

# GROWTH RATES OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, BASED ON TAG RETURNS

R. MICHAEL LAURS<sup>1</sup> AND JERRY A. WETHERALL<sup>2</sup>

## ABSTRACT

Estimates of growth parameters for North Pacific albacore, *Thunnus alalunga*, were based on tag-recapture statistics, using the standard von Bertalanffy model and an extended model. Sequential estimation of  $L_{\infty}$  and  $K$  allowed us to test hypotheses concerning variation in growth rate between tagged albacore recaptured in different ocean regions.

Significantly lower growth rates were found in albacore recaptured off Japan and the United States north of latitude 40° north compared with those recaptured off the United States south of latitude 40° north. The differences in estimated growth rate were generally consistent with differences in length-frequency distributions of albacore taken off the United States north and south of latitude 38° north during the period when most recaptures were made. The findings add to a growing body of evidence that the North Pacific albacore population is not homogeneous; rather, at least two different subpopulations may exist.

Growth rates of North Pacific albacore, *Thunnus alalunga* (Bonnaterre), have been estimated by counting vertebral rings (Uno 1936; Aikawa and Kato 1938; Partlo 1955), examining scale circuli (Nose et al. 1957; Bell 1962; Yabuta and Yukinawa 1963), tracing progressions of length modes (Brock 1943; Suda 1954), and by measuring tagged fish at release and recapture (Otsu 1960; Clemens 1961). Of these techniques, only tagging provides direct estimates of growth rate, and the tagging results of Otsu and Clemens are reasonably consistent with the conclusions of Yabuta and Yukinawa's scale analysis and Suda's modal progression work. However, as Shomura (1966) noted in a review of tuna growth studies, comparisons are complicated by the biases and uncertainties peculiar to each method. For example, in the case of tagging we assume that the growth rate is unaffected by stresses resulting from capture, handling and tagging, and from the burden of carrying the tag itself. Conclusive results will require that the basic assumptions of any particular method be tested and verified.

In this paper, we present new estimates of growth parameters based on recent tag-recapture experiments conducted jointly by the National

Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation (AFRF).<sup>3</sup> We use the standard von Bertalanffy growth model, but also briefly explore an extension. Sequential estimation of the parameters  $L_{\infty}$  and  $K$  allows us to test hypotheses concerning variation in growth rate between tagged fish recaptured in different ocean regions.

Transpacific recaptures of albacore tagged in the eastern North Pacific off North America and in the western North Pacific off Japan have established the interdependence of the United States and Japanese North Pacific albacore fisheries, and have also fostered the hypothesis of a single, common stock (Ganssle and Clemens 1953; Clemens 1961; Otsu and Uchida 1963). However, our results add to growing evidence (Laurs and Lynn 1977) that the North Pacific albacore population is not homogeneous, as usually assumed, but is composed of at least two subgroups with different migration patterns and growth histories.

## METHODS

### Tagging Procedures

Albacore were caught in the eastern North Pacific and tagged aboard U.S. commercial jig and

<sup>1</sup>Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

<sup>2</sup>Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

<sup>3</sup>AFRF administers revenues derived from a landing assessment paid by the U.S. albacore industry on U.S.-caught albacore.

bait fishing vessels on charter to AFRF. Approximately 70% of the tagging was done by commercial fishermen trained in tagging procedures, the rest by NMFS technicians. Single Floy<sup>4</sup> spaghetti-dart tags were inserted on the left side below the second dorsal fin with the aid of a beveled stainless steel tube so that the tag barb was lodged in the pterygiophores of the fin. Only fish judged to be in very good condition were tagged; fish hooked in the roof of the mouth or showing signs of extreme exhaustion or severe bleeding were rejected. For each tagged fish a record was kept on 1) tag number, 2) date and time of release, 3) fork length at time of release, 4) condition at tagging, and 5) longitude and latitude of release. Additional tagging details are given in Laurs et al. (1976).

### Recovery Procedures

Recoveries were made by sport and commercial fishermen, unloaders, and cannery workers. Information was obtained on 1) tag number, 2) date of recapture, 3) fork length at time of recovery, and 4) longitude and latitude of recapture. Most recapture locations were given as loran coordinates, which were converted to longitude and latitude, but the recapture locations for tags recovered by unloaders and cannery workers were often reported inexactly, e.g., as "off central California." Direct measurements of fork length were available for about one-half the fish recovered. For most of the remainder only the weight at recovery was given, and fork length was estimated using Clemens' (1961) weight-length relation. Observed fork lengths were measured to the nearest centi-

meter. Bias in estimating fork length from observed weight using the inverted weight-length relationship was judged to be  $<0.5$  cm in absolute value over the length range represented in the recapture sample, so subsequent growth analyses were based on the combined sets of observed and estimated lengths.

### Data Screening

The tag return data were screened to exclude cases where information was incomplete, unreliable, or clearly inaccurate. Out of 741 tag returns made from 1971 through 1978, 305 were rejected (Table 1). In 15 cases length at release was not measured, in 116 cases the recapture date was unknown, and in 68 cases neither length nor weight was measured at recovery. In 79 other rejected cases the length at recovery was not measured and the weight only guessed without the use of scales. Additionally, in 27 instances a gross error was apparent in the measurement of fork length either at release or recovery.

