Abstract.–Length-frequency data, vertebral-ring-counts, and length measurements of tagged fish were analyzed to independently estimate von Bertalanffy growth parameters for south Pacific albacore (*Thunnus alalunga*). As a working hypothesis, we assumed that the length-frequency modes and vertebral-rings are annual features. The MULTIFAN model fitted to length-frequency data provided estimates of L_∞ and K of 97.1 cm and 0.239 year^{-1}, respectively. Nine age classes were detected in the data. Growth varied seasonally: growth rate decreased to almost zero during August and peaked during February. Two to thirteen rings were visible in the vertebrae, and estimates of L_∞ and K of 121.0 cm and 0.134 year^{-1}, respectively, were obtained. No significant differences in growth parameters were detected between males and females. The growth rates predicted by the length-frequency and vertebral-ring-count models were very similar throughout the range of presumed age classes present in both data sets. These growth rates were consistent with length increment observations from 28 tag returns, which lends support to our assumptions of annual vertebral-rings and length-frequency modes.

Determination of age and growth of South Pacific albacore (Thunnus alalunga) using three methodologies

Marc Labelle
John Hampton

Tuna and Billfish Assessment Program
South Pacific Commission, Noumea, New Caledonia

Kevin Bailey
Talbot Murray

Ministry of Agriculture and Fisheries
Fisheries Research Center, P.O. Box 297
Wellington, New Zealand

David A. Fournier
John R. Sibert

Otter Research Ltd., Box 265, Station A
Nanaimo, B.C., Canada

Albacore (*Thunnus alalunga*) have been fished in the south Pacific by Japanese longliners since 1952, and by Korean and Taiwanese longliners since 1958 and 1963, respectively (Wang, 1988). Japanese longliners ceased targeting albacore in the mid-1960's, but longline fishing for albacore by Korean and Taiwanese fleets has continued. Since 1960, annual longline catches have fluctuated between 25,000 metric tons (t) and 40,000 t (Anonymous, 1991). In the 1980's, a surface fishery for juvenile albacore developed, comprising drift gillnet vessels from Japan and Taiwan and troll vessels mainly from the United States, New Zealand, Fiji, and French Polynesia. By 1989, the annual surface-fishery catches of albacore had reached about 30,000 t (Anonymous, 1991). The rapid expansion of the surface fishery catalyzed concerns over potential overfishing and possible effects on longline catch rates of larger albacore. This in turn highlighted the need for detailed information on the fisheries and on the dynamics of the albacore population.

Investigations of albacore biology have been conducted since 1985 by scientists from the United States, France, New Zealand, and the South Pacific Commission. The goal of this research has been to obtain information on a range of biological and fishery-related processes, including growth, catch age structure, stock structure, and mortality. Albacore catch rates and size composition in the troll and drift gillnet fisheries have been monitored through a fishery observer program since 1988 (Hampton et al., 1989, 1991; Sharples et al., 1991; Labelle, 1993a). Albacore tagging programs were established in 1986 to provide information on movement, mortality, growth and approximate stock boundaries (Anon., 1986; Pianet et al., 1990; Labelle, 1993b). Catch sampling at major landing sites has been carried out to monitor catch size composition, to collect logbook data, and to obtain samples of bony structures and gonads for estimation of growth rates and spawning periodicity. Estimates of growth rates, and, in particular,

estimates of von Bertalanffy (VB) growth parameters, are important because they are necessary elements in the population dynamic models used in stock assessment.

We used three independent data sets to estimate albacore growth rates: length-frequencies, vertebral-ring-counts, and tag release-recapture statistics. Estimates of VB growth parameters were derived from the length-frequency and vertebral-ring-count data. In both cases, we assumed that the length-frequency modes represent year classes and the vertebral-rings represent annual features. This assumption was tested by using the length increment data from the tag returns.

Materials and methods

Collection of length-frequencies

Length-frequency data were collected by observers from seasonal surface fishery catches between December 1986 and May 1991. All albacore measured were caught by troll vessels on the principal fishing grounds for juvenile albacore, namely the Tasman Sea, along the central east coast of New Zealand, and near the Subtropical Convergence Zone (STCZ), mainly within the area bounded by 35–42°S and 130–170°W (Fig. 1). Throughout each fishing season (typically extending from December to April), observers sampled as many albacore as possible from the daily catches. Albacore

were selected at random (i.e., unsystematically), placed on a graduated board, and measured from the tip of the snout (with the mouth closed) to the end of the median caudal ray. These fork-length measurements were rounded down to the nearest centimeter and recorded with the sampling date and fishing location. Tagged albacore were measured in an identical fashion and were combined with the length-frequency samples when it was appropriate.

Most of the length-frequency sampling occurred during 1988–1991 in the STCZ, where catch rates and fishing activity were greatest (Labelle, 1993a). In this region, over 100,000 albacore were measured; sufficient numbers were obtained to stratify samples by month for December–April each season. The number of measurements per month ranged from 351 to 18,908. These data were compiled into length-frequency histograms (Fig. 2), from which VB growth parameters were estimated by using the MULTIFAN computer program (Fournier et al., 1990).

Vertebra collection and processing

Caudal vertebrae were collected during the austral summers of 1986 and 1987 from albacore caught by research vessels trolling in the STCZ, the Tasman Sea, and over the Chatham Rise east of New Zealand (Fig. 1). Vertebrae were also collected during the austral winters of 1987, 1988, and 1989 from albacore caught by Japanese longline vessels fishing off the north east coast of New Zealand near East Cape
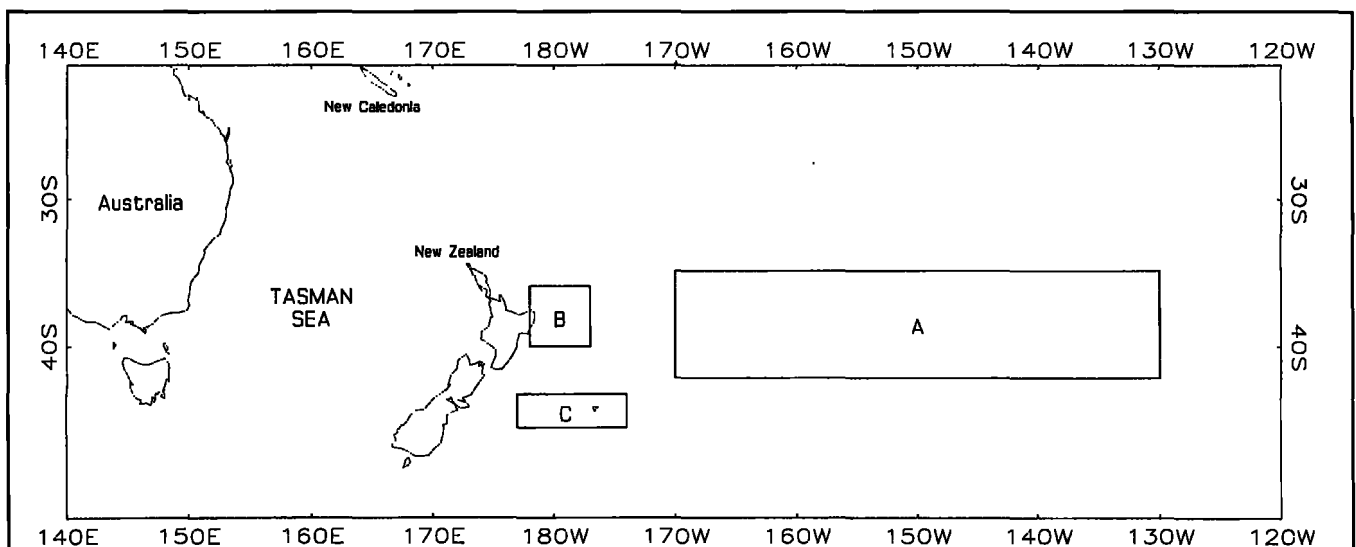

