonal distributions of effort, and sizes of albacore caught). The observed tag returns, \( r_{ijf} \), were thus grouped by tag release group \( i \), quarter and year of recapture \( j \), and recapture fleet \( f \). Tag returns to the end of 1992 were considered in the analysis.
Figure 4
Size distribution of North Pacific albacore tag releases, 1971–89.

Table 1

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<th>Vessel or gear type</th>
<th>Nationality</th>
<th>Number of returns</th>
<th>%</th>
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<td></td>
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<td>312</td>
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Nuisance parameters

We assumed that tag shedding was the only source of type-1 and type-2 tag loss and therefore used values for α and ψ of 0.12 and 0.0245 per quarter, respectively, based on analysis of double-tagging data (Laurs et al., 1976). There are no independent estimates of nonreporting of North Pacific albacore tags, although Kleiber and Baker (1987) stated that “nonreporting losses are small for the major fisheries that recovered the tags”; they assumed β = 0.9. We also made this assumption but tested the sensitivity of our results to values of β in the range 0.1 to 1.0. The value of γ(0.87) was estimated directly from the tag-return data.

Reparameterization of fishing mortality

To create sufficient degrees of freedom to enable a statistical estimation of parameters, the number of fishing mortality parameters to be estimated, $F_{ijf}$ needs to be reduced. If we assume for the moment that $F_{ijf}$ is independent of release group i, $F_{jf}$ may be reparameterized as a function of fishing effort, $E_{jf}$, and catchability, $q_{jf}$:

$$F_{jf} = q_{jf} E_{jf}.$$  (2)

We may then propose models that constrain $q_{jf}$ in some sensible way. Let $S_{j}$ denote a matrix that contains, for each $f$, a season for each time period indexed by $j$. We tested two seasonal schemes: no seasonal variation for any fleet and seasonal variation (Q1=Jan-Mar, Q2=Apr-Jun, Q3=Jul-Sep, Q4=Oct-Dec) for all fleets.
Additionally, we tested constraints on $q_f$ that specified how catchability might vary over longer (multiyear) time periods. Let $T_{jf}$ be a matrix that, for each $f$, maps time period $j$ into a series of multiyear periods within which the seasonal pattern of catchability for that fleet may be assumed to be constant. We tested two schemes for $T_{jf}$: a constant pattern of catchability over time for all fleets and catchability patterns for all fleets specific to four time periods ($1=1971$ Q4 to 1974 Q4, $2=1975$ Q1 to 1979 Q4, $3=1980$ Q1 to 1984 Q4, and $4=1985$ Q1 to 1992 Q4). Incorporating the notation for seasonal and multiyear effects, Equation 2 may then be rewritten as

$$F_{jf} = q_{sj} T_{sf} E_{jf}. \tag{3}$$

Quarterly effort statistics for fleets 1 and 3 were obtained from NMFS databases. Statistics for fleets 2 and 4 were obtained from Secretariat of the Pacific Community databases. An arbitrary, constant level of effort was assumed for fleet 5. Effort data were compiled for the period from 1971 Q4 to 1992 Q4 to correspond to the period of the tagging experiment.

**Changes in availability of the tagged population**

The model as described thus far implies that the availability of the tagged population to the various fisheries remains constant for the duration of the experiment. There are two reasons why this assumption may not be satisfied, necessitating some adjustment to the model. First, the spatial distribution of the tagged population of any release set in relation to the spatial distribution of fishing effort by the recapture fleets was not constant over time. In particular, because most releases occurred in the eastern Pacific, the tagged population would have been initially more available to the U.S. baitboat and troll fleets and less available to the Japanese baitboat and longline fleets, which have a more westerly distribution. Over time, as the tagged population dispersed, the effects of such differential spatial availability would be expected to dissipate. Second, the availability of the tagged population to the recapture fleets would also be affected by the size distribution of the tagged population. Tagged fish at release were generally of a size similar to sizes of fish captured by the surface fisheries but were considerably smaller than those captured by the longline fishery. Therefore, the availability of the tagged population at release would not be limited initially by size for the surface fisheries but would be reduced for the longline fishery. As the tagged fish grew, their availability to the longline fishery would become less restricted by their size, but their availability to the surface fisheries might be reduced as they "grew out" of the size range typically exploited by those fisheries. Because our model has neither spatial nor size structure, the effects of size and spatial distributions cannot be explicitly incorporated. However, we developed an approximate means to allow for such effects in ag-
Table 2
North Pacific albacore tag-release and tag-return data, summarized by release group.