The final accepted data set of 436 cases includes observations on 28 albacore showing negative estimated growth. We assume these are a result solely of measurement error or error in estimation in cases where the recovery weight was converted to length, and we assume such error occurs throughout the data set independently of size or time between release and recapture (time out).

One of the common steps in screening tag recovery data for growth studies is to partition the data according to length at release, compute linear regressions of growth increment on time out within each subset, and then reject rare observations, usually those departing from expectations by more than two standard deviations (Schaefer et al. 1961; Joseph and Calkins 1969). We abandoned this step because the number of

TABLE 1.—Summary of number of tagged fish released, recovered, rejected, and accepted for analysis of albacore growth.

Year	No. tagged fish released	No. tagged fish recovered	Rejected tag recoveries (no.)					Total	No. tag recoveries accepted for analysis
			Missing release length	Missing recapture date	Missing recovery size	Weight at recovery estimated	Measurement error		
1971	887	34	2	6	5	1	0	14	20
1972	1,557	132	1	23	13	16	10	63	69
1973	1,805	111	0	23	10	12	2	47	64
1974	2,486	175	4	22	16	22	8	72	103
1975	1,349	115	1	17	13	15	2	48	67
1976	1,581	85	0	15	8	10	3	36	49
1977	1,221	25	0	4	0	3	0	7	18
1978	2,719	58	1	6	3	0	2	12	46
Unknown	—	6	6	—	—	—	—	6	0
Total	13,805	741	15	116	68	79	27	305	436

<sup>4</sup>Mention of a commercial company or product does not constitute an endorsement by the National Marine Fisheries Service, NOAA.

"outliers" it identified was consistent with the number expected due to chance alone, because the procedure has no sensible stopping rule, and because even with length at release fixed, the expected relationship between growth increment and time out is nonlinear.

### Grouping of Data

The selected data were cross-classified by location of tagging and location of recapture (Table 2). Nearly 66% of the 436 tagged fish were released inshore,<sup>5</sup> and of these 74% were released south of lat. 40° N, the remainder north of this latitude. Eighty-four percent of recaptured fish released inshore south of lat. 40° N were recovered in the same area, 5% were recovered inshore north of lat. 40° N, 1.4% were taken in the offshore area east of long. 180°, and 8.4% were recovered in the western Pacific. Of the recovered fish tagged and released inshore north of lat. 40° N, only 8.2% were recaptured inshore south of lat. 40° N, 1.4% were taken east of long. 180° in the offshore area, 27.4% were recovered in the area of tagging and 63% were recovered in the western Pacific. Of the recovered fish tagged offshore, 70.5% were recaptured either inshore north of lat. 40° N or west of long. 180°, and only 27.5% were recovered in the southern inshore area.

For purposes of constructing and testing hypotheses about differences in growth rates, tag returns were grouped into three categories depending on recapture location: 1) Group A includes all fish recaptured inshore south of lat. 40° N, except those released inshore north of lat.

40° N (221 fish). 2) Group B consists of tag recoveries made inshore north of lat. 40° N, excluding those released inshore south of lat. 40° N (75 fish). 3) Group C consists of all tag recoveries made west of the 180° meridian (114 fish). The three groups together comprise 410 recaptures. Excluded are 6 fish tagged inshore north of lat. 40° N and recovered south of this line the following year or later; 11 fish released south of lat. 40° N and recaptured in the northern inshore area (1 the same season, 10 in following years); 6 fish recaptured offshore east of long 180°; and 3 fish whose recapture locations are unknown.

### Growth Models

We used observations of growth increment, length at tagging, and time at liberty to estimate the growth rate,  $K$ , and the asymptotic length,  $L_\infty$ , of the standard deterministic von Bertalanffy model. In addition, we considered an extension of the von Bertalanffy model which allows the growth rate to vary with age in a simple manner. In general terms, we assumed that the expected growth increment for the  $j$ th fish in the  $i$ th group ( $i = 1, \dots, m; j = 1, 2, \dots, n_i$ ), given the initial length and time out, could be stated as

$$E(\Delta L_{ij}) = \int_{t_{ij}}^{t_{ij} + \Delta_{ij}} G(u) (L_\infty - L(u)) du,$$

where  $E(\Delta L_{ij})$  = expected growth increment of  $j$ th tagged fish in  $i$ th group during  $(t_{ij}, t_{ij} + \Delta_{ij})$

$$= L(t_{ij} + \Delta_{ij}) - L(t_{ij})$$

$t_{ij}$  = age of  $j$ th fish in  $i$ th group at time of release

$\Delta_{ij}$  = time at liberty for  $j$ th fish in  $i$ th group

$L(u)$  = length at age  $u$

$L_\infty$  = asymptotic length

$G(u)$  = unspecified age-dependent growth rate.

If we set  $G(u) = K = \text{constant}$ , we have the standard von Bertalanffy model, and

$$E(\Delta L_{ij}) = (L_\infty - L_{1,ij}) [1 - \exp(-K\Delta_{ij})],$$

where  $L_{1,ij} = L(t_{ij})$ .

