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# Growth Variation and Stock Structure in North Pacific Albacore

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## INTRODUCTION

Two continuing needs in North Pacific albacore research are the development of validated age and growth models and the elucidation of stock structure. In many ways, these goals are interdependent. An accurate ageing method would assist growth modeling and provide a key to describing variation in such processes as spawning and migration. Similarly, knowledge of growth variation may be useful in defining stock heterogeneity.

In this paper, we report results of ongoing research directed at both of these goals. Ageing of albacore was attempted by reading validated daily increments on otoliths. Growth models were developed based on the otolith data and tag return statistics. In both sets of data, geographical variation was explored to elicit hypotheses on stock structure. Although the age and growth results are interesting and useful in their own right, some of the associated inferences on stock structure are more provocative and of greater potential significance. We therefore focus more attention on them. We emphasize at the outset that this work is exploratory and more research is required to test the hypotheses generated here.

Current biological models of North Pacific albacore assume the existence of a single stock with uniform rates of recruitment, mortality, and growth. These assumptions of stock homogeneity greatly simplify fishery modeling and seem to be empirically reasonable. For example, the single stock hypothesis is supported by abundant evidence of transpacific migration. Well over 100 albacore tagged and released in the eastern Pacific fishery have been recaptured in the western Pacific. Although fewer tagged albacore have been released in the western Pacific, some of these have been caught again off the U.S. west coast.

Other evidence of a single stock with common properties is provided by the similarity of length modes in the catches. Although the average size composition of catches differs between gears, often some of the prominent modes appear in samples from several of the fisheries.

Nevertheless, because stock structure assumptions have important consequences for models of population dynamics and fishery interactions, we need to consider the possibility that the situation is more complicated. Evidence of significant stock heterogeneity was first presented by Laurs and Lynn (1977). They demonstrated consistent differences in the geographical distribution of tag returns for albacore released off the U.S. west coast. Recoveries of albacore released south of about lat. 40°N were made almost invariably in the same region in subsequent years. Few tagged fish were recovered north of 40°N or in the western Pacific. In marked contrast, albacore released in the waters north of 40°N were recaptured in disproportionately large numbers either in the area of their release or in the western Pacific, and rarely were recaptured off the United States south of lat. 40°N.

More evidence of stock heterogeneity was presented by Laurs and Wetherall (1981), who suggested on the basis of tag return data that these "north" and "south" albacore had different growth rates. Since then, we have pursued the question further by

1) seeking to develop a validated age-growth model based on otolith increment readings, as well as tag returns, and

2) exploring patterns of stock heterogeneity arising from the expanded growth analysis.

The remainder of this paper describes the daily increment analysis and some apparent problems in increment counting. Some of the otolith data are combined with extensive tag return statistics to estimate improved growth models and show that these tentative and exploratory models lead to an interesting alternative hypothesis on stock structure. This hypothesis states that the U.S. fishery south of about lat. 40°N is supported mainly by albacore born in the winter, whereas the United States and Canadian fisheries north of 40°N, and the Japanese fisheries, catch mostly albacore spawned in the summer months.

## ANALYSIS OF GROWTH

### Approach

Despite extensive research using hard parts, length-frequency data, and tag recapture statistics, biologists have not developed a validated model of North Pacific albacore age and growth. Growth rates have been inferred from the progression of modes in length-frequency distributions (Brock 1943; Suda 1954) and computed directly from length increments of tagged and recaptured fish (Otsu 1960; Clemens 1961; Laurs and Wetherall 1981). Other research on vertebral centra (Uno 1936; Aikawa and Kato 1938; Partlo 1955), scales (Bell 1952; Nose et al. 1957; Yabuta and Yukinawa 1963), and dorsal fin rays (Beamish 1981) has been aimed at absolute age assignment, but has suffered from lack of validation. Consequently, there has been no concensus on age and growth (Shomura 1966).

In recent work, we combined an extensive body of tag return data with counts of daily increments on sagittae to estimate the age-length relationship. As a first step, we successfully concluded an experiment to validate the daily frequency of increment deposition (Laurs, et al. 1985). Marginal increments were counted on sagittae from 116 recaptured albacore previously tagged, injected with tetracycline, and released. On the average, 95 growth increments were counted between a tetracycline mark and the otolith edge for every 100 days a tagged fish was at liberty. On the basis of this experiment, we assumed that when reading increments on an entire otolith, age could be estimated accurately by multiplying the total increment count by 1.05.

## Collection, Preparation, and Screening of Data

### Otolith Data

→ Sagittae were dissected from albacore sampled from jig boat catches along the U.S. west coast and in central Pacific waters west to the grounds north of Midway Island. After cleaning in weak household bleach and distilled water, the otoliths were stored dry, and prepared and interpreted by techniques similar to those in Wild and Foreman (1980).