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<th>Japan baitboat</th>
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<th>Longline</th>
<th>Other</th>
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<td>Total</td>
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<td>23,449</td>
<td>365</td>
<td>301</td>
<td>138</td>
<td>72</td>
<td>222</td>
<td>171</td>
<td>1269</td>
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ggregate in order to reduce the potential bias in the other parameter estimates of interest. We defined a fleet-specific availability coefficient, \( \phi_{tij} \), where the index \( tij \) refers to the number of time periods at liberty of release group \( i \) in time period \( j \). Equation (3) then becomes

\[
F_{ijf} = \phi_{tij} \alpha_{f} \tau_{tij} \varepsilon_{ijf}.
\]  

(4)

\( \phi_{tij} \) is therefore a proxy variable related to time at liberty that we used to correct, in an approximate way, for the effects of changing availability of the tagged population over time. However, \( \phi_{tij} \) need not be estimated for all \( tij \). Rather, ranges of \( tij \) may be specified for which the \( \phi_{tij} \) are considered to be constant at either 0 (completely unavailable) or 1 (fully available).

A scheme for constraining \( \phi_{tij} \) was devised from preliminary inspection of the data, and some knowledge of albacore dispersion (Laur and Wight, 1977), growth (Laur and Wetherall, 1981), and gear selectivity (Bartoo and Holts, 1993) in the North Pacific (Table 3). The scheme provided three time periods for spatial mixing of tagged albacore with respect to the surface fishery fleets and the “other” fleet (which has characteristics similar to the surface fishery fleets), and eight time periods to allow recruitment of tagged albacore to the longline fishery. During these periods, \( \phi_{tij} \) was estimated from the data. We assumed that tagged albacore remain fully available to the longline fishery during the constrained period for \( \phi_{tij} = 1 \) for \( tij > 8 \). For the surface fishery and “other” fleets, this may not be a good assumption, because these fishing methods may not have fully selected albacore of larger size (Bartoo and Holts, 1993). Therefore, we assumed that albacore were fully available during periods 4–11 after release (\( \phi_{tij} = 1 \) for \( tij > 12 \)) but were completely unavailable to these fleets after 15 time periods (\( \phi_{tij} = 0 \) for \( tij > 15 \)).

To allow for a gradual decline in availability during the intermediate period (11 < \( tij < 16 \), \( \phi_{tij} \) was estimated from the data.

**Parameter estimation**

We used a multinomial likelihood function to fit the various models to the tagging data. A derivation of the likelihood function as applied to tagging data is given in Kleiber and Hampton (1994). We minimized the negative log of this function to obtain the parameter estimates, i.e. by minimizing (omitting terms dependent only on the data)

\[
- \sum_{i} \left[ (R_{i} - \sum_{k} r_{ik} \ln \left( 1 - \frac{\sum_{k} r_{ik}}{R_{i}} \right)) + \sum_{k} r_{ik} \ln \left( \frac{r_{ik}}{R_{i}} \right) \right],
\]

where the \( k \) subscript indicates an individual recapture stratum (combining recapture period, fleet, and time at liberty dimensions). Minimization was carried out with a quasi-Newton routine (Otter Research, 1991). The variance-covariance matrix of the estimated parameters was estimated from the inverse of the Hessian matrix (Bard, 1974). The variance of quantities that are functions of the estimated parameters (such as exploitation rates) were determined by the delta method (Seber, 1973).

**Results**

**Model fits**

Eight different model formulations, based on different combinations of constant or variable availability, constant or seasonal catchability, and presence or absence of multiyear effects on catchability, were fitted to the North Pacific albacore tagging data. The total numbers of estimated parameters and the maximum log-likelihood function values for each fit are shown in Table 4. It is clear that the addition of variable availability, seasonal catchability, and multiyear effects on catchability all result in highly significant improvements in fit. The model incorporating all three effects, model 8, is suggested as the most appropriate of the tested models on the basis of likelihood-ratio tests (Kendall and Stuart, 1979). Model 6, which did not incorporate multiyear catchability effects, was the next preferred model.

Examples of plots of observed and predicted tag returns, aggregated over tag release groups, are shown in Figure 6 for model 2 and in Figure 7 for model 8. As expected, there are large discrepancies
Table 4

Maximum log-likelihood function values for alternative model formulations comprising constant (–) or variable (+) availability, constant (–) or seasonal (+) catchability, and absence (–) or presence (+) of multi-year effects on catchability.