We call this Model 1. (We omit subscripts on

<sup>5</sup>Fish released (recaptured) east of long. 130° W in the area south of lat. 49° N, or east of long. 135° W between lat. 49° and 54° N were considered to be released (recaptured) inshore. Demarcation of the inshore area boundary is based on analysis of tag recoveries discussed in Laurs and Lynn (1977).

TABLE 2.—Classification of selected tag data by locations of release and recapture.

Recapture location	Release location			Off-shore	Grand total
	Inshore <sup>1</sup> —from lat. 40° N				
	South	North	Total		
East of long. 180°	194	27	221	98	319
Inshore <sup>1</sup>	191	26	217	96	313
South of lat. 40° N	180	6	186	41	227
North of lat. 40° N	11	20	31	55	86
Offshore	3	1	4	2	6
West of long. 180°	18	46	64	50	114
Unknown	2	0	2	1	3
Grand total	214	73	287	149	436

<sup>1</sup>See text footnote 5.

parameters, even though group-specific parameters are implied.)

In Model 1 we assume that the ratio of instantaneous growth rate,  $dL(u)/du$ , to potential growth,  $L_\infty - L(u)$ , is  $K$ , a constant. Instead, we may suppose generally that this ratio varies with age. We considered one such situation. In this model, Model 2, we assume that stresses due to capture, handling, and tagging will initially reduce the growth rate of a tagged fish below its usual level, but that as time passes the normal growth process will be restored. Specifically, in our analysis of Model 2 we assume the standard model holds for untagged fish but that when a fish is tagged its normal growth pattern is interrupted, such that

$$G(u) = K, \quad 0 < u < t_{ij}$$

$$G(u) = K / \{1 + \alpha \exp[-\beta(u - t_{ij})]\} \quad t_{ij} \leq u.$$

We assume  $K \geq 0$ ,  $\beta > 0$ , and  $\alpha \geq 0$ . Model 2 says that following tagging the growth rate is immediately reduced to a fraction  $(1 + \alpha)^{-1}$  of its normal value,  $K$ , and then returns to  $K$  asymptotically (Figure 1).  $L_\infty$  is assumed to be unaffected.

### Parameter Estimation

In the standard von Bertalanffy model as applied to tag recapture data, there are two parameters to be estimated,  $K$  and  $L_\infty$ . The usual approach is to estimate them simultaneously, and we did so using the FORTRAN program BGC 4 written by Tomlinson (1971). This routine finds  $\hat{K}$  and  $\hat{L}_\infty$  as those parameter values which minimize

$$S = \sum_{j=1}^{n_i} \left\{ L_{2,ij} - [L_\infty - (L_\infty - L_{1,ij}) \exp(-K\Delta_{ij})] \right\}^2,$$

where  $L_{2,ij} = L(t_{ij} + \Delta_{ij})$ . Since  $E(L_{2,ij})$  is a non-linear function of  $K$ , parameter estimates derived using this procedure are prone to serious bias unless observations on  $L_{2,ij}$  are made over a wide range of  $L_{1,ij}$  and  $\Delta_{ij}$ . Presumably, it is also desirable that they be made uniformly in the plane of these two variables.

The parameters of Model 2 may also be estimated jointly using nonlinear least squares methods, but estimates of  $L_\infty$  and correlated parameters suffer the same drawbacks as estimates of the standard von Bertalanffy model parameters derived from BGC 4

An alternative approach in fitting both models

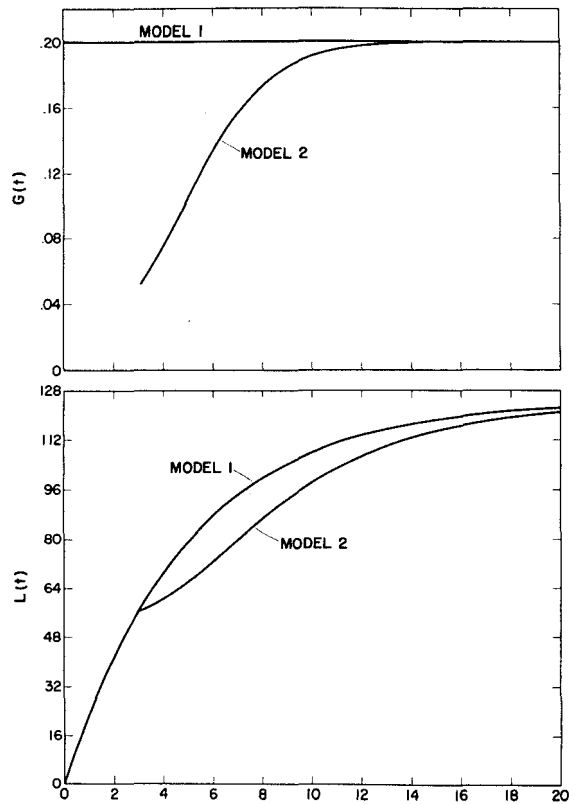


FIGURE 1.—Standard von Bertalanffy growth model (Model 1), and an extension (Model 2) incorporating a temporary reduction in growth rate,  $G(t)$ , following tagging. The resulting growth pattern,  $L(t)$ , is altered. Time units are arbitrary.