Otoliths from small albacore could be read without special treatment. However, those from larger albacore were lightly etched by repeated submersion in 0.5 N or N HCl for 3-5 seconds. Otoliths were rinsed in distilled water after each exposure to the acid. At the time of reading, etched otoliths were mounted whole on culture microslides, in immersion oil ($n_D^{23°C} = 1.515$).

Each otolith was surveyed microscopically to discover a path, leading from the primordium (core) to the tip of the postrostrum, along which increments could be counted most easily and completely. Such exploratory counting was repeated until consistency in counts was achieved and until, in the judgment of the reader, the entire record of growth was included. Counts were made from the margin to the core under magnifications of 110 to 800X. The lower powers were used near the core or on smaller otoliths where average increment width was greater.

Once the optimal reading path was defined, four final replicate counts were made, and the average count was computed. Age was estimated by multiplying the mean count by 1.05 to correct for undercounting. The data set was screened to remove cases where information on the length of the albacore or the date or location of capture was unreliable. The resulting data set consisted of 225 albacore (Table 1) ranging in fork length from 29.5 to 92.8 cm.

### Tag Return Data

Albacore were caught and tagged in the eastern North Pacific by National Marine Fisheries Service scientists and trained commercial fishermen aboard albacore bait boats and jig vessels on charter to the American Fishermen's Research Foundation. Recoveries were made by sport and commercial fishermen, unloaders, and cannery workers. The tag return data were screened to exclude cases where information on date of recapture or size at release or recapture was incomplete, unreliable, or clearly inaccurate. Details of tagging methods, recovery procedures, and the screening of recapture data have been described in Laurs and Wetherall (1981). Our analyses were based on the 410 recaptures used in that paper, plus 111 tags returned since 1978, or a total of 521 recaptures (Table 1).

## Geographical Grouping of Data

Tag recovery data were sorted into categories representing a "north" stock and "south" stock, according to criteria in Laurs and Wetherall (1981):

> "South" fish are defined as those tagged and recaptured in the eastern Pacific south of lat. 40°N and east of long. 135°W.
>
> "North" fish are those recaptured west of the 180° meridian and those released and recaptured in eastern Pacific zone north of lat. 40°N.

Otolith data were similarly classified. For albacore whose otoliths were read, only a single observation of location was available for each fish. Stock membership was determined accordingly:

> "South" fish are those caught in the eastern Pacific south of lat. 40°N
>
> "North" fish are those caught elsewhere.

## Fitting Growth Models

### Otolith Data

The otolith data and tag recapture statistics were analyzed separately to estimate parameters $L_\infty$, K, and $t_o$ of the von Bertalanffy growth model:

$$L(t) = L_\infty(1 - e^{-K(t - t_o)})$$

where L(t) is the fork length at age t.

In analyzing the otolith data, a stochastic version of the von Bertalanffy model was employed. In this extended model, we assumed that variation in observed length-at-age was additive and a linear function of age; i.e., length variance at age t was

$$V(t) = \alpha + \beta t \ .$$

The stochastic model therefore involved the two additional parameters, $\alpha$ and $\beta$.

Let $\theta_1$ = the set of parameters $L_\infty$, K, and $t_o$, and

$\theta_2$ = the set of parameters $\alpha$ and $\beta$ .

Joint maximum likelihood estimates of the five model parameters were computed by a two-step, iteratively reweighted Gauss-Newton algorithm, repeated until $\theta_1$ and $\theta_2$ converged on stable values. In the first step, given initial (or current) estimates of $\theta_1$ and $\theta_2$, $\theta_1$ was chosen to minimize

$$S_1 = \sum_{i=1}^{n} w_i \left\{ \ell_i - L(t_i) \right\}^2$$

where $\ell_i$ is the observed length of the $i^{th}$ fish in the sample of size n and the statistical weight $W_i = V(t_i)^1$. In the second step, given the residuals from the first step and the current estimate of $\theta_1$, $\theta_2$ was selected to minimize

$$S_2 = \sum_{i=1}^{n} \left\{ R_i^2 - V(t_i) \right\}^2$$

where $R_i = \ell_i - L(t_i)$. Satisfactory convergence was usually achieved in three passes through the two-step procedure.

Approximate standard errors for the parameters were computed based on asymptotic properties of the maximum likelihood estimators.

__Tag Return Data__

For tag return statistics, the only von Bertalanffy parameters directly estimable from the data are $L_\infty$ and K. These were computed iteratively by minimizing the sum of squares:

$$S = \sum_{i=1}^{n} \left\{ \ell_{2i} - [L_\infty - (L_\infty - \ell_{1i}) \exp(-K \Delta_i)] \right\}^2$$

where $\ell_{1i}$ is the observed length at release, $\ell_{2i}$ is the observed length at recapture and $\Delta_i$ is the time between release and recapture.

The von Bertalanffy parameter $t_0$ was computed from estimates of K and $L_\infty$ and an estimate of the mean length of 1-year-old albacore derived from otolith data. The average length at 1 year was estimated from a linear model fit to the otolith data for fish under about 1.5 years of age. Implicit here is the assumption of negligible bias in the increment counts for very small albacore (see discussion below).

