

Abstract—Southern bluefin tuna (SBT) (*Thunnus maccoyii*) growth rates are estimated from tag-return data associated with two time periods, the 1960s and 1980s. The traditional von Bertalanffy growth model (VBG) and a two-phase VBG model were fitted to the data by maximum likelihood. The traditional VBG model did not provide an adequate representation of growth in SBT, and the two-phase VBG yielded a significantly better fit. The results indicated that significant change occurs in the pattern of growth in relation to a VBG curve during the juvenile stages of the SBT life cycle, which may be related to the transition from a tightly schooling fish that spends substantial time in near and surface shore waters to one that is found primarily in more offshore and deeper waters. The results suggest that more complex growth models should be considered for other tunas and for other species that show a marked change in habitat use with age. The likelihood surface for the two-phase VBG model was found to be bimodal and some implications of this are investigated.

Significant and substantial differences were found in the growth for fish spawned in the 1960s and in the 1980s, such that after age four there is a difference of about one year in the expected age of a fish of similar length which persists over the size range for which meaningful recapture data are available. This difference may be a density-dependent response as a consequence of the marked reduction in the SBT population. Given the key role that estimates of growth have in most stock assessments, the results indicate that there is a need both for the regular monitoring of growth rates and for provisions for changes in growth over time (possibly related to changes in abundance) in the stock assessment models used for SBT and other species.

Estimating long-term growth-rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data

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Estimating growth rates has been a major focus of fisheries research throughout the twentieth century, and a large body of literature exists on the topic (e.g. Lee, 1912; Ford, 1933; Walford, 1946; Manzer and Taylor, 1947; Allen, 1966; Yukinawa, 1970; Pitcher and MacDonald, 1973; Kimura, 1980; Fournier et al., 1990). This literature reflects, at least in part, the fundamental importance of information on growth rates in stock assessments and the subsequent provision of management advice for commercially harvested fish populations. For example, growth information is required for yield-per-recruit analyses and for the estimation of spawning stock biomass in the estimation of stock-recruitment relationships. In addition, for a number of species, estimates of growth rates have been the primary or only source of information that can be used to estimate the age of individual fish and the age distribution of commercial catches (particularly for tropical species and for tunas and billfish). Such information on age is a critical component required in the analyses and models used to assess and manage these fish stocks (Bayliff, 1991; Clay, 1991; Caton, 1991; Wild, 1994; Wild and Hampton, 1994; Polacheck et al.¹).

Almost all the work on modeling growth has centered on modeling growth rate as a continuous, smooth, monotonically decreasing function of

age, and the von Bertalanffy (1938) growth (VBG) equation, and its extensions, have been the most common approach used. In addition, the growth process has frequently been modeled as static. Temporal variations in average growth for fish of the same size, or age, (due, for example, to changes in the physical environment or population density) are often ignored or considered to be relatively minor (with some notable exceptions—e.g. Le Cren, 1958; Southward, 1967; de Veen, 1976; Toresen, 1990; Ross and Nelson, 1992; Kaeriyama, 1996; Sinclair and Swain, 1996).

For the large pelagic tunas and billfishes, the von Bertalanffy growth equation and extensions has been the standard used for modeling growth (Bayliff, 1980). For a variety of tuna species, numerous growth studies have been conducted, and generally a reasonable range of parameter values has been estimated (e.g. see the sets of parameter values estimates for the eight scrombrid species in Bayliff, 1980).

¹ Polacheck, T., A. Preece, A. Betlehem, and N. Klaer. 1998. Treatment of data and model uncertainties in the assessment of southern bluefin tuna stocks. *In* Fishery stock assessment models (F. Funk et al., eds.), p. 613–637. Alaska Sea Grant College Program Report AK-SG-98-01. Univ. Alaska, P.O. Box 755040, Fairbanks, AK 99775-5040.

Bayliff (1988) also investigated regional growth differences in Pacific skipjack and yellowfin tunas. Interpretation as to whether any differences found are merely an artifact of the data collection or procedures used or whether they reflect real temporal or spatial difference has generally not been possible because the basic data (e.g. tagging, hard parts, length-frequency data), data collection procedures, analytic approaches, and the areas and time periods from which the data were collected have varied greatly among studies.

For southern bluefin tuna (SBT) (*Thunnus maccoyii*), extensive juvenile tagging programs were conducted in the 1960s and 1980s, and a large number of returns with measured lengths were recovered. From both periods, some returns were received after times at liberty in excess of 10 years. These two sets of tagging experiments provide the basis for the direct comparison of growth over a time span of 30 years. Also, because of the large number of tags returned in these studies, a more detailed examination of the adequacy of the von Bertalanffy growth equation as a model of the growth process is possible than with many data sets. These tagging data (primarily those from the 1960s) have been used as a basis for a number of analyses of growth rates (Murphy, 1977; Kirkwood, 1983; Hearn, 1986; Hampton, 1991; Lucas²). In the present paper, we present results of the analyses of the growth increment data from these two sets of tagging experiments. We examine these data both in terms of 1) whether SBT growth differed between the tagging periods and 2) whether there was a change in the growth process between adult and juvenile SBT (i.e. whether a more complex model than the simple von Bertalanffy equation is required to provide an adequate description of SBT growth).

The results presented here incorporate and build upon the already cited published analyses of these tag-return data, unpublished reports, and discussions of SBT growth in scientific meetings on SBT (e.g. Hearn and Hampton³; Hearn and Polachek⁴; Anonymous⁵).

² Lucas, C. 1974. Working paper on southern bluefin tuna population dynamics ICCAT (International Commission for the Conservation of Atlantic Tunas), SCRS/74/4. Collective Volume of Scientific Papers, vol. 111, p. 110–124. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

³ Hearn, W. S. and J. Hampton. 1990. SBT growth change. Ninth trilateral meeting on SBT, Hobart, Australia, September 1990, SBFWS/90/8, 19 p. [Available from CSIRO and the Commission for Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

⁴ Hearn, W. S., and T. Polachek. 1993. Estimating SBT age-at-length relations for the 1960s and 1980/90s. Twelfth trilateral meeting on SBT, Hobart, Australia, October 1993. SBFWS/93/4, 21 p. [Available from CSIRO and the Commission for Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

⁵ Anonymous. 1994. Report of the southern bluefin tuna trilateral workshop; Hobart, Australia, January/February 1994, 161 p. [Available from CSIRO and the Commission for the Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

Background: the SBT stock and fishery

SBT is a highly-migratory species that begins to spawn at about 10–12 years of age in waters south of Java during the southern summer, mainly from September to April (Farley and Davis, 1998). During the first year of life they tend to be transported south by the tropical Leeuwin Current to inshore waters between Perth and Esperance, Western Australia. From ages 1 to 4 years, they appear to mainly inhabit, at least in the summer months, the waters off the Great Australian Bight, southern New South Wales (NSW) and eastern Tasmania. Many move to oceanic waters during the winter months and apparently progressively so as they age. By five years of age almost all have migrated to oceanic waters between 30° and 50°S at all longitudes, but mostly in the Eastern Hemisphere.

Substantial surface fisheries operated off the south coast of Western Australia from 1969 to the mid 1980s, off the south coast of NSW from 1963 to the early 1980s, and off South Australia from 1964 to the present. Since 1959 a major Japanese longline fishery has operated in oceanic waters between 30° and 50°S, mainly from the mid-Atlantic and westwards to a few degrees west of New Zealand.

Materials and methods

Tagging programs

Description Large numbers of tagged fish were released by CSIRO staff in the period from 1959 to 1968 and again in the period from 1980 to 1984. The releases from these two periods are used in our present study. Most of the tagged fish were initially caught with pole-and-line gear with barbless hooks, although a relatively small number were caught with troll lines. After a fish was hooked, it was hauled aboard the vessel and placed on a measuring board (in the 1960s) or a vinyl cradle (in the 1980s), and its nose to caudal fork length was measured. The fish was then tagged by an operator who inserted a 12-cm plastic spaghetti dart tag into the fish about 4 cm to the rear of the second dorsal fin on either side of the fish and re-released it into the water within about 30 seconds. After 1963 almost all fish were double tagged. The tag numbers and length of each fish were recorded, together with location and date of release. This information was later transferred to a computer database.

Tagging operations in both the 1960s and 1980s were concentrated in the nearshore, surface-water fisheries bordering the central and western southern coast of Australia and the southern coast of NSW. In the 1980s no tags were released from the NSW coast area because this component of the fishery had collapsed, and surface schools of juvenile SBT could no longer be found (Caton, 1991). The South Australian tagging took place in the Great Australian Bight or in the adjacent shelf waters generally between longitudes 128° and 136°E. Releases in Western Australia occurred in the Albany (between longitudes 112° and 119°E) and Esperance (between longitudes 119° and 125°E) areas. There were 33,309 juvenile SBT tagged by

CSIRO personnel during the 1960s (1959 to 1968) and 10,743 during the early 1980s (1980 to 1984). Of these fish, 1972 and 4280, respectively, were later recaptured.