is to estimate  $L_\infty$  and the other parameters sequentially. Where the oldest members of the population have been intensively sampled and an upper asymptote to length is clearly demonstrated in the data, a reasonable estimate of  $L_\infty$  is the length of the largest fish seen in the catches, or the average length of the largest specimens observed. Which estimator to use depends on one's conceptual model of the growth process— $L_\infty$  can be regarded as the mean of a distribution of asymptotic lengths in the population, or strictly as an upper bound to the length any fish in the population can achieve. With the value of

$L_\infty$  determined, the other parameters may be estimated by the least squares method using the general model:

$$Y_{ij} = -\ln\left(\frac{L_\infty - L_{2ij}}{L_\infty - L_{1ij}}\right) = \int_{t_{1ij}}^{t_{2ij} + \Delta_{ij}} G(u) du + \epsilon_{ij},$$

where we assume that  $\epsilon_{ij}$  are independent errors with zero means and variances  $\sigma^2_{ij}$ .

This approach handily accommodates any well-behaved form of  $G(u)$ . In the case of Model 1, the problem of estimating  $K$  reduces to a simple linear regression:

$$Y_{ij} = K\Delta_{ij} + \epsilon_{ij}. \quad (1)$$

When a reasonably accurate estimate of  $L_\infty$  can be made by sampling the catches, this sequential estimation procedure for Model 1 has the advantage that the range of observations on  $L_{1ij}$  and  $\Delta_{ij}$  is not so critical.

With Model 2, the sequential method may be applied to estimate  $K$ ,  $\alpha$ , and  $\beta$  using the equation:

$$Y_{ij} = K\Delta_{ij} - \left(\frac{K}{\beta}\right) \ln \left\{ (1 + \alpha) / [1 + \alpha \exp(-\beta\Delta_{ij})] \right\} + \epsilon_{ij}. \quad (2)$$

The desirability of fitting this nonlinear model to any particular set of data may be judged by examining the residuals around the least squares fit of Model 1 (Equation (1)). As is evident from Figure 2, the detection of nonlinearity in this manner requires that observations be available uniformly over a broad range of  $\Delta_{ij}$ .

### Covariance Analysis

One of our chief objectives was to determine whether growth rates differed between groups of fish, based on estimates of parameters of the standard von Bertalanffy model. Since BGC 4 estimates of  $K$  and  $L_\infty$  are highly correlated, particularly when few large fish are in the sample, and since probability statements concerning intergroup comparisons of both  $K$  and  $L_\infty$  were not possible, we used the sequential estimation procedure. For the  $i$ th group of fish we assumed

$$E(Y_{ij}) = K_i \Delta_{ij}, \quad (3)$$

$$\text{where } Y_{ij} = -\ln\left(\frac{L_\infty - L_{2ij}}{L_\infty - L_{1ij}}\right)$$

and specified a fixed value for  $L_\infty$ . Then we developed and applied a weighted zero-intercept covariance analysis to test hypotheses of the form:

$$H : K_1 = K_2 = \dots = K$$

on the basis of  $F$ -statistics. Statistical weights were computed on the assumption that  $\sigma^2_{ij} \sim \Delta_{ij}$ , as suggested by Figure 2.

## RESULTS

### Standard Model

Joint estimates of  $K$  and  $L_\infty$  for Groups A, B, and C, based on the BGC 4 program, are shown in Table 3. We consider the estimates inaccurate, owing to sampling biases discussed earlier. In particular, we think the unexpectedly low  $L_\infty$  estimates (and correspondingly high  $K$  estimates) are

due to the absence of very large albacore in the release and recovery samples. Of the 410 selected tag returns, 141 exceeded 80 cm fork length at recapture, but only 42 were >85 cm and just 11 were >90 cm. The average fork length of tagged albacore at time of release was 63.7 cm (range 45-89 cm), and at recovery, 75.7 cm (range 51-103 cm).

Because of the difficulties with BGC 4 estimates, we based intergroup comparisons on estimates of  $K$  from the sequential estimation procedure. A preliminary  $F$ -test showed no significant difference in  $K$  between fish whose lengths at recovery were measured and those whose lengths were estimated from the inverted weight-length relationship. Further sequential analyses (as well as the earlier BGC 4 estimates) were therefore based on all data, regardless of how recovery length was determined.