## ESTIMATES OF LENGTH-AT-AGE

### Discrepancies Between Otolith and Tag Results

Resulting estimates of the growth model parameters for each group of data are given in Table 2. Because von Bertalanffy parameter estimates are extremely prone to bias unless the data encompass a wide range of lengths and an upper asymptote to growth is strongly evident, comparisons involving the figures in Table 2 are of dubious value. Instead, we turn directly to the estimates of mean length-at-age associated with each model. These are shown in Table 3. Estimates of the standard deviations of length-at-age for the otolith data are in Table 4.

The estimates of mean length at 1 year of age, based on the linear models fit only to otolith data from small fish, are 35.2 cm for "north" and 37.8 cm for "south" albacore. These are similar to estimates of length at first birthday reported in Yoshida (1969), based on analysis of juvenile albacore in stomachs of central Pacific billfishes.

Beyond age 1, the models estimated from the otolith data predict much faster growth that is shown by the tag returns (Table 3, Figures 1-3). For example, at 3 years of age, the otolith model predicts the "south" albacore will be 80 cm, whereas the tag data give an expected fork length of only 73 cm at this age. For "north" fish, the corresponding estimates are 77 cm and 65 cm.

Such discrepancies could be due to biases in the tag data or errors in increment counting or interpretation. One possibility, assuming the difference is due to bias in the tag-based model, is that tagging impairs an albacore's ability to swim and feed normally, with the result that tag return data underestimate the growth rate experienced by untagged fish. Hampton (1986) showed that condition factors of tagged southern bluefin tuna were significantly lower than those of untagged fish of the same size. However, this apparent effect of tagging was confined primarily to the first 20 days or so after release and, in any case, implied reduced growth in weight, not length. The latter would be less likely.

Moreover, the tag data are consistent with the pattern of modes appearing in length-frequency statistics and the commonly assumed 1-year interval between adjacent modes. We return to this observation later.

The discrepancy may also indicate that the increment counts on whole otoliths are negatively biased, so that the growth rates based on otoliths are overestimated. Since the smallest albacore in the tetracycline experiments was 51 cm at time of release, there was no validation of daily increment deposition for perhaps the first 2 years of life. Still, based on findings with other species, it is reasonable to assume that the daily deposition pattern holds for the smaller fish.

A more likely source of error in the analysis of whole otoliths would be systematic undercounting of increments deposited during early life. As new increments are deposited, those laid down earlier are partially hidden.

Constant refocusing is necessary to avoid missing the obscured increments. If the tag-based growth curves are approximately correct, the implied degree of increment undercounting would be about 10% for a 50 cm albacore and 15% for a 70 cm fish, in addition to the 5% average rate of undercounting already assumed. On an 85 cm albacore, the total increments missed would amount to roughly 45% of all those deposited during the first 2 years.

### Geographical Variation

Although the otolith and tag return growth models predict different lengths-at-age, they both indicate faster growth for albacore in the "south" group than in the "north" group. In both sets of data, there is considerable overlap (see Figures 2 and 4), and we have yet to establish whether or not the indicated differences are statistically significant. But the earlier results of Laurs and Wetherall (1981) showed a significant difference based solely on tag data. To show the tag-based models together with the observations, we computed an auxiliary growth rate variable

$$Y = \ln[(L_\infty - \ell_1)/(L_\infty - \ell_2)]$$

which is linearly related to the time at liberty (the slope is the von Bertalanffy parameter K). The relationships are displayed in Figure 5 and show the striking difference between "north" and "south" albacore. These results appear to be robust with respect to the assumptions on mean length at age 1.

Differences in growth are conceivable in view of the possibility that albacore in the "north" and "south" groups have different migration routes and foraging areas. Nishimoto and Laurs (this workshop) show that the general variation in tag return patterns between fish tagged east of long. 145°W in the "north" and "south" zones becomes even more interesting when analyzed by age group. Most returns of albacore in the 60-70 cm range at time of tagging were made in subsequent years in the area of release. Recaptures from fish in the 70-80 cm range and the 80-90 cm range when tagged were made in increasingly higher proportion away from their area of release, with a greater percentage coming from the central and western Pacific fisheries. However, albacore in the largest size class and tagged in the "north" area of the eastern Pacific had a much greater chance of being recaptured in the western Pacific than their "south" counterparts. The latter were still recaptured mainly in the region where they were released, or offshore east of the dateline. This apparent difference in migration behavior of the larger albacore is particularly interesting because these are mature fish. This difference suggests the possibility of separate spawning areas.

## BIRTH-DATE DISTRIBUTIONS

A validated age-length model leads directly to estimates of birth-date distributions, provided one has either length or age samples representative of a set of complete spawning cycles. We assume that, in these estimates, a day's chance of appearing in the sample is independent of its position in the cycle. Various biases can result from size selection, stochastic growth, and other factors.