Figure 1

Sampling locations for the collection of length-frequency measurements and vertebrae. Region A covers the main troll fishing grounds centered over the STCZ. Region B delineates the longline fishing area adjacent to East Cape. Region C delineates the Chatham Ridge area where troll fishing occurs.
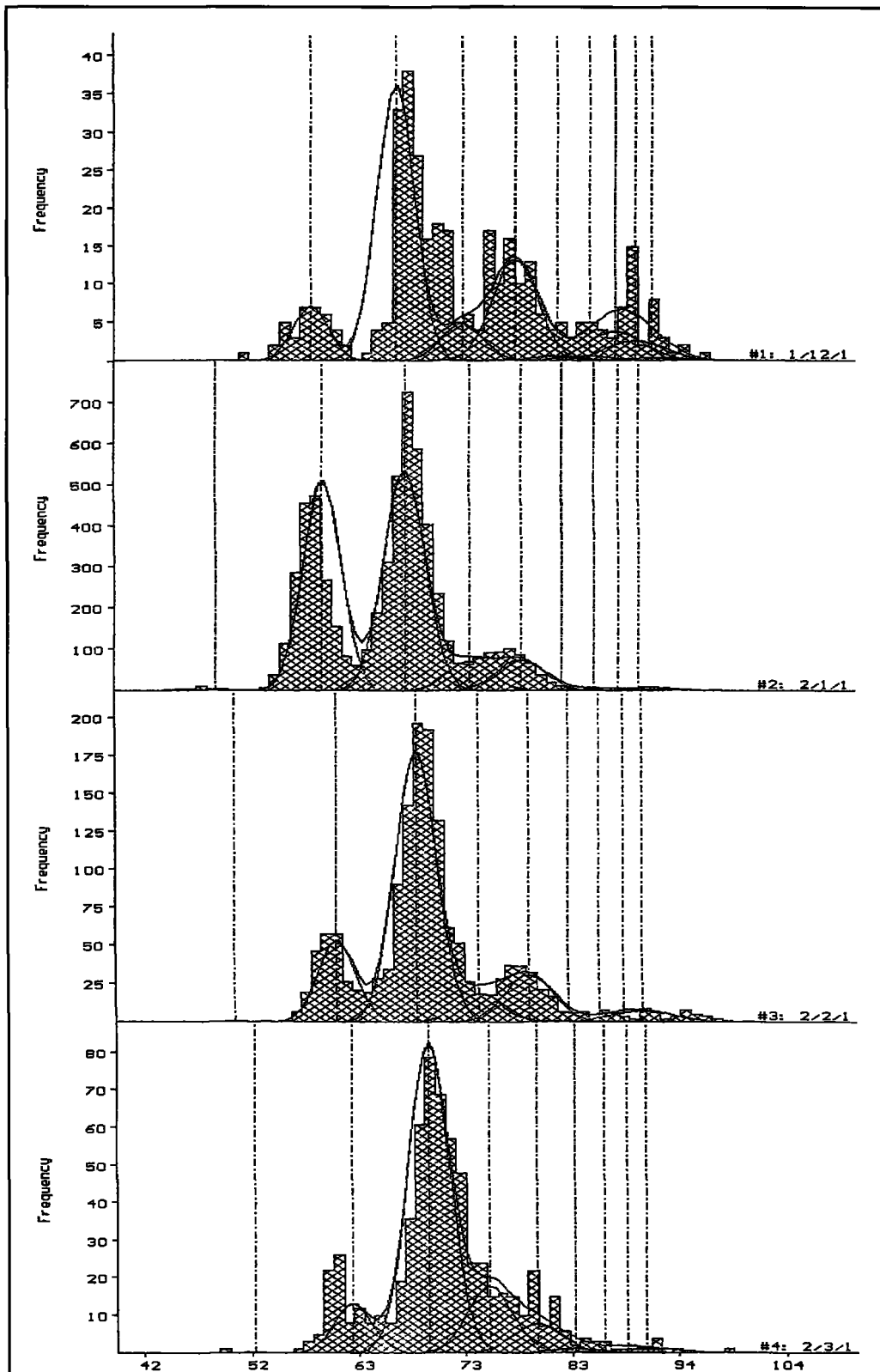
Figure 2