$L_\infty$  was fixed at 125 cm, a reasonable choice well supported by available length-frequency data. Although Otsu and Sumida (1970) reported an albacore measuring 132.7 cm from the

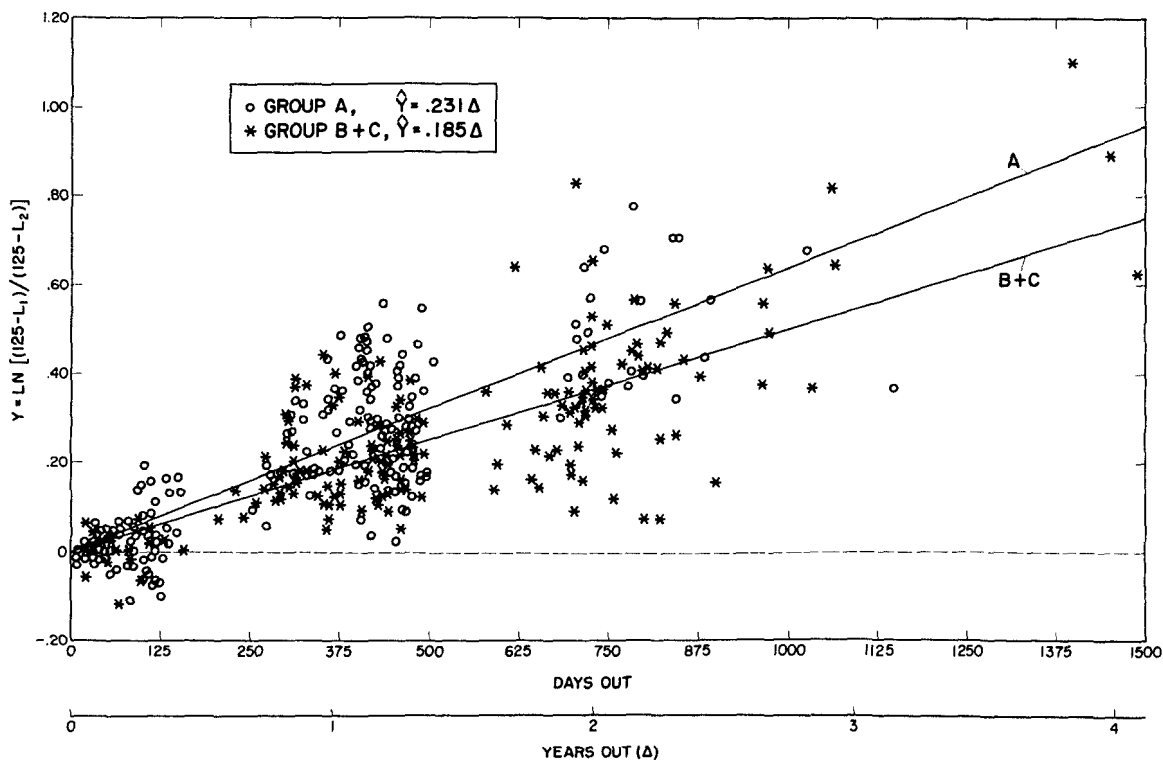


FIGURE 2.—Regression of growth variable,  $Y$ , on years between release and recapture for albacore of Groups A (221 fish) and B + C (189 fish). The slopes are estimates of the von Bertalanffy growth parameter,  $K$ , and they are significantly different.

TABLE 3.—Estimates of von Bertalanffy growth parameters for North Pacific albacore by recapture group and estimation method, assuming stock boundary at lat. 40° N.

Recapture group	Sample size	BGC4 estimates		Sequential estimates		Average time out $\Delta$ (d)
		$L_{\infty}$ (cm)	$K$ (yr $^{-1}$ )	Fixed $L_{\infty}$ (cm)	$K$ (yr $^{-1}$ )	
A	221	94.5	0.505	125.0	0.231	313
B	75	107.5	.272	125.0	.193	400
C	114	98.5	.345	125.0	.184	588
B + C	189	102.1	.310	125.0	.185	513
A + B + C	410	100.9	.342	125.0	.199	405

Hawaiian longline fishery, which harvests the largest North Pacific albacore known, specimens >125 cm are extremely rare. With  $L_{\infty}$  fixed at 125 cm, Group A had the highest growth rate estimate,  $\hat{K}_A = 0.231/\text{yr}$  (Table 3). Group B and  $\hat{K}_B = 0.193$ , and Group C had the lowest growth rate estimate,  $\hat{K}_C = 0.184$ . When Groups B and C were pooled into a "North" category, the resulting  $\hat{K}_N$  was 0.185. The estimate of  $K$  for all three groups combined was 0.199.

Table 3 also shows the statistics on average time between release and recapture. Group A fish were at liberty an average of 313 d, while Group B fish were out 400 d, and Group C fish, 588 d.

Tagged fish from Groups B and C combined were at large an average of 513 d.

The estimates suggest that the North fish, Groups B and C, had a lower growth rate than the South fish of Group A. Such a difference might arise if, as we suppose, the North fish budget more of their available energy for migration compared with the South fish, and relatively less energy for growth. Tag release and recovery results indicate that the North fish make longer migrations, traveling between coastal waters off the United States Pacific Northwest and coastal waters off Japan, while the South fish undertake shorter migrations between coastal waters south of Cape

Mendocino, Calif., and the central North Pacific east of 180° (Laurs<sup>6</sup>).

The hypothesis of equal growth rates was tested using the weighted zero-intercept analysis of covariance, and was rejected at the 0.5% significance level (Table 4, Figure 2). In pairwise comparisons between individual groups, the only nonsignificant difference in growth rate was between Groups B and C.