We estimated birth-date distributions by using the tag release and return statistics, and the growth models computed from the tag data. Each of the 521 albacore provided two estimates of its birth date, one based on release length and date and another on corresponding recapture statistics.

The estimated birth-date distributions for the "north" and "south" albacore are shown in Figure 4. These suggest that the "north" fish are born primarily during the April-October period, with a peak in July, whereas the "south" albacore appear to be born mostly during November-June, with a peak in February. The peak of "north" spawning follows the "south" peak by roughly 5 months. The breadth of the overall spawning season is generally consistent with observations on ripe albacore or the occasional occurrence of early juveniles in samples. Of course, systematic errors in the growth curves would bias these birth-date distributions. In particular, if increments on the small albacore used to establish $t_0$ were undercounted, peaks of the spawning periods would occur earlier than indicated.

Another way to estimate spawning periods is to assign ages to modes in the catch length-frequency distributions. We did so using historical length-frequency statistics compiled for the U.S. west coast jig fishery during 1972-78 (Figure 5). When we applied the tag-based growth models, the 64 and 75 cm modes appearing in the "north" group were aged at about 3 and 4 years, respectively, while the 65 and 79 cm modes of the "south" group were aged at 2.5 and 3.5 years (Table 5). These results also suggest spawning periods for "north" and "south" fish roughly 6 months apart, with the spawning of "north" albacore generally peaking in summer and that of "south" fish in winter. One of the aberations in this analysis of modes is the implied interval between the 54 cm and 65 cm modes in the "south" albacore. Tag return and otolith data estimate this interval to be only 6-7 months rather than 12 months.

## RECOMMENDATIONS

In analyzing the otolith and tag return statistics, we have explored several hypotheses concerning growth, spawning season, and stock structure. We regard this work as an ongoing, experimental process by which major assumptions of our present models of population dynamics can be examined. We have pointed out numerous problems, and potential errors and biases that could invalidate our results. Any inferences we made should be viewed circumspectly. We hope that our results stimulate further inquiry and the experiments and sampling required to test a range of hypotheses, including those suggested here. Only by this process can we improve North Pacific albacore stock models.

Additional work is required in several areas:

(1) The apparent bias in otolith increment counts needs to be explained. The possibility that hidden increments were not detected during the counting can be studied by comparing counts on whole mounted sagittae with those made on other preparations, e.g., sectioned otoliths viewed under a scanning electron microscope. We plan to begin this work soon.

(2) Otolith microstructure should be studied to describe variation in early life conditions that may point to patterns in stock structure. Samples should be collected systematically from different segments of the fishery and different areas and time periods.

(3) Better size-frequency sampling is required for analyses of stock structure hypotheses. We found that sample sizes, and geographical sample coverage, varied greatly among years. While there are practical and financial constraints to implementing an ideal sampling plan, the adequacy of the existing sampling effort and procedures should be reviewed in the light of present research needs.

(4) New tagging experiments should be designed and carried out to test specific hypotheses regarding migration and stock structure. As a basis for the experimental design, existing data should be thoroughly analyzed to elicit a set of constructive and testable hypotheses (this work has begun). Although opportunistic tagging has provided a wealth of information, it should be encouraged only if efforts to fund and implement more systematic tagging experiments fail.

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Table 1. Sample sizes for otolith and tag return data sets used to estimate growth models and birth-date distributions for "north" and "south" groups of albacore.

| Albacore group | Otolith data | Tag return data |
|---|---|---|
| "North" | 98 | 257 |
| "South" | 127 | 264 |
| Total | 225 | 521 |

Table 2. Estimates of von Bertalanffy growth parameters for "north" and "south" albacore based on otolith and tag return data (standard errors in parentheses).

| Albacore group | $L_\infty$ | $K$ | $t_0$ |
|---|---|---|---|
| <u>Otoliths</u> | | | |
| "North" | 94.1 (4.5) | 0.61 (0.08) | 0.21 (0.07) |
| "South" | 136.7 (10) | 0.28 (0.04) | -0.12 (0.08) |
| <u>Tag Returns</u> | | | |
| "North" | 136.0 (10.7) | 0.18 (0.03) | -0.70 |
| "South" | 122.9 (7.9) | 0.27 (0.04) | -0.37 |

Table 3. Mean fork length (cm) at 6-month intervals for "north" and "south" albacore, predicted by the otolith-based and tag-based growth models.

| Age (years) | Otolith model "North" | Otolith model "South" | Tag return model "North" | Tag return model "South" |
|---|---|---|---|---|
| 1.0 | 36.0 | 37.0 | 35.2 | 37.8 |
| 1.5 | 51.2 | 50.1 | 43.8 | 48.4 |
| 2.0 | 62.5 | 61.5 | 51.6 | 57.8 |
| 2.5 | 70.8 | 71.4 | 58.7 | 66.0 |
| 3.0 | 76.9 | 80.0 | 65.2 | 73.1 |
| 3.5 | 81.4 | 87.5 | 71.2 | 79.4 |
| 4.0 | 84.7 | 94.0 | 76.7 | 84.8 |
| 4.5 | 87.2 | 99.6 | 81.7 | 89.6 |