On recapture, fishermen recovered the tags and recorded the fish's length (if measured), location, and date. The tags with the recorded information were returned to the scientific staff at CSIRO, who then provided a reward. Most of the recapture lengths were measured by fishermen or factory staff, but about 31% were measured by scientists. Those measured by scientists cannot be considered a representative sample. In particular, all of the measurements for longer-term recaptured fish come from fishermen aboard Japanese longline vessels. In addition to length, longliners often reported the dressed weight and sometimes the whole weight, or both, of recaptured fish. In the 1960s Australian fishermen seldom reported any weight measurements, but in the 1980s they commonly reported the whole weight of recaptured fish.

Data selection The tagging experiments were conducted mainly within a narrow range of months at each site; therefore returns within a few months would be most strongly influenced by the seasonal differences found in SBT growth (Hearn, 1986; Burgess et al., 1991; Leigh and Hearn 2000). A nine-month period at liberty coincides with a low frequency in the times at liberty for the experiments; therefore we excluded data from analyses with less than 270 days at liberty. We also excluded data for which fish were tagged by fishermen, or when the recovery length, year, or month were reported by the tag finder to be unknown or uncertain.

Previously reported weight-length relationships (Wara-shina and Hisada, 1970; Hampton, 1986; Robins⁶) were used to identify and screen out dubious recapture data. The details of the screening procedures are documented by Hearn⁷ and Anonymous.⁵ Longline recaptures were excluded if the expected weight of a recaptured fish for its reported length was either less than 2/3 of the reported weight or greater than 1.5 times the reported weight. Some of the major inconsistencies were thought to be due to measuring the length of a fish without its tail or without its head (Lucas²). For surface fish in the 1980s, a high proportion of the weight-length data for recaptured fish from four vessels was inconsistent with the weight-length relationships noted above. All tag-return data from these four vessels were excluded. Another 2.5% of the 1980 data were excluded because of highly unlikely values for the ratio of the reported weight to length of the recaptured fish.

For the screening methods used, no assumption was made about the underlying growth curve, and these methods were designed so that they would not induce a bias into the results. The selection process yielded data sets that were sufficiently large for valid analyses, being 730 and 1450 for the 1960s and 1980s data sets, respectively. Note that for other tuna species the selection process used in our study (particularly the deletion of recaptured fish with short times-at-liberty) may cause problems because of smaller data sets (e.g. skipjack and yellowfin tunas in Bayliff, 1988).

Experimental assumptions The use of the tag-return increment data for estimating growth rates requires the following assumptions about the tagging protocols and data collection procedures:

- 1 Tagging does not retard growth.
- 2 The tagged fish are uniquely and correctly recorded at release and recapture.
- 3 The lengths of fish are measured without bias at release and recapture.
- 4 A wide range of fish sizes are represented, in recaptures at least.
- 5 There are no significant size-selection processes for fish within similar age ranges.

With respect to tagging effects, Hampton (1986) and Hearn (1986) have shown that there can be a significant weight loss of 7–12% for tagged fish in the first month after release. However, tagged fish recover this weight loss within a year at liberty, and there is no apparent difference between tagged and untagged fish after this time (Hearn, 1986). (There is little information available on weight loss of tagged fish at liberty between one month and one year.) In terms of length, Hearn and Hampton³ could not detect a reduction of growth from growth increment residuals in the tag-return data even within the first 30 days after release. Limited data from the effect of handling and tagging fish in commercial farm pens indicated no retardation in growth in length after 150 days. These farm fish did show a loss in weight when first caged, but the weight was regained over a period of a few months (Anonymous⁵); therefore we do not think that tagging had any substantial effect on the growth rate of tagged fish in our study. With respect to the other assumptions, all fish were tagged with uniquely numbered tags. During tagging operations, tags were arranged in blocks of sequential numbers to avoid confusion and the misrecording of tag numbers. Return of the physical tag was required for fishermen to obtain the reward, and the double tagging of almost all fish since 1963 has allowed cross verification of tagging numbers, which allows little scope for error in the recording of tag numbers. Approximately 23% of the length measurements for the selected recaptured fish were measured by scientists. Mainly due to the deletion of short-term recaptured fish (i.e. < 270 days), this is less than that for all data (31%). For the fishermen-measured lengths, there was no reason to suspect any consistent bias, and comparison of the residuals for fishermen- and scientist-

⁶ Robins, J. P. 1963. Synopsis of biological data on southern bluefin tuna, *Thunnus thynnus maccoyii* (Castlenau) 1872. FAO Fisheries Report 6(2), p. 562–587. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

⁷ Hearn, W. S. 1982. Fish tagging: data processing, editing and storage. In CSIRO data base for southern bluefin tuna (*Thunnus maccoyii* (Castlenau)) (J. Majkowski, ed.), p. 8–9. CSIRO Marine Laboratories, Rep. 142. [Available from CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.]

measured returns in the fitted models below did not indicate any systematic pattern. The recaptured fish used in our study ranged in size from 60 to 175 cm, although the number of fish in the larger size ranges was relatively small—less than 2% were larger than 140 cm. (The consequences of the small number of fish in the large-size category are discussed below.) Within both the surface and longline fishery, a range of sizes and age classes is harvested within a single operation. No indication exists that within the size range encompassed by a cohort at a given age, there existed significant gear or fishery size selectivity. Overall, the above basic assumptions seem reasonable in modeling growth from these SBT tagging data.

Analytical methods

Models Two basic models were used to analyze growth information from the tag-return data. The first was the simple VBG model:

$$l_t = L_\infty \left(1 - e^{-k(t-t_0)}\right), \quad (1)$$

where L_∞ = the length that fish grow to asymptotically;
 l_t = the length of a fish at age (or time) t ;
 k = the exponential rate at which the growth rate slows; and
 t_0 = the hypothetical age (or time) when a fish is of length zero.

When applied to tag-return data, this equation can be used to predict the growth increment as a function of the length at release and the time at liberty:

$$\delta l = (L_\infty - l) (1 - e^{-k\delta t}), \quad (2)$$

where δl = the growth increment;
 δt = the time at liberty; and
 l = the length of release.

Note, in this study we simplified the growth model by not accounting for seasonal growth. However, data on recaptured fish with short times at liberty were specifically deleted to ensure that our results were robust after this simplification.

Preliminary analyses of the tag-return data suggested that a simple and time invariant von Bertalanffy growth model may not provide an adequate description of the growth rate for SBT. These preliminary analyses suggested

- 1 Growth rates in the 1960s and the 1980s were not equal;
- 2 There were systematic deviations from a VBG curve, possibly corresponding to different growth processes or models for adults and juveniles.

Consequently, in the present study, we considered a more complex model than the simple VBG and conducted separate, as well as combined, analyses of the tag data from the two periods. The more complex model selected was the two-phase growth model developed by Bayliff et al.

(1991). In this model, fish grow according to one model (or parameter set) up to a certain length and according to another thereafter. In our analyses, we assumed that fish have VBG throughout their lives but grow according to one set of VBG parameters ($L_{\infty 1}$ and k_1) up to length L^* and according to a second set ($L_{\infty 2}$ and k_2) at larger sizes, the two-phase VBG model. Thus, the predicted length as a function of time for this model is

$$l_t = \begin{cases} L_{\infty 1} \left(1 - e^{-k_1(t-t_0)}\right) & \text{for } t \leq t^* \\ L^* + (L_{\infty 2} - L^*) \left(1 - e^{-k_2(t-t_0)}\right) & \text{for } t > t^* \end{cases}, \quad (3)$$

where t^* = the predicted time for a fish to reach L^* .

Note that t^* can be solved for in terms of four of the parameters of the model (t_0 , k_1 , $L_{\infty 1}$, and L^*):

$$t^* = t_0 - \frac{1}{k_1} \log \left(1 - \frac{L^*}{L_{\infty 1}}\right), \quad (4)$$

where $t_0 = t_1 + \frac{1}{k_1} \log \left(1 - \frac{l_{t_1}}{L_{\infty 1}}\right)$,

and l_{t_1} = the length of a fish at the time of tagging, t_1 .