Are the observed differences in growth rates of tagged albacore consistent with other information? To check this, we examined the length composition of albacore catches along the U.S. west coast (Figure 3). The length-frequency plot for catches north of lat. 38° N during the period when most recaptures were made, 1972-78, showed modes at about 64 and 76 cm and a hint of one at 54 cm. Catches south of lat. 38° N showed the 54 cm mode, but had primary modes at about 66 and 79 cm. The discrepancy between modes of the older albacore is further evidence of a slower growth rate for North fish, assuming these modes represent fish of the same age. To see if length-frequency data and tag data agreed, we computed the expected fork lengths under each  $K$  at annual time steps and compared these with observed modes in the length-frequency distributions. Starting with some initial fork length,  $L_1$ , we used the equation  $L_i = a + bL_{i-1}$ ,  $i = 2, 3, \dots$ , where  $a = L_\infty (1 - \exp(-K))$  and  $b = \exp(-K)$ . Setting  $L_1 = 54$  and  $L_\infty = 125$  cm, we found the sequence of lengths 54.0, 66.0, and 76.0 cm for the North group albacore; and 54.0, 68.6, and 80.3 cm for the South fish. These are reasonably consistent with the observed sequences of length modes.

### Extended Model

Plots of residuals from the standard model against days out (Figure 4) showed a tendency toward negative deviations during the first several months after tagging, suggesting that some of the residual variation could be attributed to "lack of fit" (Draper and Smith 1966). For example, of the 221 recaptures analyzed in Group A, 90 were taken within 6 mo of tagging, and 70% of the Model 1 residuals corresponding to these early recaptures were negative. We therefore fit Model

TABLE 4.—Analysis of covariance comparing growth rate of Group A North Pacific albacore with growth rate of Group (B + C) albacore, assuming stock boundary at lat. 40° N. Probability of obtaining  $F$  statistic this large under null hypothesis is  $< 0.005$ .

Source of variation	df	Residual SS	MS	$F$
Individual lines:				
A	220	1.1476		
B + C	188	1.7362		
Pooled	408	2.8837	0.0071	
Common line	409	3.1009		
Difference	1	.2172	.2172	30.72

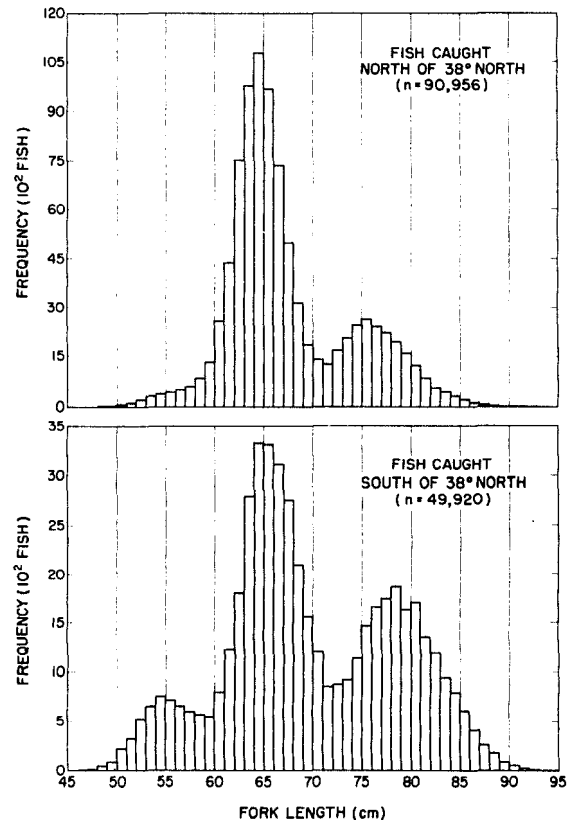


FIGURE 3.—Composite length-frequency distributions for North Pacific albacore caught north of lat. 38° N and south of lat. 38° N off the U.S. west coast during the 1972-78 fishing seasons.

2 to each set of data, using the sequential estimation procedure (Equation (2)) with  $L_\infty = 125$  cm. Resulting estimates of  $K$  were 3-6% larger than the corresponding estimates from the standard linear model; thus, if Model 2 is correct, systematic bias in the latter estimates does not appear to be serious.

However, estimates of  $\alpha$  and  $\beta$  were relatively large in all cases, suggesting that the growth rate may drop abruptly to near zero immediately after

<sup>6</sup>Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-17, 10 p.