The south Pacific albacore length-frequency data set. The corresponding sampling period are given in the lower right of each histogram. The sampling data format is year/month/week; year 1 was 1988. No sampling was conducted during December 1989. The horizontal bars over the first three modes of sample no. 6 correspond to the user supplied bounds on the mean length of these age classes. The dashed vertical lines represent the estimated mean lengths-at-age in each sample. The inner smooth curves are the estimated numbers at age and the outer smooth curve is the estimated frequency distribution.
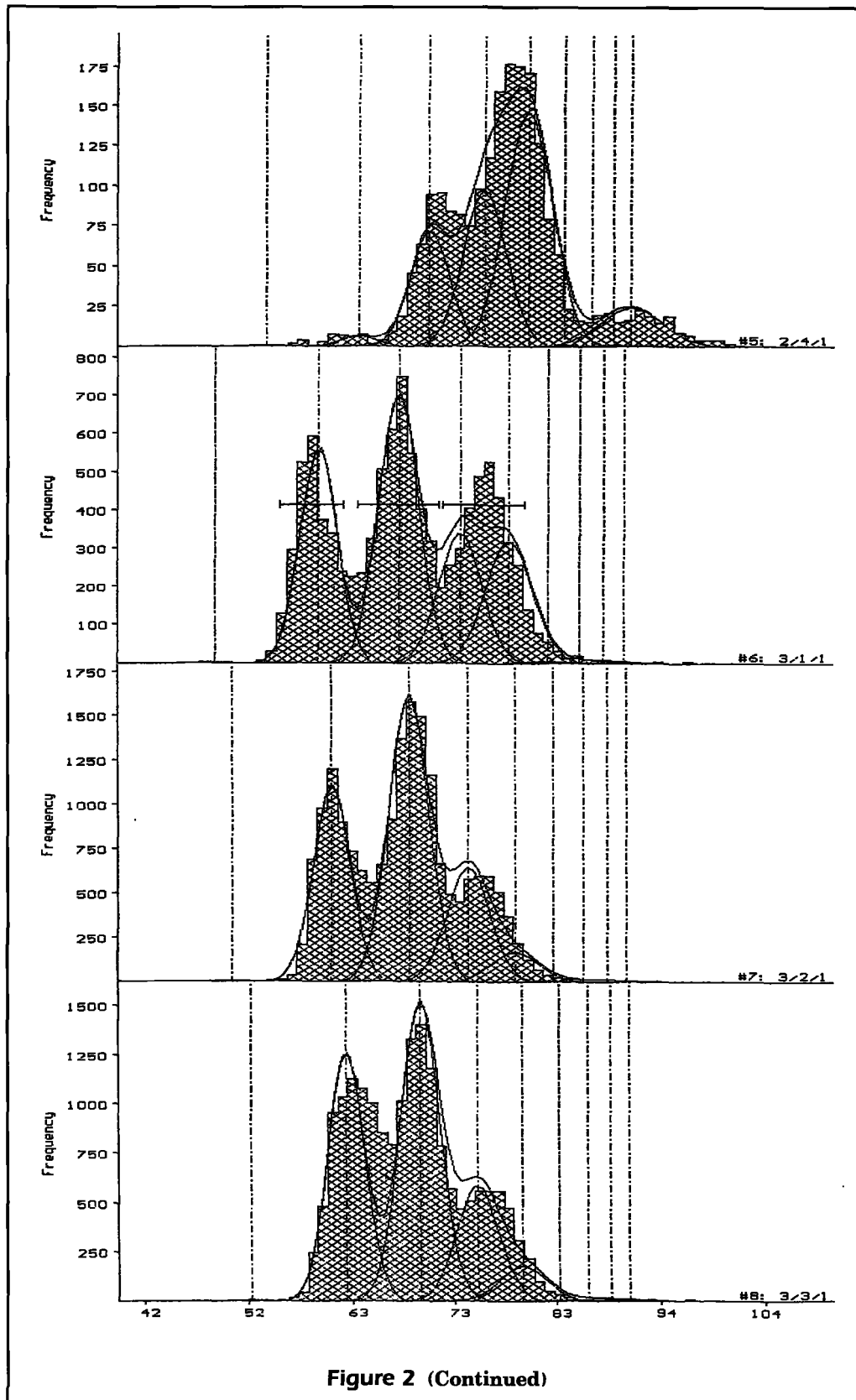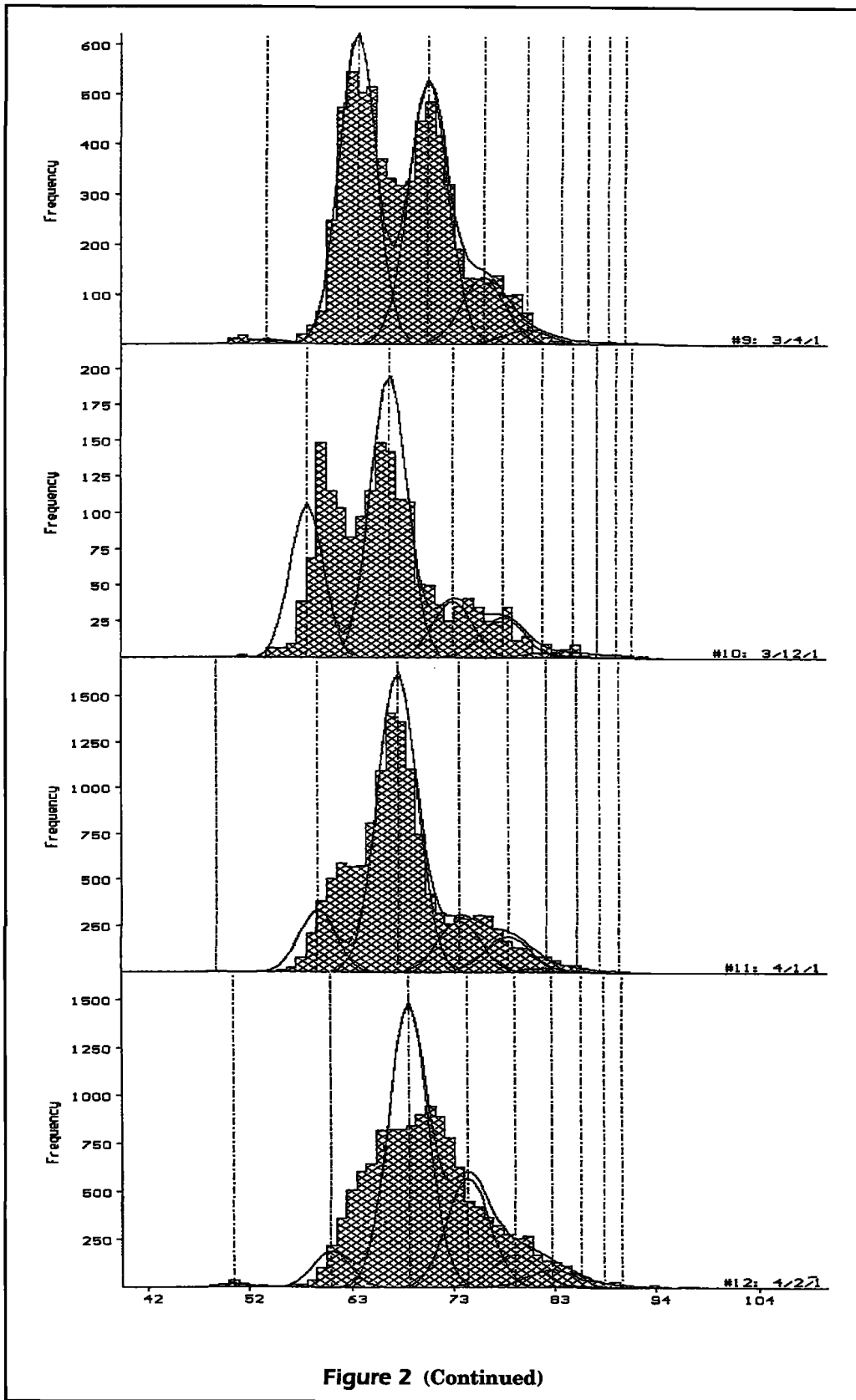
Figure 2 (Continued)
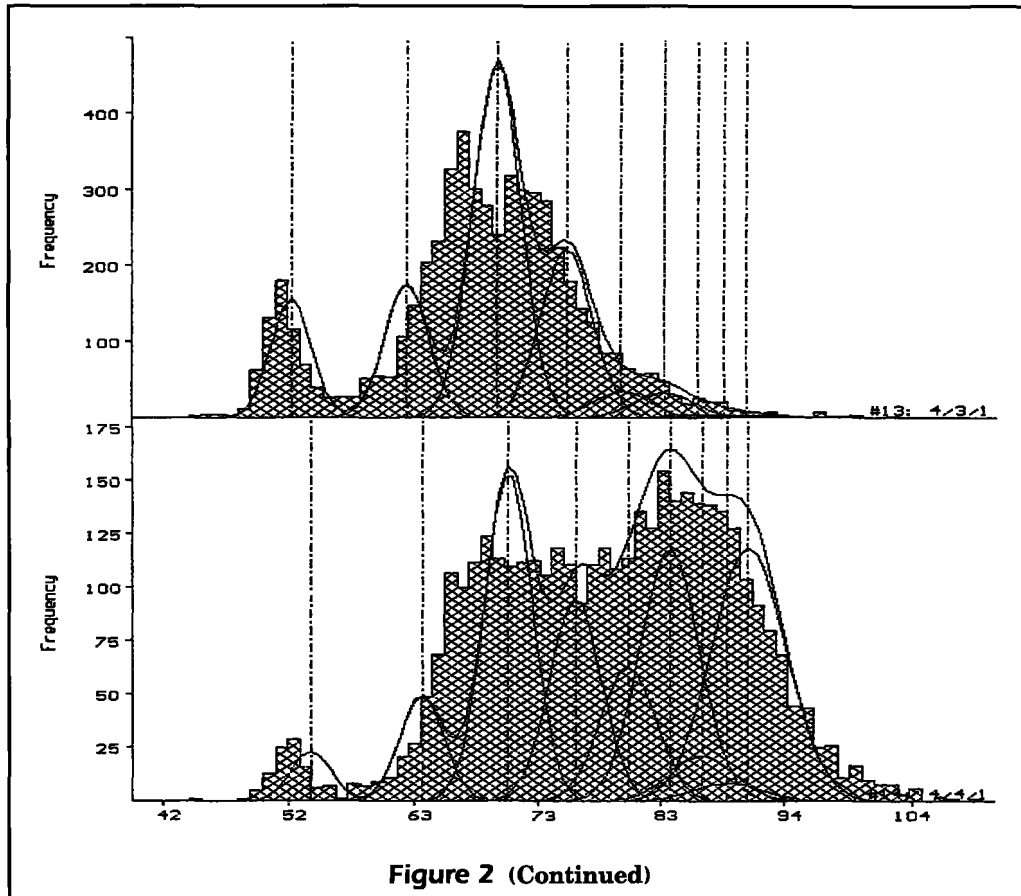
Figure 2 (Continued)

Figure 2 (Continued)

(Fig. 1). Altogether, 494 vertebrae were collected, of which 66% were from troll-caught albacore. All albacore sampled were first measured according to the procedure described previously. Vertebrae were removed by severing the caudal peduncle immediately anterior to the large bony keels. Vertebrae in the caudal peduncle were selected because they were easy to collect and their removal did not affect the market value of the fish. The caudal fins were trimmed, and the entire peduncle was placed in a plastic bag and frozen. Sex was recorded as often as possible (128 cases), but logistic difficulties prevented internal examination of the majority of the albacore sampled.