Table 4. Estimated standard deviations of fork lengths (cm) for "north" and "south" albacore as function of age, based on otolith daily increment growth models.

| Age (yrs) | "North" | "South" |
|---|---|---|
| 1.0 | 2.2 | 1.3 |
| 1.5 | 2.9 | 2.1 |
| 2.0 | 3.4 | 2.7 |
| 2.5 | 3.8 | 3.2 |
| 3.0 | 4.3 | 3.7 |
| 3.5 | 4.6 | 4.0 |
| 4.0 | 5.0 | 4.4 |
| 4.5 | 5.3 | 4.7 |

Table 5. Predicted ages (yrs) of prominent modes in the U.S. jig catch length-frequency distribution, for "north" and "south" albacore, computed from otolith-based and tag-based growth models.

| | "North" Modes (cm) | | "South" Modes (cm) | | |
|---|---|---|---|---|---|
| | 64 | 75 | 54 | 65 | 78 |
| Otoliths | 2.1 | 2.8 | 1.7 | 2.2 | 2.9 |
| Tag returns | 2.9 | 3.8 | 1.8 | 2.4 | 3.4 |

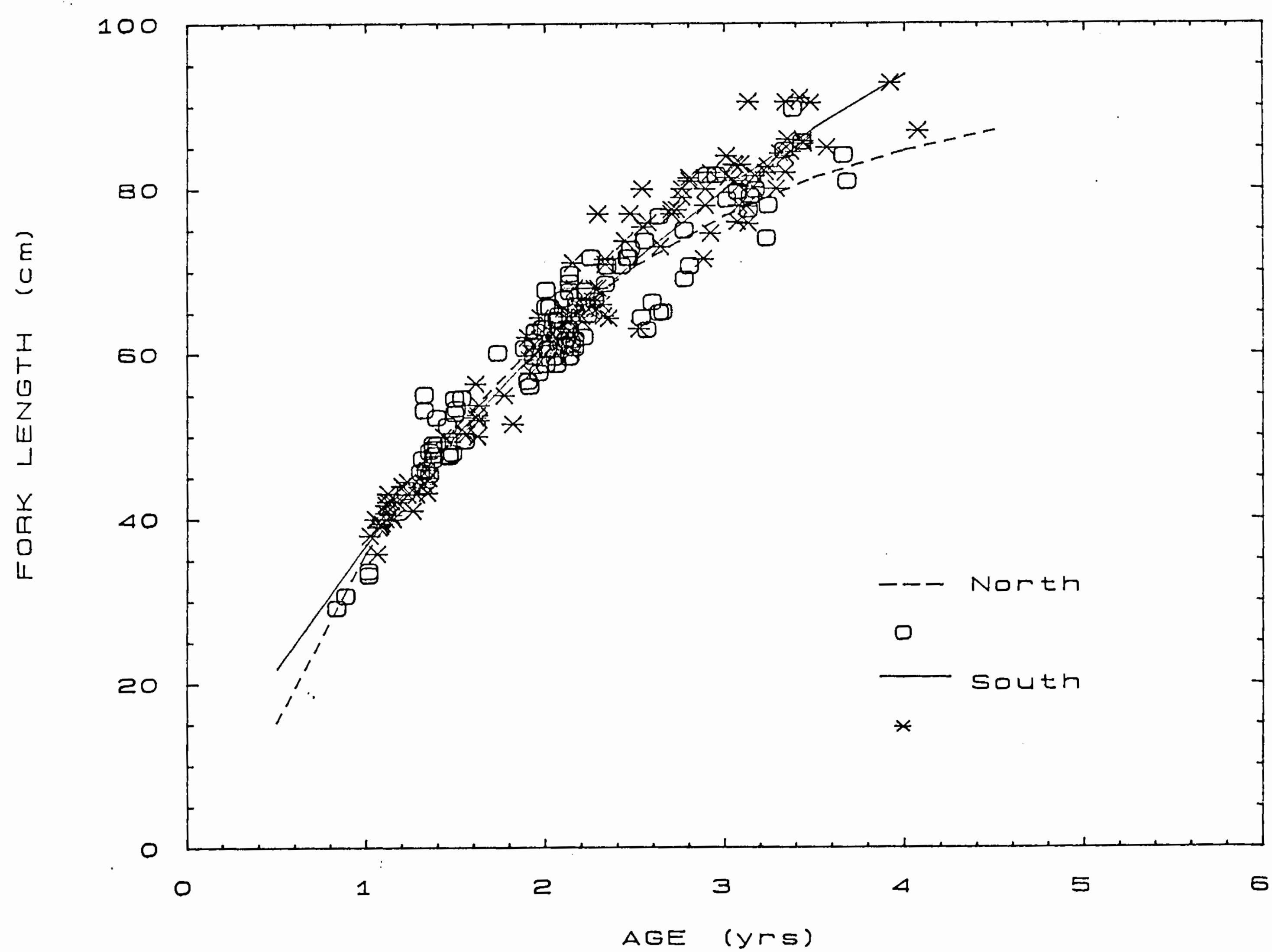


Figure 1.--Estimated von Bertalanffy growth models for "north" and "south" groups of North Pacific albacore, and observed length-at-age, based on otolith data.