As with this simple VBG model, Equation 3 can be solved to predict the growth increment as a function of the release length and the time of liberty $\delta t = t_2 - t_1$:

$$\delta l = \begin{cases} (L_{\infty 1} - l_{t_1}) (1 - e^{-k_1 \delta t}) & \text{if } t_2 \leq t^* \\ (L^* - l_{t_1}) + (L_{\infty 2} - L^*) \left(1 - e^{-k_2(\delta t - (t^* - t_1))}\right) & \text{for } t_1 < t^* \text{ and } t_2 > t^* \\ (L_{\infty 2} - l_{t_1}) (1 - e^{-k_2 \delta t}) & \text{if } t_1 \geq t^*. \end{cases} \quad (5)$$

It should be noted that in some of the analyses considered below, the estimate of $L_{\infty 1}$ did not converge (i.e. the estimate for $L_{\infty 1}$ was essentially infinite). In such cases, the estimated growth rate is linear, with growth rate R_1 , and for the first phase we replaced the von Bertalanffy growth function with a simple linear one:

$$\delta l = R_1 \delta t,$$

and $t^* = t_1 - (L^* - l_{t_1})/R_1$. (6)

Model-fitting procedure A large body of literature exists on statistical approaches for estimating growth from tag-return data (e.g. Fabens, 1965; Sainsbury, 1980; Kirkwood and Somers, 1984; Francis, 1988; James, 1991; Hampton, 1991; Wang et al., 1995). The most appropriate approach depends on the error structure assumed for the model. We followed the maximum-likelihood approach and general error structure described by Hampton (1991). The measured growth increment of fish “ i ” is

$$\delta l_i = E[\delta l_i] + \varepsilon_i + e_i, \quad (7)$$

where ε_i is due to measurement error in the observed growth increment (i.e. the combined effect of any errors in measuring the lengths at the time of release and recapture) and e_i is due to process or model error. The latter may be a function of l_1 , δt , δl , and the model parameters.

For the measurement error component, we allowed for different variances, depending upon whether the recaptured fish was measured by an independent and scientifically trained individual or by a fisherman. Scientifically trained individuals (i.e. scientists) included fishery observers, port samplers, and CSIRO staff. We assumed that the measurement error was normally distributed, with mean zero and variance σ_x^2 , where x is one of f or s for recaptured fish measured by fishermen or scientists.

The choice of the functional form for the process error in growth models is a complex issue. One approach has been to consider that process error stems from variability among individuals in the expected value of the growth parameters (e.g. Sainsbury, 1980; Hampton, 1991; Wang et al., 1995). This approach in the case of the two-phase VBG model would result in many potential structures for the process error component because there could be individual variability in the expected value of any single or possible combination of parameters (of which there are 25 combinations). There is little theoretical basis for deciding which of these 25 combinations to use. As an alternative, we selected a more empirical approach. A function that increases with longer times at liberty seemed appropriate, and was also consistent with preliminary analyses. We explored both linear and quadratic functional relationships between the times at liberty and the process error component. The quadratic term was found to be insignificant, and therefore we chose to report only results for a simple linear functional relationship, namely $\sigma_m^2 \delta t$. Hence the corresponding variance of the expected growth increment of fish i is $V(\delta l_i) = \sigma_x^2 + \sigma_m^2 \delta t_i$. It should be noted that without independent data on measurement error any constant component in process error would be totally confounded with the measurement error term in the model. Therefore, σ_x^2 should be considered as a combined measurement and process error term. Both σ_x and σ_m were estimated empirically by maximum likelihood tag increment data.

Assuming a Gaussian error distribution, the likelihood function is

$$L = \prod_{i=1}^n \left\{ 2\pi V(\delta l_i) \right\}^{\frac{1}{2}} \exp \left\{ -\frac{\{\delta l_i - E[\delta l_i]\}^2}{2V(\delta l_i)} \right\}. \quad (8)$$

The estimates of the parameters are found by minimizing

$$-\ln(L) = \frac{1}{2} \sum_{i=1}^n \left[\log \{ 2\pi V(\delta l_i) \} + \frac{\{\delta l_i - E[\delta l_i]\}^2}{V(\delta l_i)} \right]. \quad (9)$$

The minimum value was obtained for all models by using the minimizing subroutine MINIMD (programmed by

D.E. Shaw, CSIRO Div. Maths. and Stats.), which uses the Nelder and Mead (1965) method.

Model selection The estimation of the full two-phase VBG models across both tagging periods contains 16 parameters (five model parameters plus three variance parameters for each time period). We examined a variety of alternative hypotheses to test whether the number of parameters could be reduced by eliminating some or equating them. For the model parameters, we considered whether the L_∞ or k terms were equal either between time periods or between the first and second phases within a time period. We also considered the simple VBG model, for which L^* doesn't exist.

For the L^* parameter, we considered whether the estimates were different between the two time periods. We also examined models in which the value of L^* was determined by assuming that the expected growth rate for a fish of length L^* was equal for both growth phases (i.e. by assuming that the changes in growth rates as a function of length is a continuous function). Under this assumption

$$L^* = \frac{L_{\infty 1} k_1 - L_{\infty 2} k_2}{k_1 - k_2}. \quad (10)$$

This model is referred to as the continuous rate two-phase model in the "Results" section. However, this model is not smooth because it has a discontinuity in the derivative of the growth rate at L^* . For the variance parameters, we considered whether any of them could be eliminated and also whether $\sigma_s = \sigma_f$. We used the log-ratio test and AIC criterion (Akaike, 1974) to identify the most parsimonious model.

Results

Best fits to the 1960s and 1980s data

Table 1 contains the maximum likelihood solutions for various assumptions when fitting growth models to either the 1960s or 1980s tag-return data separately. Using the AIC criteria, we found the best-fit model for the 1960s tag-return data was one with linear growth in the first phase and with the change between the two phases at approximately 74 cm (row 1, Table 1A). The fit to this model compared with all other parameter combinations yielded both the lowest AIC and negative log-likelihood values. The fit, however, was only marginally better than the fit (row 3, Table 1A) to the two-phase VBG curve with common k parameters (e.g. where the difference in the negative log-likelihood values is 1.21). Except for the first phase growth parameters, the estimates for the other parameters are nearly identical between these two models. This similarity reflects the fact that growth is nearly linear over the initial part of a VBG curve. Thus, by having a relatively high $L_{\infty 1}$ (271 cm), essentially similar growth rates can be achieved up through the 74 cm size range when $k_1 = k_2$, as compared with linear growth in the first phase. It should

Table 1

(A) Estimation of SBT growth parameters, and tests, from 1960s tag-return data with time at liberty of at least 270 days; (B) Estimation of SBT growth parameters, and tests, from 1980s tag-return data with time at liberty of at least 270 days. "na" = not applicable because this is the normal von Bertalanffy curve, i.e. with only one phase.

Common parameters	Number of parameters	$L_{\infty 1}$	k_1	$L_{\infty 2}$	k_2	L^*	σ_s	σ_f	σ_m	-Log likelihood	AIC
A											
none	6	22.23 ¹	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992	2055.53	4123.07 ²
$L_{\infty 1}=L_{\infty 2}$	6	212.73	0.1451	212.73	0.1044	75.75	0.000	3.134	2.999	2057.39	4126.77
$k_1=k_2$	6	271.35	0.1060	211.35	0.1060	74.71	0.000	3.130	2.997	2056.74	4125.49
$L_{\infty 1}=L_{\infty 2}$ $k_1=k_2$	5	172.67	0.1723	172.67	0.1723	na	2.201	3.782	2.855	2099.04	4208.08
continuous rate	6	114.14	0.4289	205.45	0.1128	81.55	0.000	3.203	3.021	2065.89	4143.78
$\sigma_m=0$	7	760.47	0.03425	191.33	0.1330	70.00	3.478	5.258	0.000	2088.19	4190.39
$\sigma_s=\sigma_f$	6	22.20	0.0000	209.65	0.1085	74.04	2.301	2.301	3.180	2068.33	4148.66
$\sigma_s=\sigma_f=0$	6	454.10	0.05660	214.26	0.1033	74.70	0.000	0.000	3.752	2071.57	4155.15
B											
none	8	226.70	0.1649	182.52	0.1841	84.90	2.305	4.501	3.018	4509.99	9035.97
$L_{\infty 1}=L_{\infty 2}$	7	183.09	0.2276	183.09	0.1832	85.65	2.266	4.497	3.031	4510.44	9034.88
$k_1=k_2$	7	210.24	0.1841	182.61	0.1841	84.99	2.276	4.492	3.030	4510.02	9034.03 ³
$L_{\infty 1}=L_{\infty 2}$ $k_1=k_2$	5	156.45	0.2884	156.45	0.2884	na	1.626	4.209	3.405	4530.88	9071.76
continuous rate	7	141.07	0.3590	182.25	0.1842	97.70	2.148	4.473	3.085	4514.54	9043.09
$\sigma_m=0$	6	206.71	0.1883	180.82	0.1883	84.85	4.149	5.920	0.000	4526.06	9064.11
$\sigma_s=\sigma_f$	6	210.74	0.1858	182.23	0.1858	85.36	3.948	3.948	3.183	4529.25	9070.49
$\sigma_s=\sigma_f=0$	5	209.46	0.1875	181.49	0.1875	85.30	0.000	0.000	4.737	4545.25	9100.49

¹ Here k_1 is zero, i.e. the growth rate is constant in the first phase; therefore we give the estimate of the growth rate instead of $L_{\infty 1}$.