<table>
<thead>
<tr>
<th>Model number</th>
<th>Variable availability</th>
<th>Seasonal catchability</th>
<th>Multi-year effects on catchability</th>
<th>Number of parameters</th>
<th>Log likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>6</td>
<td>−9,511.2</td>
</tr>
<tr>
<td>2</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>19</td>
<td>−9,210.7</td>
</tr>
<tr>
<td>3</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>19</td>
<td>−9,386.1</td>
</tr>
<tr>
<td>4</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>50</td>
<td>−9,036.9</td>
</tr>
<tr>
<td>5</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>37</td>
<td>−9,089.9</td>
</tr>
<tr>
<td>6</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>47</td>
<td>−8,834.4</td>
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<tr>
<td>7</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>47</td>
<td>−8,973.3</td>
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<tr>
<td>8</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>79</td>
<td>−8,666.5</td>
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</table>

between observed and predicted returns for model 2, particularly in the time periods soon after release. Major discrepancies were eradicated in the model 8 fit, which has greater flexibility in fitting the returns for these initial periods. Notice also that model 8 not only better predicts the returns for time periods in which \( \phi_{\text{tij}_f} \) was estimated (periods 1–8 for the longline fleet, periods 1–3 and 12–15 for all other fleets) but performs much better in predicting returns from periods of assumed full availability as well (e.g., periods 5 and 6 for U.S. baitboat and troll, periods 10–15 for longline).

Table 5

Estimates of natural mortality rate \( M \) and \( \phi_{\text{tij}_f} \) obtained from fitting model 8 (see Table 4) to the North Pacific albacore tagging data. Underlined zeros indicate parameters set to zero because of zero tag return in those time periods.

<table>
<thead>
<tr>
<th>Recapture fleet</th>
<th>U.S. baitboat</th>
<th>Japan baitboat</th>
<th>Troll</th>
<th>Japan longline</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>CV</td>
<td>Estimate</td>
<td>CV</td>
<td>Estimate</td>
</tr>
<tr>
<td>( M ) (1 year)</td>
<td>0.608</td>
<td>0.090</td>
<td>0.176</td>
<td>0.207</td>
<td>0.035</td>
</tr>
<tr>
<td>( \phi_{\text{1}} )</td>
<td>0.256</td>
<td>0.168</td>
<td>0.067</td>
<td>0.076</td>
<td>0.601</td>
</tr>
<tr>
<td>( \phi_{\text{2}} )</td>
<td>0.297</td>
<td>0.273</td>
<td>0.169</td>
<td>0.511</td>
<td>0.286</td>
</tr>
<tr>
<td>( \phi_{\text{3}} )</td>
<td>0.103</td>
<td>0.763</td>
<td>0.000</td>
<td>—</td>
<td>0.414</td>
</tr>
<tr>
<td>( \phi_{\text{4}} )</td>
<td>0.277</td>
<td>1.012</td>
<td>0.299</td>
<td>0.398</td>
<td>1.000</td>
</tr>
<tr>
<td>( \phi_{\text{5}} )</td>
<td>0.415</td>
<td>0.594</td>
<td>0.554</td>
<td>0.469</td>
<td>0.313</td>
</tr>
<tr>
<td>( \phi_{\text{6}} )</td>
<td>0.486</td>
<td>0.470</td>
<td>0.237</td>
<td>1.018</td>
<td>0.000</td>
</tr>
<tr>
<td>( \phi_{\text{7}} )</td>
<td>0.000</td>
<td>—</td>
<td>0.260</td>
<td>1.016</td>
<td>0.000</td>
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</table>

Parameter estimates

Estimates of \( M \) and \( \phi_{\text{tij}_f} \) for the model 8 fit (\( \beta=0.9 \)) are given in Table 5 by way of example. The model 8 estimate of \( M \) (0.608/yr, coefficient of variation 0.09) is similar to estimates obtained by Bertignac et al.\(^1\) from albacore tagging data in the South Pacific but

higher than previous estimates obtained from fishery data by Suda (1966) and Fournier et al. (1998). Model 1–4 estimates of $M$ (0.496–0.536/yr) are lower than those of models 5–8 (0.576–0.632/yr) because in the former, the models attempt to accommodate the low numbers of initial tag returns by depressing $M$, whereas in the latter, reduced availability for the initial time periods rather than reduced $M$ is found to be a more likely solution. We noted that the correlation coefficients between the estimates of $M$ and the $\phi_{ij}f$'s for the initial time periods were always negative and were in the range of –0.09 to –0.45.

The coefficients of variation of the $\phi_{ij}f$ estimates were variable (0.16–1.0) and were particularly high for the surface fleets at time periods at liberty beyond three years when very few tagged albacore were recovered.

For model 8, considerable differences in catchability estimates among time periods for all fleets were detected, although no consistent trends were evident (Fig. 8). The confidence intervals on these estimates were large in some cases.

Estimates of the total exploitation rate (percentage of the population harvested) in year $y$, calculated by
where $k$ is a quarter occurring in year $y$, are shown in Figure 9 (model 8, $\beta=0.9$). Estimated exploitation rate has been <10% for most of the time series; it declined between 1976 and 1988 and increased slightly afterwards.