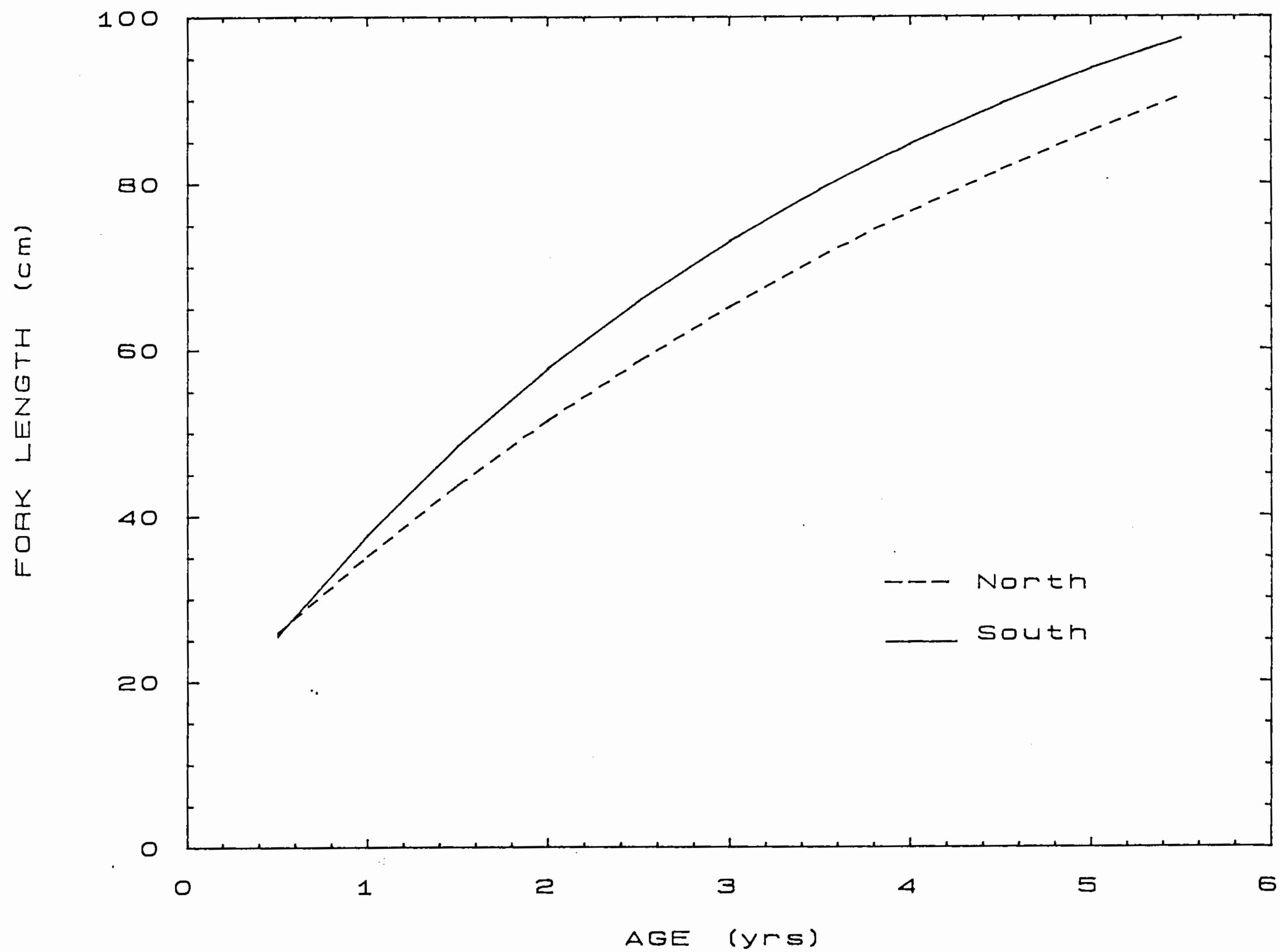


Figure 2.--Estimated von Bertalanffy growth models for "north" and "south" groups of North Pacific albacore, based on tag return data. Location of curves with respect to age axis fixed using estimates of mean length of 1-year-old fish computed from otolith daily increment counts on small albacore.