All vertebrae were processed in the laboratory according to the methods described by Berry et al. (1977), Berry (1978), and Lee et al. (1983). Caudal peduncles were thawed and the flesh trimmed from around the vertebrae. The 35th and 36th vertebrae were separated from the others with a knife and a fine-toothed hand saw. Each vertebra was then clamped in a vise by the keel, and sawed in half along the sagittal (dorsoventral) plane. Remnants of the cone jelly were removed and the anterior portion of the cone was lightly scrubbed.

The left lateral section was normally used for staining unless it had been damaged by cutting. Sections were soaked for 5–20 minutes in Alizarin red-S stain with Berry's (1978) "school tuna" solution, and then rinsed in fresh water. Sections stained too darkly were soaked in a 5% hydrogen peroxide solution until the stain faded sufficiently. Stained vertebrae examined under high intensity visible light displayed distinct band couplets on the anterior cone (see Johnson, 1983). Within each couplet, the bands are uniformly spaced around the cone and separated by a thin translucent zone. Each couplet is separated from adjacent ones by a wide opaque zone that becomes somewhat depressed towards the outside edge of the cone. Each couplet of twin bands was considered to be a distinct growth ring. The vertebral-ring-count was given by the number of complete couplet bands observed.

The investigators examined 20 stained vertebrae to derive criteria to be used in interpreting the ring structures. Vertebrae were then processed by the team: one biologist read 20 vertebrae while the other recorded data, and vice versa. At least 25% of the samples processed each day were examined by both persons to check consistency. Identical counts were obtained in

>95% of the cross-checks; samples were rejected if the discrepancies in counts could not be resolved. A linear relationship (r^2=0.94) was detected between ring counts for the 35th and 36th vertebrae of the first 200 albacore processed, and no significant difference in age composition was found between counts from the two sets of vertebrae (χ^2 test, P=0.9). Even though the 35th and 36th vertebrae were both suitable for study, we chose the 35th vertebrae because it was larger and easier to read in most cases.

Tagging operations

For tagging, albacore were caught mainly with commercial troll gear (Dotson, 1980). The tagging procedure was similar to that described by Laurs et al. (1976). Immediately after a strike, the fishing line was retrieved manually. Once the specimen was on board, the hook was removed and the albacore was quickly inspected for injuries to the gills, eyes, mouth, and palate. Albacore that were vigorous and not visibly injured were placed on a measuring board or tagging cradle (Kearney and Gillett, 1982) and were tagged as rapidly as possible with a stainless steel tube applicator that contained a 13-cm-long serially numbered spaghetti-type plastic tag with a single barbed nylon head. The tag was inserted at an oblique angle so that the barb was anchored among the pterygiophores of the second dorsal fin. Fork length was measured and recorded on audio tape, along with the date, time, albacore condition, and tag number. Albacore were returned to the water head first immediately after tagging.

Labelle (1993b) described the albacore tagging operations conducted in the south Pacific, and summarized the corresponding release-recapture statistics. Approximately 17,000 albacore were tagged and released from troll fishing vessels during 1986–92; the season totals ranged from 815 to 6,524. As of November 1992, recaptures of 42 tagged albacore had been reported; we obtained complete information on sizes and dates of release and recapture for 27 of 42 albacore. Most of these 27 tags were returned by fishermen, although some were detected during catch sampling at canneries and landing sites. Recreational fishermen also tagged and released an additional 3,646 albacore along the south east coast of Australia during 1973–92 (Matthews and Deguara, 1992). As of November 1992, 14 of these had been recovered but only one tag recovery record was sufficiently complete to allow inclusion of the data.

Data analysis

Length-frequency analysis The MULTIFAN computer program was used to estimate VB growth parameters from the length-frequency data under the assumption that the modes in the data represent year classes. A detailed description of the model is given by Fournier et al. (1990) and the program is described in the MULTIFAN 3 *User's Guide and Reference Manual* (Otter Research, 1991). MULTIFAN can incorporate specific structural hypotheses into models being fitted to the length-frequency data. The simplest structural hypothesis assumes that the mean lengths-at-age lie on a VB growth curve and that the standard deviations of length-at-age are identical for all cohorts. More complex structural hypotheses can be tested to determine if they provide a statistically significant improvement in fit to the data. The more complex hypotheses tested assume that the following processes can occur in the population sampled:

1 Sampling bias for the first cohort. This could result from selectivity during the sampling process induced by the fishing gear or the sampling method. Size selectivity was assumed to apply only to the first cohort and to decrease linearly with age until fish reach the second cohort.

2 Age-dependent standard deviation in length-at-age. For some fish populations, variation in length-at-age is not constant across cohorts. This hypothesis allows the standard deviation of length-at-age to increase or decrease linearly with age.

3 Seasonally oscillating growth. Seasonal growth patterns are known to occur in some fish populations (Pauly and Gaschütz, 1979). This process was incorporated into the growth model by adding two parameters, one representing the magnitude of the seasonal effect and the other determining the time of the year at which growth is slowest because of the seasonal effect.

We systematically fitted models incorporating all possible combinations of the above structural hypotheses and used likelihood ratio tests to identify the most parsimonious model structure. Fitting and testing procedures were done automatically by MULTIFAN, although some user-specified input was needed to ensure that the model exhibited stable behavior (see Fournier et al., 1990, for explanations).

Estimates of the VB growth parameters K and L_∞ were obtained along with parameters for sampling bias, age-specific standard deviations, and seasonal growth. In the absence of information on the age of the first age-class, MULTIFAN assumes that the VB curve passes through the origin (i.e., t_0=0). Estimates of age-at-length are based on this assumption.

Analysis of vertebrae data The VB growth parameters were estimated from vertebral-ring-count data and length data, under the assumption that ring counts indicate total age (in years). We did not attempt to

estimate fractional age based on an assumed birth date; therefore, all ages are integers. Maximum-likelihood estimates (MLE) were obtained according to the procedure described by Kimura (1980). The objective function (Φ) minimized to obtain the parameter estimates was the negative log-likelihood of the VB model:

$$\Phi = \frac{N \log_e (2 \pi \sigma^2)}{2} + \frac{\sum_{i=1}^{N} \{l_i - [L_\infty (1 - e^{-K(t_i - t_0)})]\}^2}{2\sigma^2} \quad (1)$$

where: l_i = fork length of individual i,
   t_i = presumed age of individual i,
   N = number of individual measurements,
   L_∞ = estimated asymptotic fork length,
   K = estimated growth coefficient,
   t_0 = estimated hypothetical age at zero length,
   σ^2 = estimated variance associated with the length-at-age.

The objective function was minimized by using the Quasi-Newton algorithm in the NONLIN statistical module of the SYSTAT microcomputer program (Wilkinson, 1989). Asymptotic standard errors and parameter correlations were obtained from the Hessian matrix once the iteration process was complete (see Wilkinson, 1989). As suggested by Kimura (1980), the initial values supplied for the parameters were obtained from the Walford plot (Ricker, 1975).

Comparison of growth curves with tag-return data
We used the growth curves fitted to the two data sets and the observed length increments from the available tag-return data to test our assumption that the length-frequency modes represent year classes and vertebral-rings represent annual features. It must be acknowledged that there is no statistically correct means of comparing the models and the length increment data, because the growth curves derived from length frequencies and vertebral-ring-counts are based on age-length data. The only statistically correct predictions possible from these growth models are predictions of length (the dependent variable) from age (the independent variable). However, the length increment data can be related to the growth curves by first generating predictions from the fitted growth models which are then compared to the length increment data. This was accomplished by predicting lengths-at-recapture by using the standard Fabens (1965) length increment model:

$$l_{r_i} = l_i + (L_\infty - l_i)(1 - e^{-K \Delta t_i}) \quad (2)$$

where: l_i = length at release of individual i,
   Δ_{t_i} = time at liberty of individual i,
   l_{r_i} = estimated length-at-recapture of individual i,

and L_∞ and K are the VB parameters estimated from the length-frequency or vertebral-ring-count data. As noted above, this procedure is not correct in the strict statistical sense because the growth models are not used to predict length from age (see Francis, 1988). However, for comparative purposes, the second method should reveal any gross departures from the "annual features" assumption applied in fitting the growth models. Some justification for this is presented later.