² The least AIC value for estimates from the 1960s data. Na= not applicable because this is the normal von Bertalanffy curve, i.e. with only one phase.

³ The least AIC value for estimates from the 1980s data.

also be noted that the two-phase VBG model with common L_{∞} (row 2, Table 1A). was very similar to the common k parameterization, reflecting the high correlation between L_{∞} and k in the VBG models. For the 1960s, the continuous two-phase VBG model was rejected, $P < 0.005$ (row 5, Table 1A).

For the 1980s data, the best-fit model based on the AIC values was for the two-phase VBG model with a common value for the k parameter in both phases (row 3, Table 1B). The estimate of the size at which the change between the two phases occurs was 85 cm (compared to the estimate of 74 cm for the 1960s data). As with the results of the 1960s data, the common- k model, common- L_{∞} model, and the full two-phase model yielded very similar values for both the likelihood and parameter estimates in the second phase, but not for those in the first phase. This similarity reflects the high correlation between k and L_{∞} in the VBG model, so that over the limited size range below L^* nearly identical growth rates can be achieved in the common- k model by decreasing the value of $L_{\infty 1}$. For the 1980s (as with the 1960s), the continuous two-phase VBG model (7 parameters), was rejected, $P < 0.005$ (row 5, Table 1B).

For both the 1960s and 1980s data, the two-phase model provided a substantially and significantly better fit to

the tag return data than a simple VBG model. This can be seen in Table 1 (A and B) by comparing the negative log-likelihood and AIC values for the simple VBG model (row 4) with any that include a two-phase component, particularly the continuous rate two-phase VBG model. We also fitted a smooth Richards' (1959) growth model (a generalization of the VBG model) to the data, which fitted better than the simple VBG model, but worse than the two-phase VBG models.

Note, however, that the log-ratio test and AIC criterion may not be fully applicable for testing the differences between the simple and two-phase VBG models because the simple VBG model can arise in more than one way as a submodel of the two-phase model (e.g. with common L_{∞} and k parameters or from L^* equaling zero or infinity) (Davies, 1977, 1987). Nevertheless, the large magnitude of the differences in the log-likelihood values indicates a significance difference.

For the 1960s data, it should be noted that the scientist measurement error (σ_s) was estimated to be essentially zero when it was included as an explicit term in several of the models. In these cases, we refitted the models excluding this parameter. Common sense dictates that measurement errors would not be zero. The most informative data

Table 2

Comparison of SBT growth parameter estimates for the 1960s and 1980s, between absolute maximum likelihood and local maxima likelihood.

Common parameters	Number of parameters	$L_{\infty 1}$	k_1	$L_{\infty 2}$	k_2	L^*	σ_s	σ_f	σ_m	-Log likelihood	AIC
1960s											
none	6	22.23 ¹	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992	2055.53	4123.07
none	8	118.08	0.3957	186.04	0.1500	91.23	1.061	3.398	2.855	2062.76	4141.51
1980s											
$k_1=k_2$	7	210.24	0.1841	182.61	0.1841	84.99	2.276	4.492	3.030	4510.02	9034.03
$k_1=k_2$	7	145.37	0.3371	169.03	0.3371	120.47	2.293	4.514	3.025	4512.98	9039.96

¹ Here k_1 is zero, i.e. the growth rate is constant in the first phase; therefore we give the estimate of the growth rate instead of $L_{\infty 1}$.

on measurement error would come from fish with short times at liberty because in these cases the amount of process error would be small. However, as explained above, fish with times at liberty of less than 270 days were excluded to eliminate seasonal effects. Process and measurement errors are partially confounded in the model. The estimation procedure could not distinguish an additional constant component to the linear, temporally increasing process error from the measurement error for recaptured fish measured by scientists. For the 1980s data, the estimation procedure was able to estimate a nonzero value for the scientist measurement error. The results for the 1980 returns suggest that the measurement error for the scientist was about 50% of that for fishermen.

For both the 1960s and 1980s data, the estimation procedure is able to distinguish between fishermen and scientist measurement error. The assumption that the measurement error of fishermen and scientists are the same is rejected by a statistical test (i.e. the second last line of both Table 1, A and B).

Examination of the residuals indicated no systematic lack of fit in either the 1960s or 1980s data (Fig. 1, A–D).

Shape of the likelihood function

It is worth noting that the likelihood function is bimodal with respect to the parameter determining the length at which growth changes between the two phases (L^*). Figure 2 shows the negative log-likelihood ($-LL$) values as a function of L^* for the 1960s and 1980s data for the best-fit model. For the 1960s data, the $-LL$ function has an absolute minimum at $L^* = 74$ cm and a second, local minimum at $L^* = 91$ cm. For the 1980 data, the absolute minimum occurs at $L^* = 85$ cm and the second, local minimum at $L^* = 120$ cm.

Monte Carlo and bootstrap simulations were conducted to evaluate the bimodal nature of the likelihood function. The Monte Carlo simulations were done by assuming the two-phase VBG growth model and were conditional on the SBT release lengths. Both types of simulations confirmed that the minima with the lowest absolute value for the

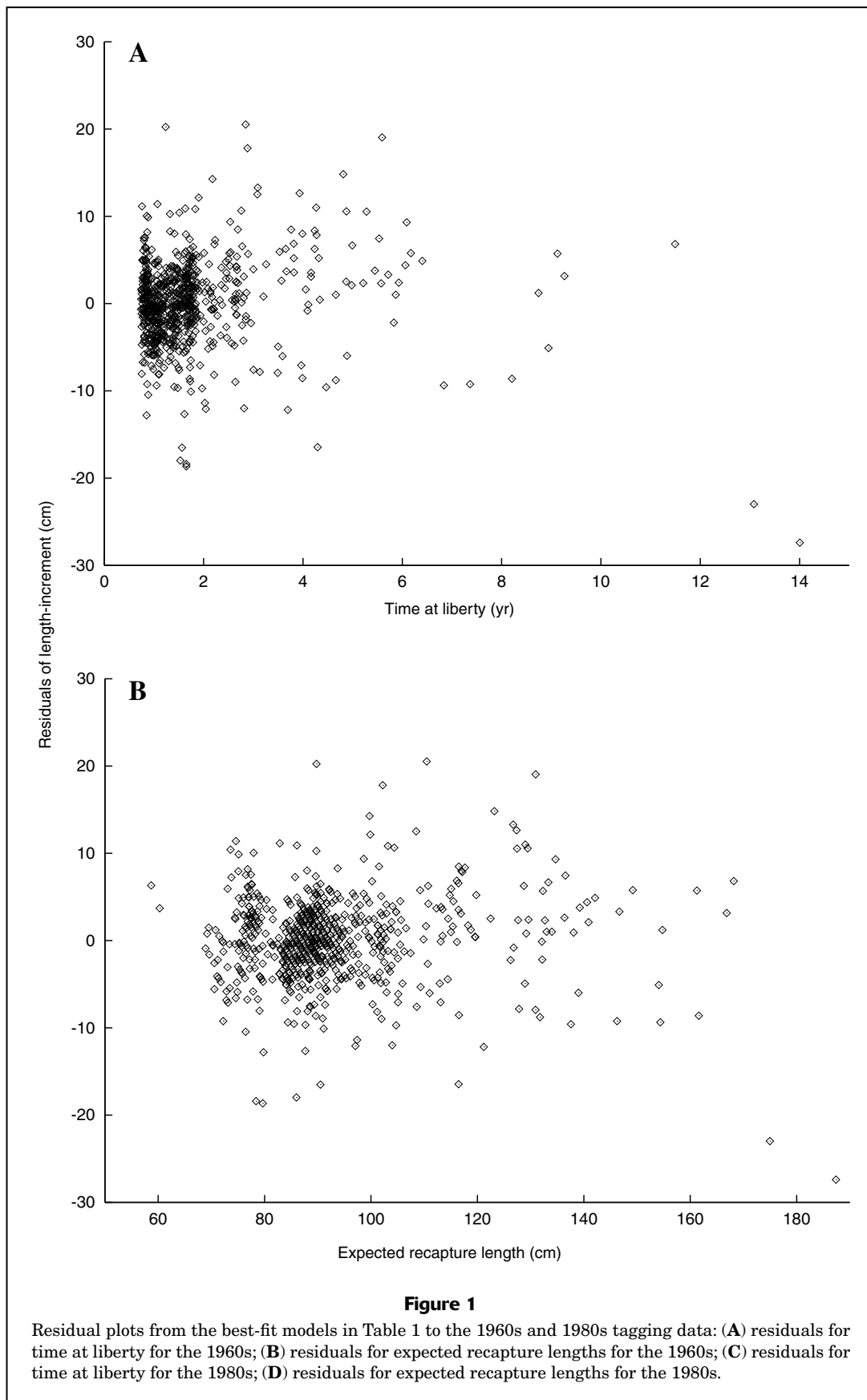
negative log-likelihood function would switch between individual realizations within the simulations. Only the results of the bootstrap simulations are presented in this article. These were based on 1000 individual simulations for which the tag increment data were randomly sampled with replacement. For each individual simulation, the value of L^* that yielded the absolute minimum value for the negative log-likelihood function was determined. For the 1960s data, the best-fit estimate of L^* was near 74 cm in 930 of the simulations and 91 cm in 70. For the 1980 data, the absolute minimum in the negative log-likelihood function occurred 767 times when L^* was near 85 cm and 233 times when L^* was near 120 cm (Fig. 3). Thus, although the lower value for L^* was the most likely for both the 1960s and 1980s data, the 95% confidence intervals based on the bootstrap results would encompass both values. The estimated value of the other parameters determining the expected growth curve are correlated with that of L^* . Thus, the alternative minima in the log-likelihood function are associated with substantially different estimates for the k and L_{∞} parameters (Table 2). This in turn has implications for possible biological interpretations of the parameter estimates (see below).