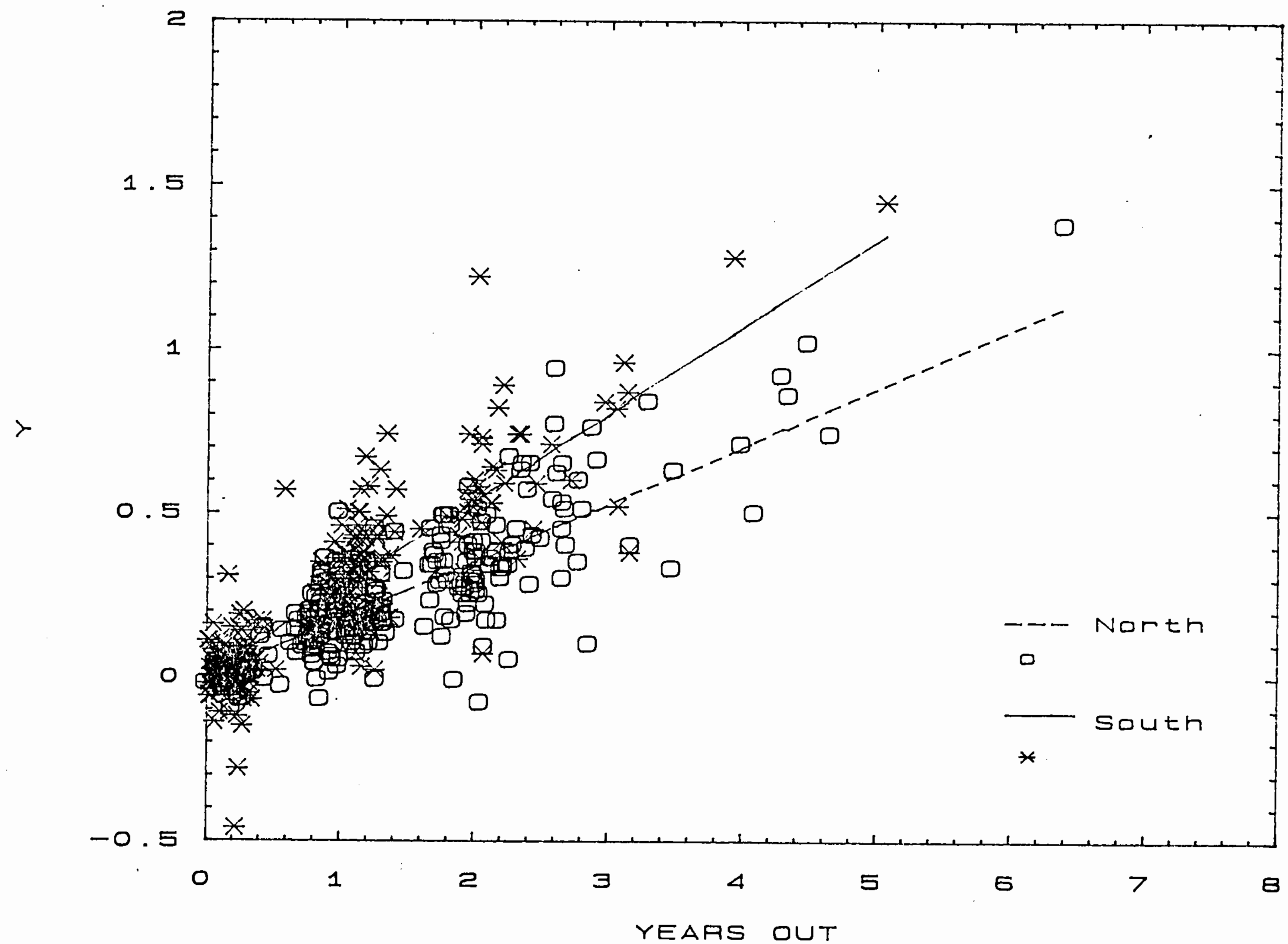


Figure 3.--Growth rate variable $\underline{Y}$ as function of days at liberty for "north" and "south" tag returns, and expected values based on fitted von Bertalanffy models.