Results

Growth analysis based on length-frequencies

The most parsimonious model structure for the albacore length-frequency data set included seasonal growth and age-dependent standard deviation in length-at-age. The incorporation of first length bias did not significantly improve the fit. Parameter estimates and estimates of the means and standard deviations of length-at-age are given in Table 1. Note that we use the term "relative age class" to denote that estimates of absolute age are based on the assumptions that the length modes represent annual cohorts and $t_0=0$.

The seasonal growth phase estimate of 0.216 indicates that fastest growth occurs in February, and slowest growth occurs six months later in August at the end of the austral winter. The seasonal growth amplitude estimate (0.949) is near the upper limit of 1.0, indicating that growth is almost non-existent at that time of the year. Standard deviation in length-at-age increased progressively with age for the nine significant age classes detected.

The predicted aggregate length-frequency distributions fitted the observed distributions very well over the entire range of sizes (Fig. 2), and the predicted modes closely matched the actual modes in most months. The predicted modal distribution pattern indicates that there were usually four prominent age classes in troll catch samples.

Growth analysis based on vertebral-ring counts

The fork lengths of the albacore sampled ranged from 44 to 110 cm (Table 2), which corresponds to the size range of albacore caught in the surface and longline

Table 1

Estimated parameters from the MULTIFAN analysis, with predicted fork lengths (FL) and standard deviations (SD) of lengths-at-age.

Parameter	Estimated value	Relative age class	Predicted FL ($\bar{x}$, cm)	Length-at-age SD
von Bertalanffy K (cm·yr⁻¹)	0.239	3.04	48.86	1.74
von Bertalanffy L_∞	97.100	4.04	59.12	2.03
Brody's rho (ρ)	0.788	5.04	67.19	2.29
Age of first age class (yr)	3.040	6.04	73.55	2.53
Mean length sampling bias	0.000	7.04	78.56	2.72
Seasonal growth phase	0.216	8.04	82.50	2.89
Seasonal growth amplitude	0.949	9.04	85.60	3.03
Mean SD	2.373	10.04	88.05	3.14
Ratio of first to last SD	1.861	11.04	89.98	3.24

Table 2

Summary statistics on sizes of albacore aged from vertebral-ring-counts.

Ring count	Sample size	Range (FL, cm)	Mean FL	Length-at-age SD	Coefficient of variation	Mean size increment
1	7	45–51	47.2	2.21	4.68	—
2	79	44–65	50.1	4.23	8.38	2.9
3	71	46–72	57.1	6.86	12.03	7.0
4	68	48–78	65.9	6.63	10.01	8.8
5	61	57–95	73.6	8.01	10.88	7.7
6	53	58–99	79.6	8.74	10.98	6.0
7	54	70–105	85.1	8.42	9.89	5.5
8	26	73–102	88.9	7.34	8.25	3.8
9	20	80–101	95.0	4.58	4.81	6.1
10	32	88–110	96.6	4.61	4.77	1.6
11	20	92–107	97.6	3.69	3.78	1.0
12	2	103–108	105.5	3.53	3.35	7.9
13	1	107–107	107.0	—	—	1.5

fisheries (Labelle, 1993a). Up to 13 rings, assumed to be annuli, were visible in the vertebrae sampled. Sample sizes for all relative age classes were greater than 20, except for classes 1, 12, and 13. Significant differences in the standard deviation of length-at-age were detected among the age classes (Bartlett's test, χ^2=64.683, P<0.001), and the standard deviation was greatest for relative age classes 5–7. This trend differs from the results obtained in the length-frequency analysis, which indicated increasing standard deviation with age (although only linear trends were possible in this analysis).

Differences in mean size between the successive age classes were calculated to reveal other anomalies in growth patterns. In theory, absolute growth should be rapid at first and decrease progressively in later life (see Ricker, 1975). The pattern observed for albacore agrees with these theoretical expectations, except for the high growth rates observed between relative ages 8→9 and 11→12 (Table 2). No statistical or biological criteria justified the omission of the data associated with ages 8→9 from the analysis. However, the large growth increment obtained for age 11→12 could simply be biased because of the small sample size (2) for relative age class 12.
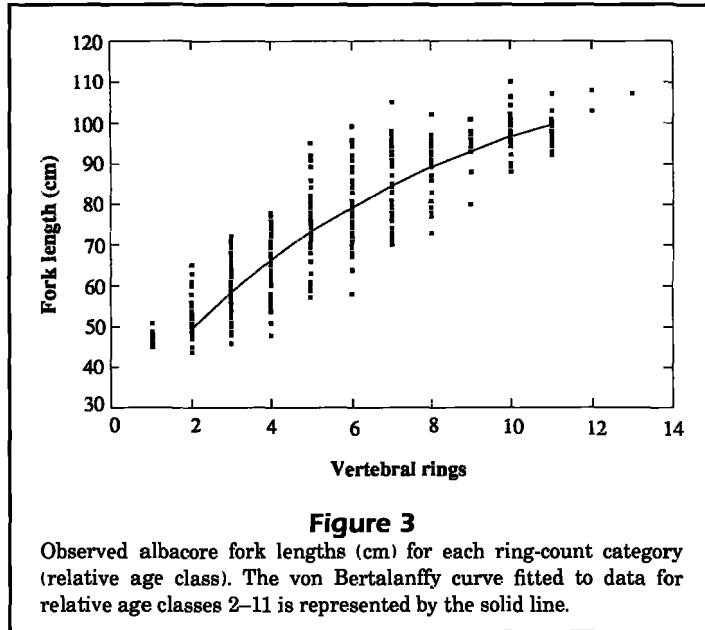
The VB model was fitted to the aggregate vertebral-ring-count data for relative age classes 2–11. The data for relative age classes 1, 12, and 13 were excluded because of their small sample sizes. The VB model provided a good fit to the remaining data (Fig. 3). The residuals were generally well centered around zero and the slope of a linear regression of residuals against relative age was not significantly different from zero (F-test=0.001; P=0.973).

Of the albacore sexed, 59 were females and 70 were males. As these were distributed in a similar fashion with respect to relative age class as the pooled data set (females, males, and unsexed), the VB parameters were estimated for each sex (Table 3). Likelihood ratio tests (Kimura, 1980) were used to test for differences in growth parameters between sexes. No significant differences were detected for any of the tests carried out (Table 4). Therefore, the growth parameters estimated from the pooled data set were considered to be representative of growth patterns of male and female albacore within the size range sampled.

Comparison of growth curves

A direct comparison of the VB growth curves estimated from length-frequencies and vertebral-ring-counts is slightly complicated by the assumption of $t_0 = 0$ for the length-frequency analysis and the estimation of $t_0 = -1.922$ year for the vertebral-ring model. This inconsistency would result in the growth curves being out of phase by almost two years, apart from any other differences that might be present. One way of comparing the two curves is to compare the expected growth of

Figure 3

Observed albacore fork lengths (cm) for each ring-count category
(relative age class). The von Bertalanffy curve fitted to data for
relative age classes 2–11 is represented by the solid line.