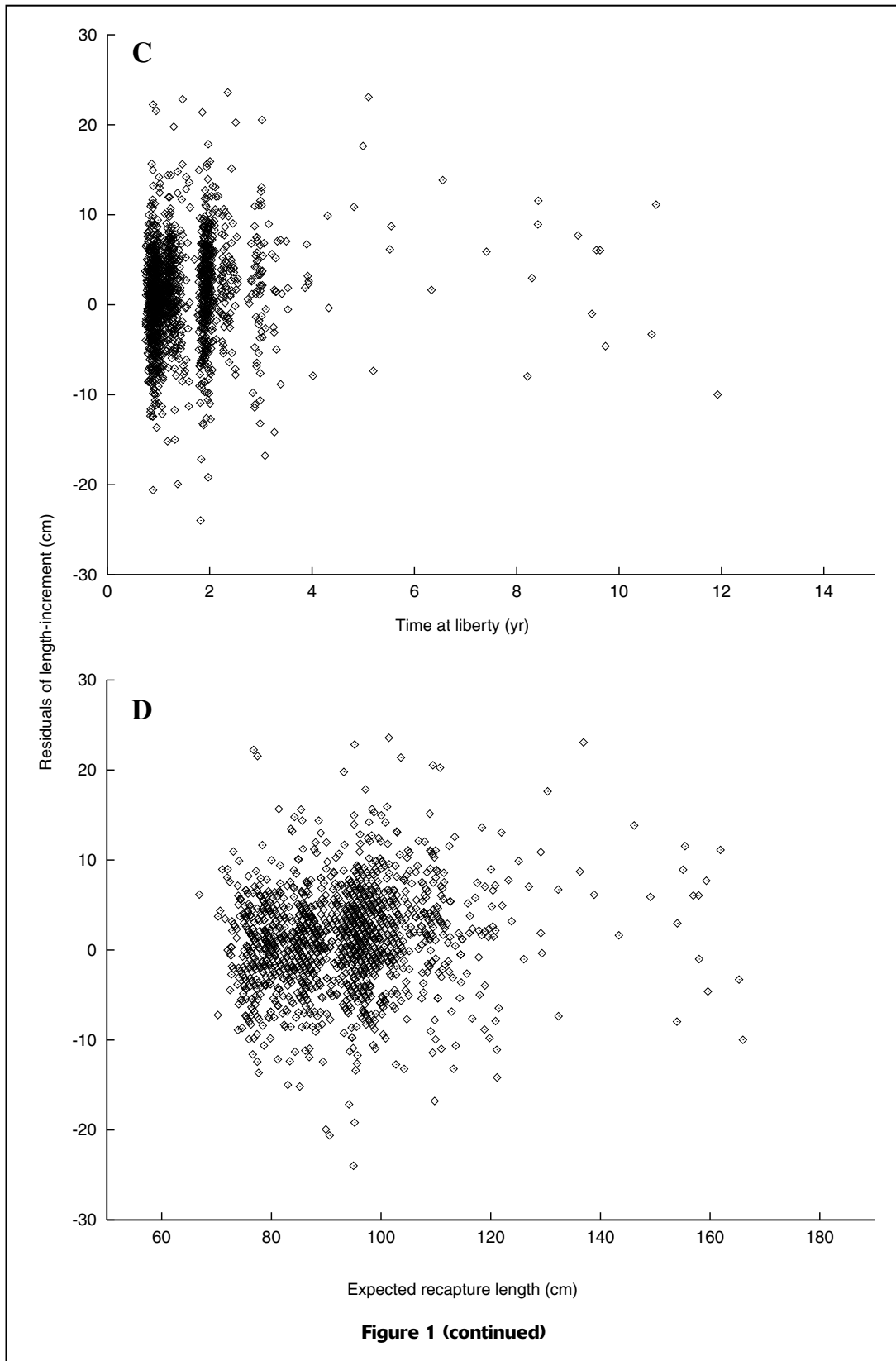
Joint analyses of the 1960s and 1980s data

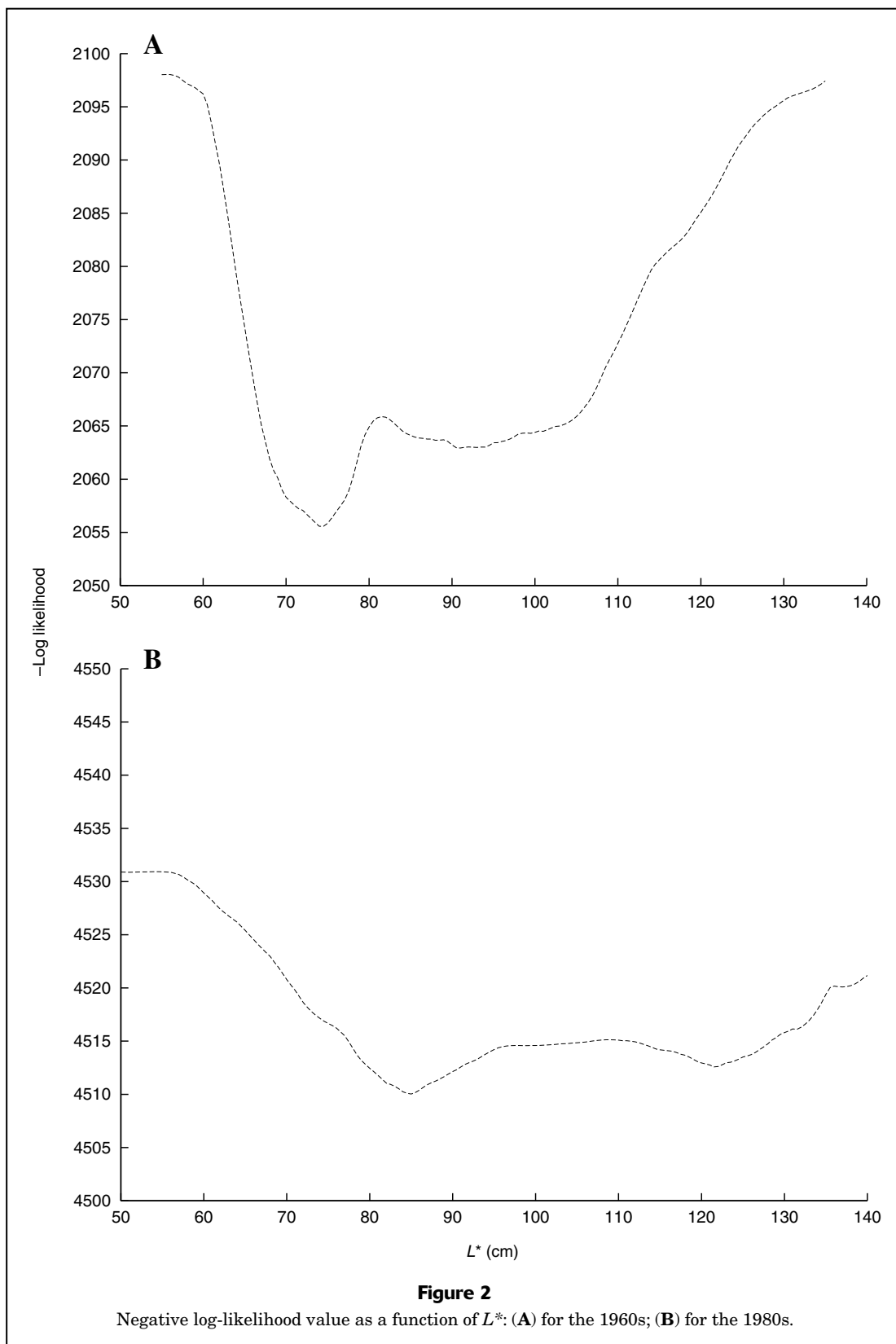
Results of jointly modeling the 1960s and 1980s tag return data to test for common parameters are presented in Table 3. The model error (σ_m) was the only parameter found not to be significantly different in the combined analyses. Having a single parameter value for the model error component had virtually no effect on the parameters determining the expected growth rates, compared to those estimated in the separate analyses.