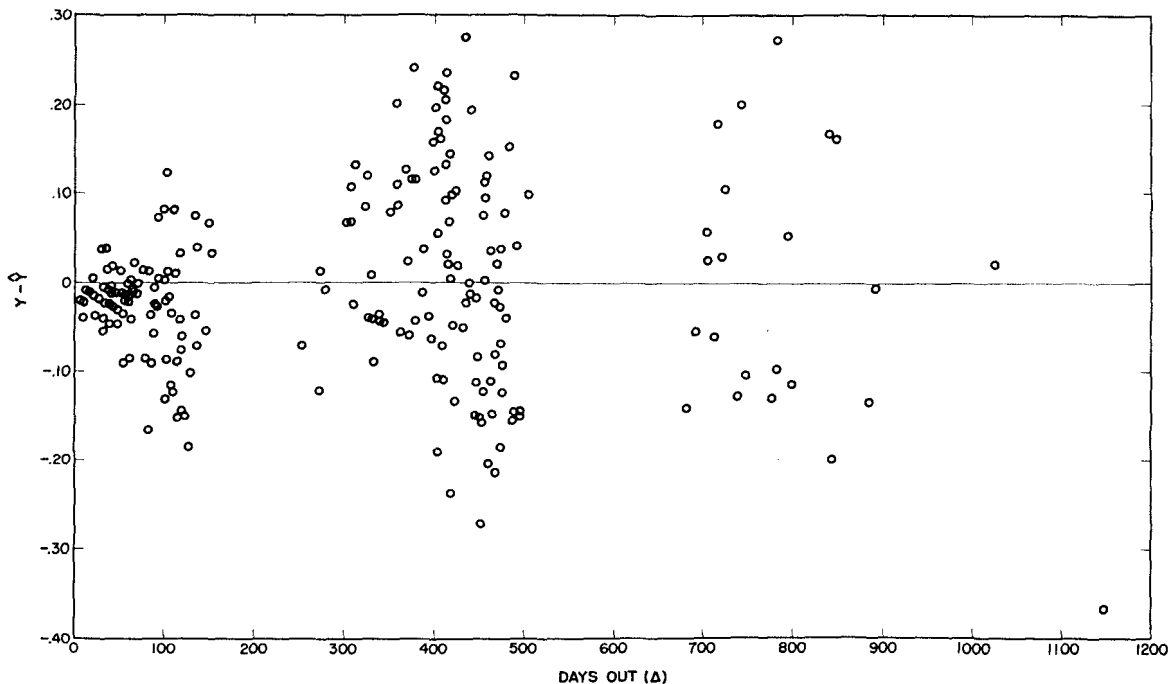


FIGURE 4.—Residuals from the fit of Model 1 to the Group A albacore data, as a function of days out.

tagging and then recover to normal within the first year of liberty. While this basic response to tagging stress appears to be a reasonable hypothesis, the estimates of  $\alpha$  and  $\beta$  were very unstable and little confidence could be placed on projected growth rate recovery patterns. Further, although the extended model fits the data better than the ordinary von Bertalanffy in the sense of reducing residual variation, as expected, this improvement is only slight; considering the high variance displayed in the data we do not reject the simpler von Bertalanffy model.

## DISCUSSION AND CONCLUSIONS

The results of our growth analysis are strengthened by their consistency with other findings, but the assumptions of our analysis need to be tested. In particular, we assumed that our estimate of  $L_\infty$ , 125 cm, was the same for all groups of North Pacific albacore. If  $L_\infty(B + C) > L_\infty(A)$ , our conclusions concerning differences in growth rate are reinforced. But if the South fish, Group A, actually tend toward a larger asymptote in fork length than the North fish of Groups B and C (there is no evidence of this), then the differences between estimates of  $K$  might not be significant. For

example, if we assume  $L_\infty(A) = 130$  cm and  $L_\infty(B + C) = 120$  cm, the differences vanish. More to the point, unless the  $L_\infty$ 's are the same, the comparison of growth rates between groups is no longer conveniently reduced to a comparison of  $K$  estimates. When the assumption of equal  $L_\infty$  is valid, the actual value of  $L_\infty$  assumed is relatively unimportant as far as the covariance analysis is concerned; our conclusions were the same when  $L_\infty$  was fixed at 120, 130, and 135 cm.

In Model 1, the standard von Bertalanffy model, we also assumed that the growth rate was unaltered by the presence of the tag or by the stress imposed in its application. In our analysis of Model 2 we explored the question of whether tagging might have affected growth rate in a specified way, and Model 2 fits our data only slightly better than Model 1. However, effects of the sort we hypothesized might easily be masked by high variance in the data. Nevertheless, if the effect of tagging were simply to reduce the normal growth rate,  $K$ , suddenly and permanently to a lower level,  $K'$ , it would go undetected by our analysis. To determine the validity of the tag-effect assumption, we need to compare the growth rates of tagged fish with those of untagged, "control" fish.



Such a comparison was recently made for bait-boat-caught southern bluefin tuna, *T. maccoyii*, by Hearn,<sup>7</sup> who found that fish caught 3 wk after being tagged weighed 14% less than untagged fish of the same length in the same schools. Assuming the tagged bluefin tuna also grew less in length than their untagged counterparts, this 14% weight loss would be an underestimate. At any rate, after 1 yr at liberty no difference in weight was discernible.