Growth rates of tagged albacore

The 28 tag release-recapture records with complete growth data included a wide variety of sizes (61.0–96.5 cm), times-at-large (54–1,790 days) and release-recapture locations well distributed throughout the principle fishing areas. Estimated average growth rates during the periods at large were 0.17–1.13 cm·month^{-1}. For albacore at liberty <500 days, growth rate showed the expected decline with increasing mid-size (half way between release and recapture sizes); but this decline was negligible for albacore at liberty >500 days (Fig. 5). Given the relatively small number of records available, no attempt was made to estimate the VB growth parameters based on tag release-recapture data.

Comparison of tag return growth increments with the fitted models

To compare the consistency of the VB models derived earlier with the tag-return data, we first calculated sets of predicted recapture lengths for the 28 tag return records by using the two sets of L_∞ and K estimates, derived from length-frequency and vertebral-ring-count data, in Equation 2. We also made a third set of predictions using the L_∞ estimate and twice the K estimate obtained from the length-frequency analysis (L_∞=97.1 cm, K=0.478 yr^{-1}). These parameters are consistent with an assumption that the observed

an albacore of a specific initial size over time. This is equivalent to using the L_∞ and K estimates in a Fabens-type length increment model to make an approximate comparison of predicted growth trends independent of assumed or estimated t_0. Despite substantial differences in the L_∞ and K estimates from the two analyses, there was little difference in the predicted growth of a 40-cm albacore over time within the range of the data (Fig. 4).

Table 3

MULTIFAN parameter estimates of the VB growth model based on the vertebral-ring-counts. Parameter estimates are based on all albacore of relative ages 2–11 (top); females only of ages 2–9 (middle); and males only of ages 2–10 (bottom). Lower and upper bounds are the upper and lower limits of the 95% confidence intervals. MLE=maximum-likelihood estimates.

Sample content	Parameters	MLE	SD	Lower bound	Upper bound	Correlation matrix		
						L_∞	K	t_0
All albacore	L_∞	121.024	5.193	110.846	131.202			
ages 2–11	K	0.134	0.016	0.104	0.165	−0.981		
n = 484	t_0	−1.922	0.291	−2.492	−1.350	−0.880	0.951	
	σ^2	46.102	2.964	40.293	51.910	0.004	−0.004	−0.004
Females	L_∞	169.320	54.532	62.440	276.200			
ages 2–9	K	0.077	0.045	−0.011	0.166	−0.994		
n = 58	t_0	−2.573	1.109	−4.745	−0.400	−0.900	0.940	
	σ^2	40.775	7.574	25.930	55.621	0.026	−0.026	−0.024
Males	L_∞	122.037	14.332	93.947	150.127			
ages 2–10	K	0.168	0.054	0.063	0.274	−0.980		
n = 70	t_0	−0.907	0.649	−2.179	0.365	−0.847	0.929	
	σ^2	64.262	10.862	42.972	85.551	0.002	−0.002	−0.002

Table 4

Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) albacore, based on the procedure described by Kimura (1980).

| Hypothesis	Linear constraints	Parameter estimates						Residual SS	χ^2	df	P
		$L_{\infty,1}$	$L_{\infty,2}$	K_1	K_2	$t_{0,1}$	$t_{0,2}$				
1	none	122.037	169.320	0.168	0.077	−0.907	−2.573	6863.3			
2	$L_{\infty,1}{=}L_{\infty,2}$	129.504	129.504	0.145	0.134	−1.180	−1.561	6911.0	0.104	1	>0.70
3	$K_1{=}K_2$	131.088	127.932	0.140	0.140	−1.265	−1.455	6922.4	0.129	1	>0.60
4	$t_{0,1}{=}t_{0,2}$	131.197	128.411	0.138	0.141	−1.350	−1.350	6933.6	0.153	1	>0.50
5	Same L_∞, K, t_0	131.157	131.157	0.136	0.136	−1.385	−1.385	6948.1	0.184	3	>0.50
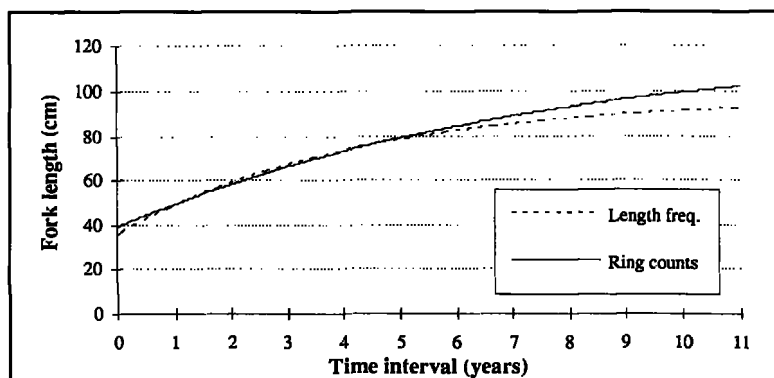
Figure 4

Growth of south Pacific albacore from an initial length of 40 cm as predicted by models fitted to length-frequency and vertebral-ring-count data.

length-frequency modes are semestral, rather than annual features. We then compared each set of predictions to the observed recapture lengths.

The growth models derived from length-frequency and vertebral-ring-count data, assuming that the modes and rings are annual features, appear to be consistent with the tag return length increment data (Fig. 6). Deviations of observed from predicted recapture lengths are both positive and negative and are generally within the range of expected individual variation. In contrast, the growth model based on the assumption of semestral length-frequency modes overestimates the recapture lengths. On this basis, the tag return length increment data lend support to our initial assumptions concerning the length-frequency modes and vertebral-rings.

Discussion

Estimates of the VB growth parameters for south Pacific albacore based on the analysis of length-frequencies and vertebral-ring-counts were generally within the ranges of values reported for albacore from other regions (Table 5). The only exception was the L_∞ estimate obtained with MULTIFAN, which was lower than all other estimates reported. This could be partly due to the fact that the data set used for the MULTIFAN analysis did not include length-frequency samples from longline catches, so the largest size classes were not well represented. Nevertheless, we do not attach any biological significance to this or to the differences in VB parameters estimated from the two data sets in this study. Despite differences in the parameters, the predicted growth patterns based on the two analyses are remarkably similar. This often noted feature of the VB growth model (e.g., Knight, 1968; Francis, 1988) highlights the potential pitfalls of comparing growth only on the basis of VB growth param-
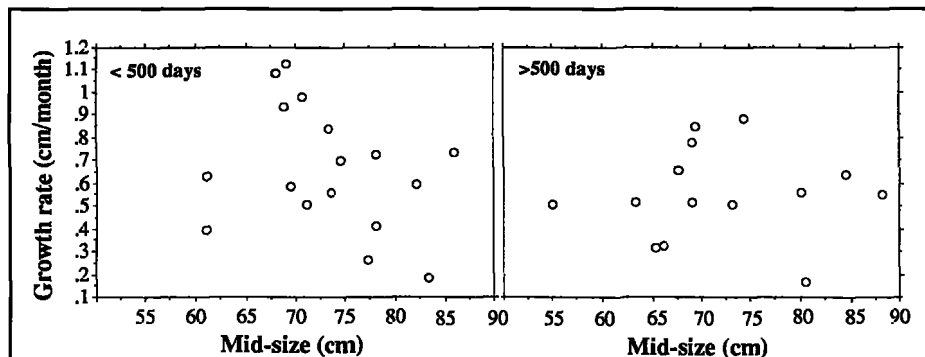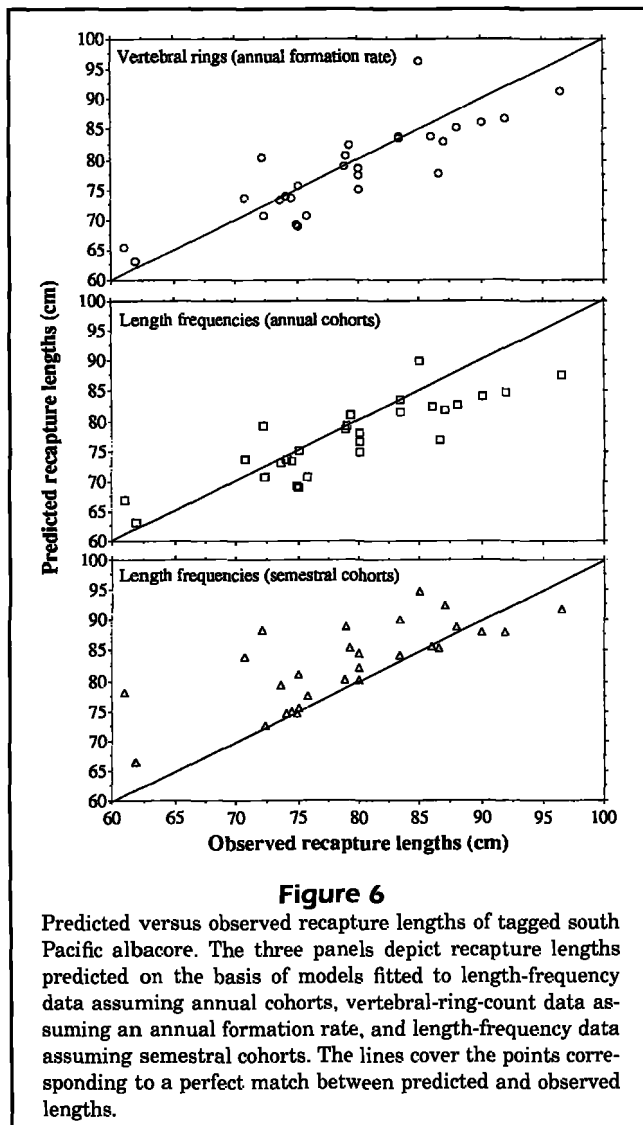