Comparison of 1960s and 1980s growth rates

The fact that all of the parameters that describe the expected growth rates significantly differ for the 1960s and 1980s data indicates that SBT growth rate changed between these two periods. For the best-fit solutions, the







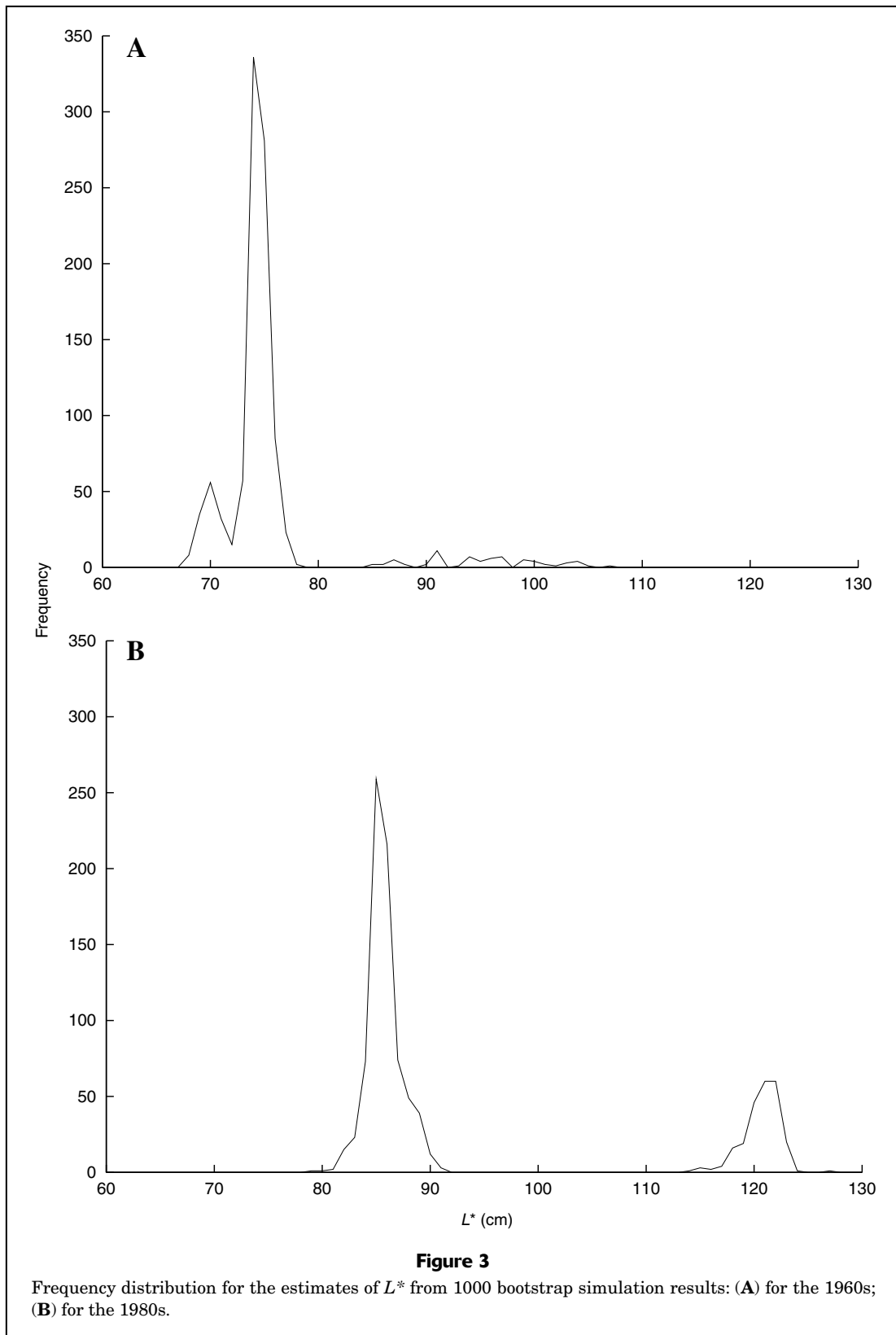


Table 3
Southern bluefin tuna growth parameters and tests, from jointly analyzing the 1960s and 1980s data.

Common parameters	Number of parameters	$L_{\infty 1}$	k_1	$L_{\infty 2}$	k_2	L^*	σ_s	σ_f	σ_m	-Log likelihood	AIC
none (60) (80)	13	22.23 ¹	0.0000	210.90	0.1063	74.24	0.000	3.122	2.992	6565.55	13157.10
		210.24	0.1841	182.61	0.1841	84.99	2.273	4.496	3.030		
$\sigma_m 60 = \sigma_m 80$	12	22.23	0.0000	210.98	0.1062	74.25	0.000	3.115	2.998	6565.56	13155.11
		210.31	0.1840	182.67	0.1840	85.00	2.309	4.514	2.998		
$L60_{\infty 1} = L80_{\infty 1}$	12	213.29	0.1462	210.49	0.1069	75.03	0.000	3.133	3.001	6567.43	13158.85
		213.29	0.1804	184.20	0.1804	85.00	2.323	4.518	3.001		
$L60_{\infty 1} = L60_{\infty 2} = L80_{\infty 1}$	11	211.41	0.1480	211.41	0.1060	75.08	0.000	3.128	3.004	6567.44	13156.87
		211.41	0.1827	183.24	0.1827	85.00	2.315	4.515	3.004		
$k60_1 = k80_1$	12	185.24	0.1804	210.46	0.1069	75.11	0.000	3.119	3.008	6568.07	13160.15
		213.26	0.1804	184.21	0.1804	85.01	2.325	4.510	3.008		
$L60_{\infty 2} = L80_{\infty 2}$	11	22.20	0.0000	195.25	0.1232	73.74	0.000	3.120	3.010	6568.89	13159.78
		233.55	0.1584	195.25	0.1584	85.22	2.302	4.516	3.010		
$k60_2 = k80_2$	11	23.85	0.0000	186.76	0.1374	70.48	0.000	3.097	3.044	6575.52	13173.03
		258.76	0.1374	207.04	0.1374	86.23	2.262	4.495	3.044		
$L^* 60 = L^* 80$	12	110.51	0.4707	196.71	0.1269	85.45	0.000	3.196	3.014	6574.09	13172.19
		211.13	0.1827	182.97	0.1827	85.45	2.306	4.505	3.014		
$\sigma_s 60 = \sigma_s 80$	12	22.22	0.0000	210.59	0.1072	74.10	1.602	3.023	3.068	6570.46	13164.92
		209.66	0.1842	182.49	0.1842	84.94	1.602	4.472	3.068		
$\sigma_f 60 = \sigma_f 80$	11	22.28	0.0000	210.43	0.1064	74.23	0.000	4.174	2.975	6577.96	13177.91
		210.40	0.1844	182.62	0.1844	85.02	2.394	4.174	2.975		

¹ Here k_1 is zero, i.e. the growth rate is constant in the first phase; therefore we give the estimate of the growth rate instead of $L_{\infty 1}$.