**Effect of assumed tag reporting rate**

Although the tag-reporting rate is thought to have been high for North Pacific albacore (Kleiber and Baker, 1987), this contention is not supported by independent data. We therefore examined the sensitivity of the results to different values of $\beta$ (assumed to apply equally to each fleet) for the model 8 fit. The estimates of $M$ were directly related to $\beta$; conversely, average exploitation rate was inversely related to $\beta$ (Fig. 10). In both cases, the sensitivity was slight for $\beta > 0.6$. If the tag-reporting rate was above this level for the main fleets, the results of our analysis should have been robust to small departures from the assumed value.
In the absence of other information, the tag-reporting rate was assumed to be constant over time. It is possible that reporting could have varied over time, owing to variation in the effectiveness of tag recovery procedures or cooperation of fishing fleets. Although it is not possible to test conclusively such hypotheses with the available data, we might note that the time-related variability in catchability estimated with model 8 (Fig. 8) could equally have been interpreted as variation in reporting rates, because catchability and reporting rate are highly correlated in these models.

Discussion

The use of a tagged sample of the population to infer characteristics of the population in general is a common technique in fisheries stock assessment. For such inferences to be valid, several assumptions, discussed in detail by Seber (1973), need to hold. For North Pacific albacore, the assumption of equal probabilities of capture of tagged and untagged fish is likely to be critical. As noted earlier, both the spatial distribution of the tagged population in relation to recapture effort, and the size distribution of the tagged fish in relation to the size-selective characteristics of the different fishing gears are likely to result in violation of this assumption. We have developed a procedure to correct for these deficiencies in an approximate way. The procedure uses time-at-liberty information and knowledge of appropriate time lags to provide some correction for nonuniform availability of the tagged population to the various fishing fleets that is due to spatial and size effects. A more elegant approach would be to develop a model that explicitly deals with the spatial and size structure of the tagged population and with the spatial distribution and size selectivity of fishing effort. Spatially disaggregated tag models are now available (e.g. Kleiber and Hampton, 1994; Sibert et al., in press). An extension of such a model to include size or age structure would provide an improved method for analyzing the North Pacific albacore data.

The natural mortality rate parameter estimated from tagging data in this study is higher than some previous estimates for albacore. We have shown that \( M \) will be overestimated if the tag-reporting rate is overestimated. Although tag reporting for the major fleets is believed to have been high, it is possible that unreported tag recaptures by the drift gillnet fleet, which reported relatively few recaptures, have resulted in a positive bias in our estimate of \( M \).

If the exploitation of tagged albacore is similar to exploitation of the North Pacific population in general, our results suggest that aggregate exploitation rates declined from the mid-1970s to 1988, after which some increase occurred. The results of our preferred model (model 8) further suggest that an-
annual total exploitation rates have been less than 10% during most of the years of the experiment. However, there is a strong indication that exploitation of tagged albacore by the troll fleet may not be representative of exploitation patterns generally by this fleet. The total number of tag returns from the troll fleet was 148 (Table 1). The U.S. baitboat fleet, which fished in an area similar to that fished by the troll fleet during the 1970s and 1980s, reported 403 tag recaptures. However, during the period of the tagging experiment, troll catches were some eight times baitboat catches (Liu and Bartoo, 1995). There is no ready explanation for this inconsistency. One possibility is that differential reporting rates existed between the fleets. However, given the earlier assertion that tag-reporting rates were high in general, differential tag reporting is unlikely to be the cause of such a discrepancy. Another possibility is that albacore become “hook shy” after they have been captured by trolling and are thereafter less likely to respond to trolled lures. Because the majority of albacore tag releases were troll-caught, such behavior would render the tagged population less available to the troll fleet than the albacore population in general. If this was indeed the reason for the paucity of troll-caught returns, relative availability of tagged albacore to the troll fleet would need to be of the order of 3.5% (compared with 100% for the U.S. baitboat fleet) to reconcile the tag-return and catch data for these fleets. Such reduced availability would result in significant underestimation of exploitation rates if not explicitly accounted for in the analysis. If we set $\phi_{tf} = 0.035$ for $3 < t < 16$ for the troll fleet, estimated exploitation rates that would apply to the untagged population are considerably higher, declining from around 40% in the 1970s to less than 10% since the mid-1970s (Fig. 11). At this point, we cannot be sure that the “hook shy” hypothesis is viable or not; therefore, both of the time series shown in Figure 11 should be considered as equally valid possibilities until additional information becomes available.

**Acknowledgments**

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Literature cited.