Figure 5

Individual growth rates of tagged south Pacific albacore for two time-at-liberty categories. Mid-size is the fork length half way between the release and recapture lengths.

Figure 6

Predicted versus observed recapture lengths of tagged south
Pacific albacore. The three panels depict recapture lengths
predicted on the basis of models fitted to length-frequency
data assuming annual cohorts, vertebral-ring-count data as-
suming an annual formation rate, and length-frequency data
assuming semestral cohorts. The lines cover the points corre-
sponding to a perfect match between predicted and observed
lengths.

eters. In this study, the VB model was preferred to
alternatives because it was used in available software
such as MULTIFAN. There were no indications from
the data that the VB model was not appropriate for
modelling albacore growth, although a Gompertz model
(Ricker, 1979) appeared to provide an equally good fit
to the vertebral-ring-count data.

In fishes, rings are thought to form in bony tissues
as a series of growth checks separated by zones, usu-
ally more opaque, that are associated with growth
(Casselman, 1983). The usual inference that rings are
formed yearly is based on the observation that growth
rate, particularly for temperate species, is frequently
seasonal as a result of its dependence on temperature.
Growth checks are thought to occur during the period
of the year when the water is coldest; high growth
rates occur during periods of warmer water tempera-
tures. Length-frequency analysis provided evidence that
juvenile albacore growth is strongly seasonal; there-
fore this seasonality could be the basis of ring forma-
tion in vertebrae. However, the relationship of water
temperature with this seasonality is unknown. Alba-
core, while being predominantly a temperate species,
are also found in tropical waters, particularly as adults.
In common with other *Thunnus* species, they occupy a
three-dimensional habitat within wide temperature lim-
its (14–20°C) and are capable of physiological ther-
moregulation, maintaining body temperatures of up to
15°C warmer than that of the surrounding waters
(Morrison et al., 1978). It is possible that ring forma-
tion in the bony tissues of albacore is influenced by
these biological characteristics and by more complex
biological cycles, such as feeding and reproduction, as
well as the temperature of the water that they occupy.

As a working hypothesis, the length-frequency modes
and vertebral-rings were assumed to be formed each

Table 5

Reported estimates of the von Bertalanffy growth parameter albacore from various regions around the world.

Data source	Sampling region	Aging method	L_∞	K	t_0	Size range (FL, cm)
Clemens (1961)	N. Pacific	Tagging	135.6	0.170	−1.870	54–77
Shomura (1966)	N. Pacific	Tagging	118.8	0.250	1.999	60–91
Shomura (1966)	N. Pacific	Scales	114.4	0.308	0.818	65–120
Shomura (1966)	N. Pacific	Scales	145.3	0.159	−0.056	50–120
Laurs and Wetherall (1981)	N. Pacific	Tagging	125.0	0.199	—	47–92
Shomura (1966)	N. Pacific	Vertebrae	104.8	0.431	1.504	69–90
Shomura (1966)	N. Pacific	Scales	145.3	0.150	−0.396	40–95
Bell (1962)	N. Pacific	Scales	108.8	0.225	−2.273	51–94
Huang et al. (1991)	Indian	Scales	128.1	0.162	−0.897	64–106
Beardsley (1971)	Atlantic	Length data	140.0	0.141	−1.830	68–114
González-Garcés and Farina-Perez (1983)	N. Atlantic	Dorsal spine	140.1	0.129	−1.570	38–110
Santiago (1992)	N. Atlantic	Length-freq.	117.9	0.200	—	48–106

year in the growth models presented in this paper. Laurs et al. (1985) validated the daily increment formation rates in sagittae of tagged north Pacific albacore that had been injected with oxytetracycline (OTC) prior to release and concluded that the increment counts, adjusted upwards by 5%, provided an accurate estimate of absolute age. Preliminary estimates of absolute age of south Pacific albacore were obtained from counts of otolith increments, assuming similar increment deposition rates as for the north Pacific population (Wetherall et al., 1989). These results indicated that south Pacific albacore grew about twice as fast as our estimates suggest. This would suggest that the length-frequency modes and vertebral-rings analysed here are more likely to be semestral than annual features.

The length increment data from 28 tag returns presented in this study clearly favor the hypothesis of annual length-frequency modes and vertebral-rings over a semestral formation rate. Given the assumption that length-frequency modes represent cohorts of albacore spawned during the same season, we would expect the temporal spacing of length-frequency modes to correspond to the frequency of spawning seasons. Both gonadosomatic indices and microscopic examination of gonad tissue of south Pacific albacore clearly indicate a single annual peak in spawning activity during the austral summer (Ramon and Bailey, 1993).

Most of the evidence therefore points towards annual length-frequency modes and vertebral-rings, although the conflicting results obtained from "daily" growth increment counts on otoliths are deserving of further study. It would be particularly useful to estimate increment formation rates in vertebrae and otoliths of tagged south Pacific albacore injected with OTC before release, as was done for the north Pacific population. During 1986–1989, 3,341 tagged south Pacific albacore were injected with OTC, and to date, three have been recaptured and the relevant hard parts obtained. It is hoped that examination of this material will, in due course, clarify increment deposition rates in south Pacific albacore.

A previous review of the available information on stock structure lead Lewis (1990) to conclude that the south Pacific population probably had very limited exchange with those of the North Pacific and the Indian Ocean. Parasite studies (Jones, 1991), tagging programs, and ongoing electrophoretic surveys have not yet revealed the existence of separate sub-stocks within the south Pacific population. Thus, the growth rates reported here could be considered as representative of the growth patterns in the entire south Pacific albacore population. However, we cannot reject the hypothesis that populations from other oceans have significantly different growth patterns. It is also plausible

that local phenomena, such as land mass effects and upwelling zones that can affect the growth rates of albacore within certain regions of the south Pacific.