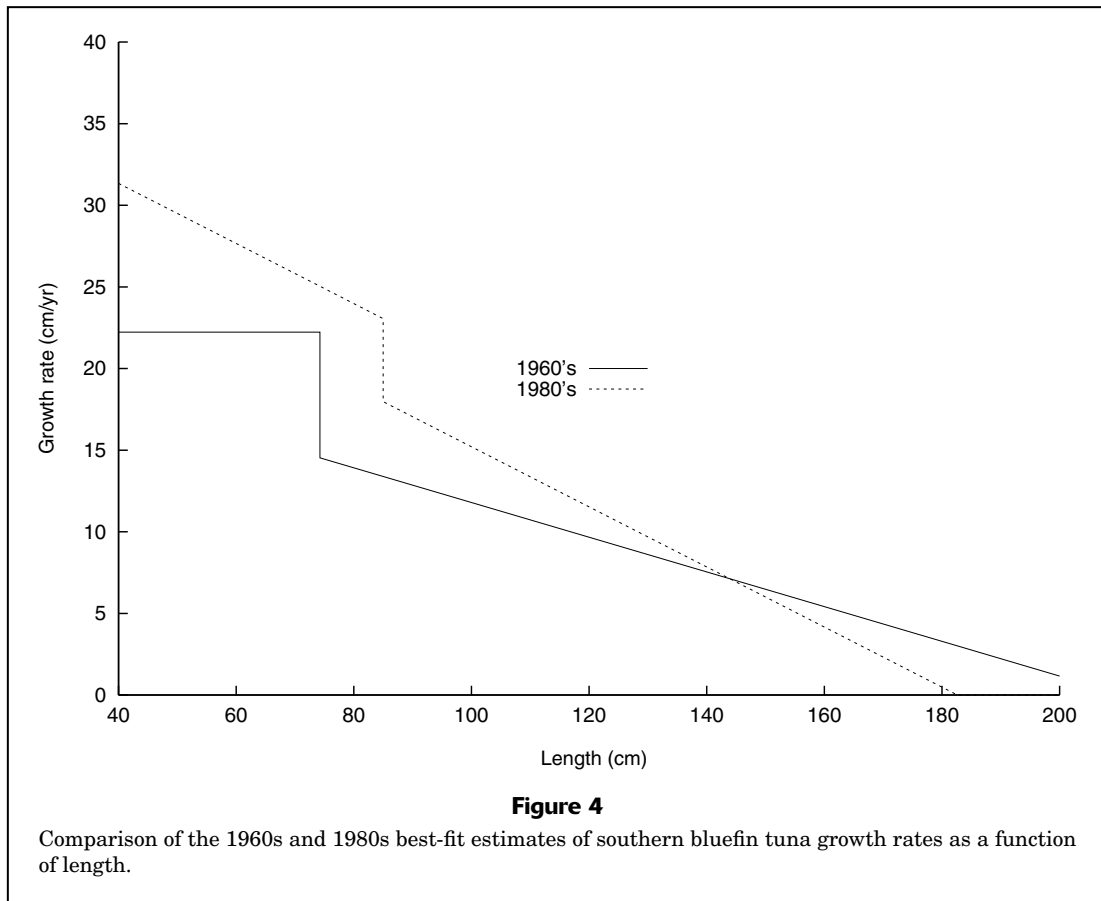
SBT growth rates in the 1960s are estimated to be less than those in the 1980s up to 144 cm (Fig. 4). Comparison of the 1960s and 1980s expected growth curves over time for a 55-cm fish are presented in Figure 5. In making this comparison, we assumed that a 55-cm fish is approximately one year of age (Anonymous⁵) and that size at age one did not change between the 1960s and 1980s, as supported by length-frequency data from these two time periods (Leigh and Hearn, 2000; Anonymous⁵). Thus, Figure 5 can also be considered as an estimate of the expected length-at-age curve. Figure 5 indicates that the overall expected growth was significantly faster in the 1980s than in the 1960s, so that a fish of 55 cm or age 1 would take approximately four years in the 1960s to achieve the same length that would have been achieved in three years in the 1980s.

A feature of the best-fitted estimated growth parameters is that the expected growth curves intersect at ~170 cm, so that after age 13 a fish from the 1960s is estimated to be larger than a fish from the 1980s. This crossover is driven primarily by the difference in the estimates of $L_{\infty 2}$. The standard log-likelihood test indicates a low probability, $P=0.01$, that $L_{\infty 2}$ for the 1960s and 1980s are the same. However, the analyses of the bootstrap estimates of $L_{\infty 2}$ indicate that the estimates are bimodal, reflecting the bimodal distribution of L^* . Random sampling from the boot-

strap distributions for $L_{\infty 2}$ showed that in 6.1% of cases the 1960s $L_{\infty 2}$ estimate was less than the 1980s estimate. For a two-sided test at the 5% significant level, at least 2.5% (and at most 97.5%) of the bootstrap samples would have been expected to have the 1960s $L_{\infty 2}$ less than that of the 1980s to justify the hypothesis that the two $L_{\infty 2}$ are equal. Thus, based on the bootstrap results, the hypothesis of equality cannot be rejected. Most of the 6.1% of cases are associated with the 1960s $L_{\infty 2}$ less than 180 cm, which are in turn associated with the upper mode of L^* in Figure 3A, i.e. near $L^* = 91$ cm. It is worth noting that only three recapture lengths were greater than 170 cm. There are, therefore, very minimal data for estimating growth rates beyond 170 cm and for precisely estimating $L_{\infty 2}$.

Discussion

The results in this study indicate that the traditional VBGM model does not provide an adequate representation of growth in SBT. There appears to be a significant change in the pattern of growth in relation to a VBGM curve during the juvenile stages of the SBT life cycle. This, in turn, may be related to the transition from a tightly schooling fish that spends substantial time in near and surface shore waters



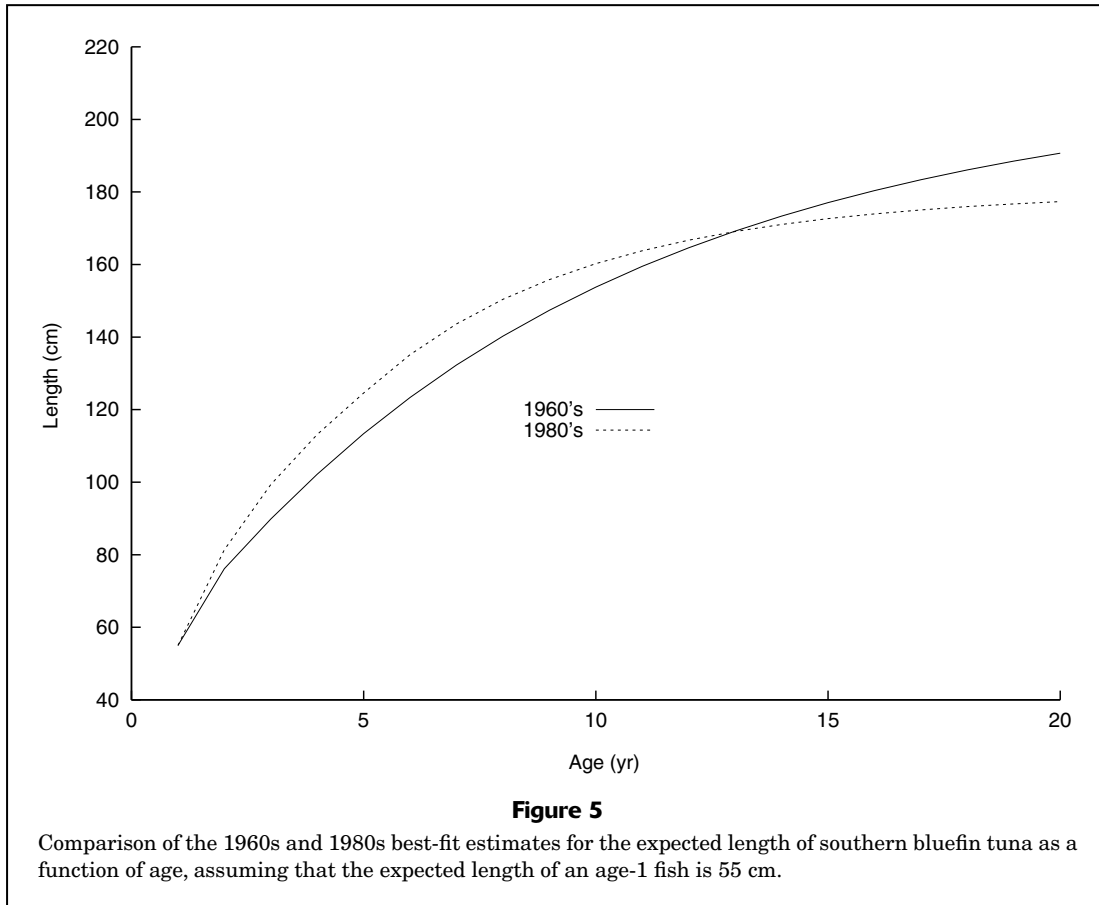
to one that is found primarily in more offshore and deeper waters. In this regard, recent information from archival tags indicates that SBT between 80 and 90 cm (about two to three years old) commonly migrate during winter months to offshore oceanic waters in the Indian Ocean and the Tasman Sea and begin to feed at substantial depth (Gunn and Block, 2001). In contrast, catches and samples off Albany, Western Australia, show that many SBT less than 70 cm stay in nearshore Australian waters during winter (Hynd, 1965; Murphy⁸; and release data analyzed in this study). Thus, the growth changes estimated to be near $L^* = 80$ cm may correspond to a marked change in the SBT behavior during these winter months.