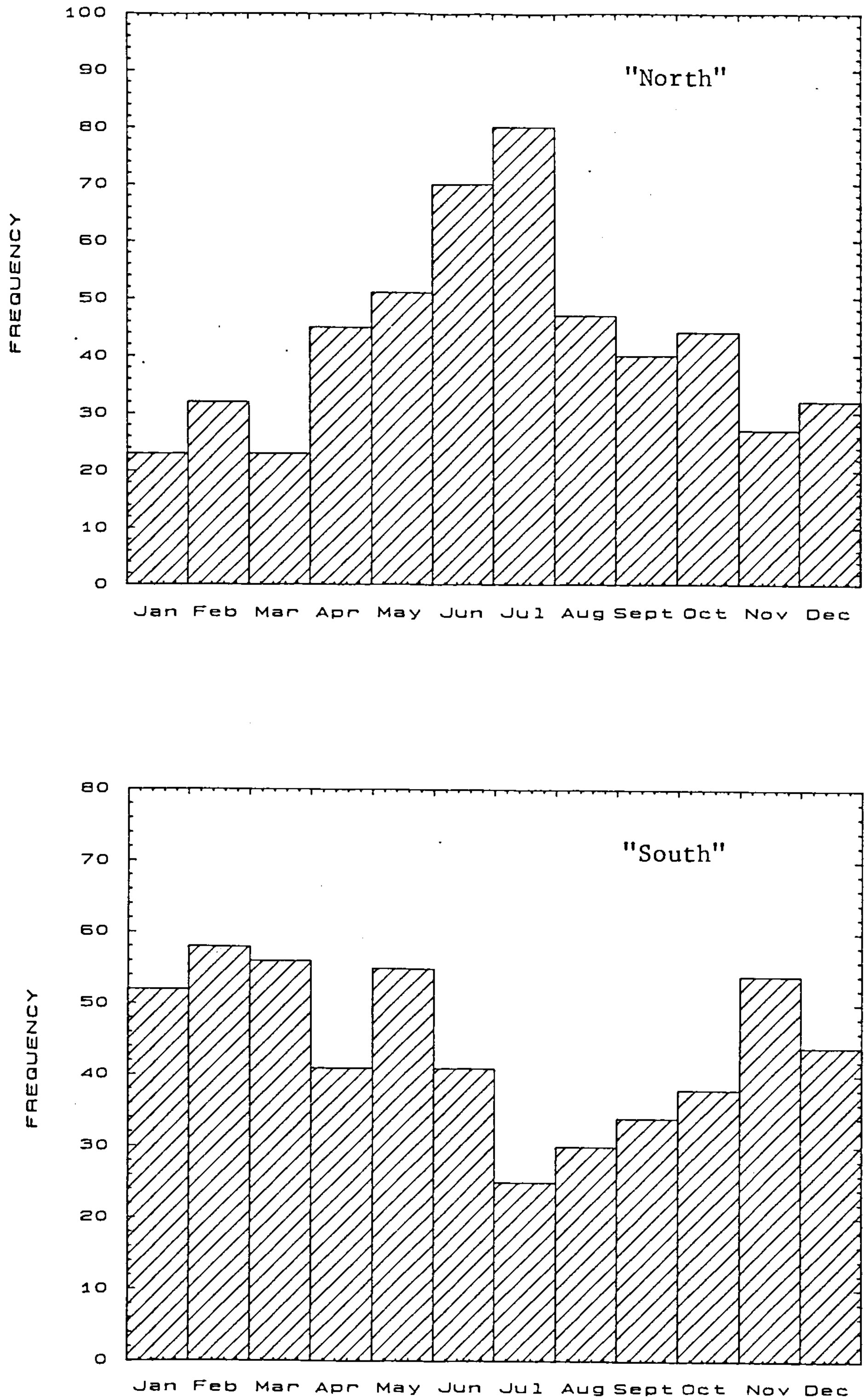


Figure 4.--Estimated birth-date distributions for "north" and "south" groups of North Pacific albacore.

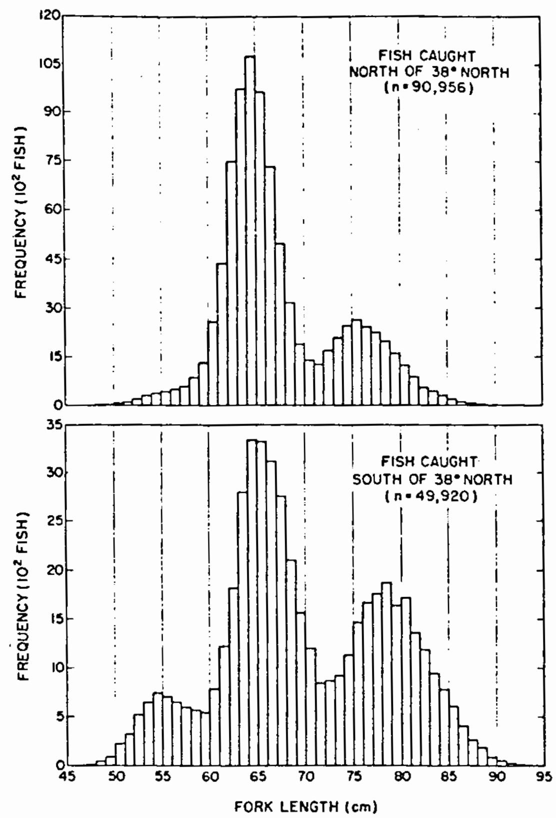


Figure 5.--Composite length-frequency distributions for North Pacific albacore caught north of lat. 38°N and south of lat. 38°N off the U.S. west coast during the 1972-78 fishing seasons.