Acknowledgments

Literature cited

Anonymous.
   1986. First South Pacific Albacore Research Workshop; Auckland, New Zealand, 9–12 June 1986. South Pac. Comm. Rep., Noumea, New Caledonia, 33 p.
   1991. Fourth South Pacific Albacore Research Workshop; Taipei, Republic of China-Taiwan. November 4–8, 1991. South Pac. Comm., Noumea, New Caledonia, 40 p.
Beardsley, G. L.
   1971. Contribution to the population dynamics of Atlantic albacore with comments on potential yields. Fish. Bull. 69(4):845–857.
Bell, R. R.
   1962. Age determination of the Pacific albacore of the California coast. Calif. Fish Game. 48(1):39–48.
Berry, F. H., D. W. Lee, and A. R. Bertolino.
   1977. Progress in Atlantic bluefin tuna ageing attempts. Collective Volume of Scientific Papers. Int. Comm. Conserv. Atlantic Tunas. 6(2):305–317.
Berry, F. H.
   1978. Vertebrae related studies. In J. J. Hunt (ed.), Proceedings of Atlantic bluefin tuna ageing workshop. Collective Volume of Scientific Papers. Int. Comm. Conserv. Atlantic Tunas. 7(2):337–339.
Casselman, J. M.
   1983. Age and growth assessment of fish from their calcified structures—techniques and tools. In E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Tech. Rep. NMFS 8:1–17.

Clemens, H. B.
1961. The migration, age and growth of Pacific albacore in the north Pacific (*Thunnus germo*), 1951–1958. Calif. Dep. Fish Game, Fish. Bull. 115, 128 p.

Dotson, R. C.
1980. Fishing methods and equipment of the US west coast albacore fleet. U.S. Dep. Commer., NOAA Tech. Memo. NMFS 8, 126 p.

Fabens, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton.
1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47:301–317.

Francis, R. I. C. C.
1988. Are growth parameters estimated from tagging and age-length data comparable? Can. J. Fish. Aquat. Sci. 45:936–942.

González-Garcés, A., and A. C. Farina-Perez.
1983. Determining age of young albacore, *Thunnus alalunga*, using dorsal spines. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Tech. Rep. NMFS 8:117–122.

Hampton, J., T. Murray, and P. Sharples.
1989. South Pacific albacore observer programme 1988–1989. South Pac. Comm. Tuna and Bill. Assess. Prog. Tech. Rep. 22, 22 p.

Hampton, J., T. Murray, and K. Bailey.
1991. South Pacific albacore observer programme 1989–1990. South Pac. Comm. Tuna and Bill. Assess. Prog. Tech. Rep. 25, 25 p.

Huang, C., C. Wu, C. Kuo, and W. Su.
1991. Age and growth of the Indian Ocean albacore, *Thunnus alalunga*, by scales. Proceedings of the expert consultation on stock assessment of tunas in the Indian Ocean; Bangkok, Thailand, July 2–6, 1990. Collective Volume of Working Documents 4:111–122. FAO/UNDP Indo-Pacific Development and Management Programme.

Jones, J. B.
1991. Movements of albacore tuna (*Thunnus alalunga*) in the South Pacific: evidence from parasites. Mar. Biol. 111:1–9.

Johnson, A. G.
1983. Comparison of dorsal spines and vertebrae as ageing structures for little tunny, *Euthynnus alletteratus*, from the Northeast Gulf of Mexico. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Tech. Rep. NMFS 8:111–115.

Kearney, R. E., and R. D. Gillett.
1982. Methods used by the Skipjack Survey and Assessment Program for tagging skipjack and other tuna. South Pac. Comm. Tech. Rep. Skip. Surv. Asses. Progr. 7:21–43.

Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77(4):765–776.

Knight, W.
1968. Asymptotic growth: An example of nonsense disguised as mathematics. J. Fish. Res. Board. Can. 25:1303–1307.

Labelle, M.
1993a. A review of the south Pacific albacore troll fishery 1985–92. South Pac. Comm. Tuna and Bill. Assess. Prog. Tech. Rep. 32, 25 p.
1993b. A review of albacore tagging in the South Pacific. South Pac. Comm. Tuna and Bill. Assess. Prog. Tech. Rep. 33, 17 p.

Laurs, R. M., and J. A. Wetherall.
1981. Growth rates of north Pacific albacore, *Thunnus alalunga*, based on tag returns. Fish. Bull. 79(2):293–302.

Laurs, R. M., W. Lenarz, and R. Nishimoto.
1976. Estimates of rates of tag shedding by north Pacific albacore, *Thunnus alalunga*. Fish. Bull. 74(3):675–678.

Laurs, R. M., R. Nishimoto, and J. A. Wetherall.
1985. Frequency of increment formation on sagittae of north Pacific albacore (*Thunnus alalunga*). Can. J. Fish. Aquat. Sci. 42:1552–1555.

Lee, D., E. D. Prince, and M. C. Crow.
1983. Interpretation of growth bands on vertebrae and otoliths of Atlantic bluefin tunas, *Thunnus thynnus*. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Tech. Rep. NMFS 8:61–70.

Lewis, A. D.
1990. South Pacific albacore stock structure: a review of available information. South Pac. Comm., Noumea, New Caledonia. Third South Pacific Albacore Research Workshop; Noumea, New Caledonia, 9–12 October 1990. WP 5, 13 p.

Matthews, J., and J. Deguara.
1992. Gamefish tagging 1991–92. NSW Fish. Res. Inst. Annual Report, 13 p.

Morrison, D. C., R. M. Laurs, and R. C. Ulevitch.
1978. Activity of albacore serum complement reflects its thermoregulatory capacity. *In* G. D. Sharp and A. E. Dizon (eds.), The physiological ecology of tunas, p. 141–150. Academic Press, New York.

Otter Research.
1991. MULTIFAN 3 user's guide and reference manual. Otter Research Ltd., Nanaimo, Canada.

Pauly, D., and G. Gaschütz.
1979. A simple method for fitting oscillating growth data, with a program for pocket calculators. ICES CM 1979/G: 24, 26 p.

Pianet, R. J. Chabane, J. Cremoux, R. Etaix-Bonnin, R. Grandperrin, R. Leborgne, G. Moarii, G. MouTham, J. Panche, M. Radenac.

1990. Rapport de la campagne PROSGERMON 87, N.O. Coriolis, 21 Février au 20 Mars 1987. ORSTOM, Noumea, 1990. Sci. Mer : Biol. mar.; 7: 69 p.

Ramon, D., and K. Bailey.
1993. Reproductive patterns of south Pacific albacore, *Thunnus alalunga*, as indicated by gonosomatic index and meiotic activity. South Pac. Comm. Fifth South Pacific Albacore Research Workshop; Papeete, Tahiti, French Polynesia. March 1993. WP 13, 27 p.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board. Can. Bull. 191, 382 p.

1979. Growth rates and models. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiology. Volume VIII: Bioenergetics and growth, 786 p. Academic Press. London.

Santiago, J.
1992. Application of "MULTIFAN" to estimate the age composition of the North Atlantic albacore catches. Int. Comm. Conserv. Atlantic Tunas (ICCAT). Collective Volume of Scientific Papers XXXIX(1):188–192.

Sharples, P., K. Bailey, P. Williams, and A. Allan.
1991. Report of observer activity on board Jamarc driftnet vessel R.V. *Shinhoyo Maru* fishing for albacore in the south Pacific ocean. South Pac. Comm. Tuna and Bill. Assess. Prog. Tech. Rep. 24, 24 p.

Shomura, R. S.
1966. Age and growth studies of four species of tunas in the pacific Ocean. *In* T. A. Manar (ed.), Hawaii Governor's Conf. Center. Pac. Fish. Res. Proc., p. 203–219.

Wang, C. H.
1988. Seasonal changes of the distribution of south Pacific albacore based on Taiwan's tuna longline fisheries, 1971–1985. Acta Oceanographica Taiwanica. 20:13–39.

Wetherall, J. A., R. N. Nishimoto, and M. Y. Y. Yong.
1989. Age and growth of south Pacific albacore determined from daily otolith increments. South Pac. Comm. Second South Pacific Albacore Research Workshop; Suva, Fiji, Nov. 1989. WP 18, 7 p.

Wilkinson, L.
1989. SYSTAT. The system for statistics. SYSTAT, Inc. Evanston, Illinoi.