We found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of lat. 40° N or in the western North Pacific off Japan was significantly lower than for tagged albacore recaptured off North America south of lat. 40° N during 1972-78. The differences in growth rate of tagged fish are remarkably consistent with differences in length-frequency distributions of albacore caught off North America north and south of lat. 38° N during the period when most recaptures were made. These findings add to a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs et al.<sup>8</sup>; Laurs and Lynn<sup>9</sup>) that North Pacific albacore are not as homogeneous as usually assumed, and that there may be at least two subgroups of albacore: one which supported the Japanese pole-and-line fishery and the United States and Canadian fisheries in waters north of about lat. 40° N from 1972 to 1978, and another which did not contribute significantly to the Japanese surface fishery, but supported the United States coastal fishery south of lat. 40° N during this period. If such a distinction is valid, the situation is surely more complex and dynamic than we have supposed, with each stock's contribution to each fishery varying from year to year. Presumably such variation would be tied directly to changes in oceanographic conditions. And undoubtedly the latitudinal boundary was not fixed exactly at lat. 40° N during 1972-78, as we assumed, but analyses based on assumed boundaries at lat. 38° and 42° N gave the

same results. If an accurate assignment of tagged fish to stock were possible, a more powerful test of growth differences could be made.

A finding that more than one subpopulation or stock is involved in the North Pacific albacore fisheries would have important consequences, of course, both for stock assessment, fishery evaluation and management policy analysis, and for development of accurate catch forecasting systems. It is important that further work be done to identify stocks, and to elucidate their origins, migratory habits, and degree of interchange.

## LITERATURE CITED

- AIKAWA, H., AND M. KATO.  
1938. Age determination of fish (preliminary report 1). [In Jpn., Engl. synop.] Bull. Jpn. Soc. Sci. Fish. 7:79-88. In W. G. Van Campen (translator), U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 21, 22 p., 1950.
- BELL, R. R.  
1962. Age determination of the Pacific albacore of the California coast. Calif. Fish Game 48:39-48.
- BROCK, V. E.  
1943. Contribution to the biology of the albacore (*Germo alalunga*) of the Oregon coast and other parts of the North Pacific. Stanford Ichthyol. Bull. 2:199-248.
- CLEMENS, H. B.  
1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Calif. Dep. Fish Game, Fish Bull. 115, 128 p.
- DRAPER, N. R., AND H. SMITH.  
1966. Applied regression analysis. Wiley, N.Y., 407 p.
- GANSSLE, D., AND H. B. CLEMENS.  
1953. California-tagged albacore recovered off Japan. Calif. Fish Game 39:443.
- JOSEPH, J., AND T. P. CALKINS.  
1969. Population dynamics of the skipjack tuna (*Katsuwonus pelamis*) of the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 13: 1-273.
- LAURS, R. M., W. H. LENARZ, AND R. N. NISHIMOTO.  
1976. Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*. Fish. Bull., U.S. 74:675-678.
- LAURS, R. M., AND R. J. LYNN.  
1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with Transition Zone waters. Fish. Bull., U.S. 75: 795-822.
- NOSE, Y., H. KAWATSU, AND Y. HIYAMA.  
1957. Age and growth of Pacific tunas by scale reading. [In Jpn., Engl. summ.] In Suisan Gaku Shusei, p. 701-716. Tokyo Univ. Press.
- OTSU, T.  
1960. Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. Pac. Sci. 14:257-266.
- OTSU, T., AND R. F. SUMIDA.  
1970. Albacore (*Thunnus alalunga*) of Hawaiian waters. Commer. Fish. Rev. 32(5):18-26.

<sup>7</sup>Hearn, W. S. 1979. Growth of southern bluefin tuna (*Thunnus maccoyii*). Commonwealth Scientific and Industrial Research Organization, Division of Fisheries and Oceanography, Cronulla, New South Wales, Australia, Unpubl. manuscr.

<sup>8</sup>Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1975. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-75-84, 49 p.

<sup>9</sup>Laurs, R. M., and R. J. Lynn. 1976. Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1976. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-36, 51 p.

- OTSU, T., AND R. N. UCHIDA.  
1963. Model of the migration of albacore in the North Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 63:33-44.
- PARTLO, J. M.  
1955. Distribution, age and growth of eastern Pacific albacore (*Thunnus alalunga* Gmelin). J. Fish. Res. Board Can. 12:35-60.
- SCHAEFER, M. B., B. M. CHATWIN, AND G. C. BROADHEAD.  
1961. Tagging and recovery of tropical tunas, 1955-1959. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 5:343-455.
- SHOMURA, R. S.  
1966. Age and growth studies of four species of tunas in the Pacific Ocean. In T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, Honolulu, Hawaii, p. 203-219.
- SUDA, A.  
1954. Studies on the albacore - I. Size composition in the North Pacific ground between the period of its southward migration. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 20:460-468. In W. G. Van Campen (translator), Japanese albacore and bigeye tuna size composition studies. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 182:6-14, 1956.
- TOMLINSON, P. K. (programmer).  
1971. Program name - BGC 4. In N. J. Abramson (compiler), Computer programs for fish stock assessment, p. 2.(5).3.1 to 2.(5).3.3. FAO Fish. Tech. Pap. 101.
- UNO, M.  
1936. *Germo germo* (Lacepede) in the waters east of Nozima promontory, Tiba Prefecture (preliminary report I). [In Jpn., Engl. synop.] Bull. Jpn. Soc. Sci. Fish. 4:307-309. (Engl. transl., 1956, 3 p.; in files of Southwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.)
- YABUTA, Y., AND M. YUKINAWA.  
1963. Growth and age of albacore. [In Jpn., Engl. synop.] Rep. Nankai Reg. Fish. Res. Lab. 17:111-120.