The von Bertalanffy growth equation and its modifications have been the standard for modeling tuna growth. The life history dynamics for most tuna species (e.g. north Pacific bluefin, albacore, bigeye, and yellowfin tuna) have a bimodal component analogous to that of SBT. Thus, juveniles are frequently found in densely packed surface schools, whereas at larger sizes individuals are rarely found near the surface and appear not to occur in densely

packed schools (although there is little direct information on schooling for these larger fish). Moreover, mature tuna expend considerable energy in the spawning process, and in some cases swim thousands of kilometers and incur considerable weight losses during spawning (Warashina and Hisada, 1970). Bayliff et al. (1991) also found that growth models with a rate discontinuity at a certain size provided a better fit to Pacific northern bluefin tuna tag-return data than a simple continuous growth model. The extent to which this may be a general phenomenon in tuna or other fish species with marked changes in habitat use with age is not clear. However, the results from our study and those of Bayliff et al. (1991) suggest that a growth rate with a discontinuity at a certain size may be more common than existing modeling of growth may indicate. Complex growth models, which deviated from a simple continuous growth curve, have generally not been considered, and the available data, in many cases, may not have sufficient power to be able to statistically identify more complex growth processes if they exist.

Although the complex two-stage growth model used in our study clearly provided a substantial and significant improvement in fit to the growth-increment data, the model itself presents problems in terms of the biological interpretation of the parameter estimates for L^* . The bimodal nature of the likelihood function means that the size and

⁸ Murphy, G. I. 1979. Southern bluefin tuna. Aust. CSIRO Div. Fish. Oceanogr. Fishery Situation Report 1, 10 p. [Available from CSIRO Marine Research, GPO Box 1538 Hobart 7000, Australia.]



age where the change in growth occurs is not well defined. This, in turn, confounds the evaluation of the plausibility of different specific possible biological hypotheses underlying the change. Moreover, although the change in growth patterns may be quite rapid, a large discontinuity in the growth rates at a specific length seems unrealistic. The continuous two-stage VBG model did not fit the 1960s and 1980s data as well as the discontinuous two-stage VBG models. However, the two-phase VBG models fitted the data better than the simple von Bertalanffy growth curve (Table 1, A and B) and its generalization—the simple Richards' (1959) curve (senior author, unpubl. results).

From both the statistical estimation and biological perspective, we think there is scope for the development of more appropriate complex growth models. In this context, there is also need for the development of estimation procedures for these complex models that can take into account alternative error structures that allow for individual variability in the growth rate parameters (e.g. Sainsbury, 1980; James, 1991; Wang et al., 1995).

In the joint analysis of the 1960s and 1980s data, σ_m was the only parameter found not to be significantly different between the two data sets. However, caution is warranted in any comparison and interpretation of growth curves determining parameter values because of the well-known negative correlation between k and L_∞ of the VBG growth

model and the bimodal nature of the likelihood surface, as already noted. In particular, the differences in the estimates of $L_{\infty 2}$ should not be taken as strong evidence that the asymptotic growth of SBT decreased or that there was a crossover in the growth rates. These complex growth changes are difficult to explain from a biological perspective and, as noted above, the bootstrap results indicate that the hypothesis that the $L_{\infty 2}$ parameters are equal cannot be rejected. Moreover, we would note that there is a paucity of tag return data for larger fish. A total of only seven tags were recovered from fish with lengths exceeding 165 cm and only three for fish with lengths in excess of 170 cm. Fitting VBG models does not provide reliable estimates of growth when extrapolated beyond the range of the data because of the large negative correlation between k and L_∞ . We, therefore, do not think that the current data are sufficient to determine whether, in fact, $L_{\infty 2}$ differed between the 1960s and 1980s.

One of the primary applications of the estimated SBT growth curves is to provide estimates of the age distribution of commercial catch in stock assessments based on catch-at-age analyses (e.g. Anonymous⁸). The predicted growth curves (assuming that an age-1 fish is 55 cm) indicate that the estimated ages of 165-cm fish have diverged by about a year for the curve based on a common $L_{\infty 2}$ compared with those for which $L_{\infty 2}$ is allowed to differ

between the 1960s and 1980s. For smaller sizes, the divergence is substantially less (e.g. for fish 140 cm or less the divergence is less than three months). In terms of using the growth rate data to estimate ages from lengths, these results indicate that for the older reproducing fish the results will be highly sensitive to assumptions about $L_{\infty 2}$.

The results from these tagging studies clearly show that growth rates for SBT hatched in the 1980s had increased in relation to those cohorts hatched in the 1960s. The increase in growth rates is substantial, so that a fish, on average, would have been expected to take four years to grow from 55 cm to 111 cm in the 1960s, but only three years to do so in the 1980s. In other words, after age 4 there is a difference of about one year in the expected age of a fish of similar length, and this difference persisted over the size range for which meaningful recapture data were available. The change in growth and its magnitude are consistent with the analyses in Leigh and Hearn (2000) of the modes in length-frequency distributions of juvenile fish captured in the Australian surface fishery. The underlying causes of the change in SBT growth rates are unknown. They could be associated with changes in environmental conditions, population size, or a combination of the two. The change in SBT growth rates between the 1960s and 1980s is associated with very substantial declines in both the adult and juvenile components of the SBT stock (Polacheck et al.¹; Anonymous⁹).

There is an increasing number of examples in which growth rates have been reported to be inversely correlated to fish population numbers because of intraspecific competition. For example, Le Cren (1958) documented an increase in the growth rate of perch after a planned reduction of a lake population. In a converse case, Kaeriyama (1996) reported a decline in the growth rate of Japanese chum salmon following a many-fold increase in its population size because of a most successful hatchery enhancement scheme. Other accounts are published in Southward (1967), de Veen (1976), Toresen (1990), Ross and Nelson (1992), and Sinclair and Swain (1996). However, the reports are mainly on species for which direct aging data are reliable and regularly collected over a lengthy period, or the fish are hatchery reared.

The hypothesis that the increase in SBT growth rates was the result of the marked reduction in SBT population size would seem plausible, given the similar associations that have been found in a number of fisheries phenomena. As discussed in Leigh and Hearn (2000), changes in juvenile SBT growth rates based on analyses of length-frequency data are also consistent with the change having a density-dependent component. In this regard, it is worth noting that preliminary analyses of tag return data from the 1990s indicate that growth rates in the 1990s were similar to those in the 1980s (Polacheck and Preece¹⁰). Thus, these preliminary results are also consistent with the change in growth being a density-dependent response

as both juvenile and adult SBT abundances remained at low levels during this period (e.g. Anonymous⁹; Polacheck and Preece¹⁰). Large uncertainty exists about possible recovery of the SBT stock in the near future (e.g. Anonymous⁹), but continued monitoring of SBT growth may provide one indicator of stock recovery.

To simplify our investigation we did not consider seasonal growth. We avoided possible bias, due to seasonal growth, by analyzing data only from fish with times at liberty more than or equal to 270 days. This restriction provided an efficient mechanism to focus on the long-term growth process and was effective because the resultant sets were large. Large numbers of recaptured fish with reliable information and times at liberty more than 9 months seem rare for other tunas, in which case the added complication of accounting for possible seasonal growth would be required to ensure the robustness of the results.

The analyses in this paper represent the first documented examples of substantial temporal changes in growth rates that persisted for an extended portion of the life span in a large pelagic tuna resource. For tuna stocks in general, estimates of growth rates play a major role in stock assessments and in the subsequent management advice derived from these assessments.

Acknowledgments

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⁹ Anonymous. 1998. Report of the 1998 Scientific Committee meeting 3–6 August 1998, Tokyo, Japan. [Available from the Commission for the Conservation of Southern Bluefin Tuna, PO Box 37, Deakin West, ACT 2600, Australia.]

¹⁰ Polacheck, T., and A. Preece. 1998. Preliminary comparisons of the growth rates of southern bluefin tuna in the 1990s with those in the 1960s and 1980s. Tenth SBT recruitment monitoring workshop, 14–17th September 1998, Hobart, Australia. RMWS/98/5, 11 p. [Available from CSIRO and the Commission for the Conservation of Southern Bluefin Tuna, P.O. Box 37, Deakin West, ACT 2600, Australia.]

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