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## Changes in growth of juvenile southern bluefin tuna (*Thunnus maccoyii*): an analysis of length–frequency data from the Australian fishery

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**Abstract.** Modal analysis is applied to historical length–frequency records of the Australian southern bluefin tuna fishery, in order to quantify the variation in mean length from year to year. In the South Australian fishery in the first half of March, the mean length has ranged between 54 cm and 64 cm for 1-year-old fish, 73 cm and 85 cm for 2-year-old fish, and 85 cm and 100 cm for 3-year-old fish. The mean lengths of 2-, 3- and 4-year-old fish, and the increment from age 1 to age 3, have increased substantially over the history of the fishery. This increase in growth is probably a response to a decline in the population due to heavy fishing. In many years in the Western Australian fishery, two or more groups of 1-year-old fish were found: the mean lengths of these groups typically differed by 10 cm. Growth rates also varied markedly according to the season of the year.

### Introduction

Growth of southern bluefin tuna, *Thunnus maccoyii* (Castlenau) has long been recognized as highly variable (Serventy 1956; Hearn 1986; Hampton 1989; Hearn and Hampton 1990). This paper aims to incorporate year-to-year variation in growth into a length–frequency analysis, so as to (a) identify the growth patterns and changes that have occurred over the history of the commercial fishery, and (b) assign ages to catches of fish.

Southern bluefin tuna is a highly migratory species that lives to ~40 years of age and begins to spawn at ~10–12 years of age in waters south of Java (Farley and Davis 1998). A major Australian fishery is based on harvesting juveniles, aged from 1 to 5 years. This fishery has historically consisted of three distinct regional fisheries, in coastal waters off Western Australia, South Australia, and New South Wales. Beyond about 5 years of age, the fish live permanently in oceanic waters, where they are caught by Japanese long-line vessels. Reviews of this species and its fisheries are given by Shingu (1978), Olson (1980), Hampton and Majkowski (1986) and Caton (1991).

Reliable estimates of ages and growth rates of southern bluefin tuna are required for an understanding of its biology, ecology and productivity (Serventy 1956; Yukinawa 1970; Murphy 1977; Murphy and Majkowski 1981; Hampton *et al.* 1984). Catch-at-age statistics are the primary input into stock assessments by virtual population analysis, which is the principal method currently used to assess the resource of southern bluefin tuna. Understanding the degree of variability in growth, and the factors underlying such changes, is impor-

tant when trying to evaluate both short- and long-term effects on yield, spawning biomass, and recruitment.

Changes in growth rates from the 1960s to the 1980s might be expected from a decline in total population size. Mounting evidence suggests that fish population size and growth rates are inversely correlated because of intra-specific competition. For example, Le Cren (1958) reports that the growth rate of perch increased after a lake population was deliberately reduced. In a converse case, Kaeriyama (1996) documents the decline in the growth rate of Japanese chum salmon following a many-fold population increase. Other accounts are found in de Veen (1976), Schmitt and Skud (1978), Toresen (1990), Ross and Nelson (1992) and Sinclair and Swain (1996). Evidence for a decline in the southern bluefin tuna population comes from (i) the fall in annual Australian catch from a peak of 81 605 t in 1960 to 36 930 t in 1984 (Caton 1991, table 12), (ii) the catch rate per hook of the Japanese long-line fishery falling seven fold (Caton 1991, table 15), and (iii) recent analysis of catch-at-age statistics (virtual population analysis) indicating that the southern bluefin tuna spawning biomass in the 1990s is between 10% and 20% of its 1960s level (Polacheck *et al.* 1999).

This paper refers solely to the Australian fishery. There, rapid growth of younger fish, very frequent representative sampling of catches, and accurate measurement of lengths to within one centimetre (Majkowski 1982) enable extraction of information on age and growth. The age at which fish enter the Australian fishery was revised downwards by one year by Gunn *et al.* (1995) on the basis of daily rings observed in otoliths.

Length–frequency measurements constitute the only source of age and growth information that fully covers the history of the Australian fishery. We recognize that the measurements are subject to errors from non-random sampling, migration and size-selectivity. Nevertheless, since other sources cover only part of the history, analysis of the length–frequency data must play a significant part in drawing conclusions about changes that have taken place in the fishery.

The method that is currently used to divide the catches of southern bluefin tuna into age-classes relies on knife-edged partition using a growth curve for predicting age from length: for example, a fish is classified as being two years old at 1 January if its length is between those for a 1½-year-old fish and a 2½-year-old one. This method, described in detail by Majkowski and Hampton (1983, p. 275), allows for changes in length with time of year, but makes no allowance for variation in ages of fish of the same length, year-to-year variation, or departure from the growth curve. It tends to underestimate differences in year-class numbers (Anon. 1994), a problem avoided in this paper. Analyses to 1993 used the growth curve of Kirkwood (1983, table 1 line ‘A combined’) that was derived from both length–frequency and tagging data collected during the 1960s and 1970s. Since then, the curves used are those developed at an international workshop (Anon. 1994) which allow for a two-stanza growth model and changes in growth rates between the 1960s and 1980s, but they do not account for seasonal growth. The changes in growth rates between the decades are represented by two growth curves (the 1960s and 1980s curves) that were derived from information on fish that were tagged during the 1960s (with birth years mainly 1960 to 1967) and 1980s (with birth years mainly 1981 to 1983).

The estimation of age-class parameters by fitting a mixture model to a length–frequency sample goes back many years (Hasselblad 1966; Macdonald and Pitcher 1979; Schnute and Fournier 1980). Fournier *et al.* (1990) developed the MULTIFAN method to simultaneously analyse many samples taken at different times.

We follow the general approach of Fournier *et al.* (1990), but differ from them in many respects. MULTIFAN, in common with Schnute and Fournier (1980), constrains all the means from different cohorts to lie on a single von Bertalanffy growth curve (Anon. 1992, section 5.4, assumption 2), but we do not. We link only mean lengths of fish of the same age at various times in the same year. We understand that it is possible for the MULTIFAN user to except some means from lying on the curve; however, we still consider it too restrictive for a growth curve to link mean lengths of fish of different ages in the same year. The ages belong to different cohorts with possibly different mean birth times and growth histories. The primary purpose of this manuscript is not to carefully compare our approach with MULTIFAN, but to assess changes in the growth rate of southern bluefin tuna.

## Materials and methods

### *Length–frequency records, sampling and hypothesis testing*

The length–frequency database of southern bluefin tuna catches by the Australian fisheries is described by Majkowski (1982), Majkowski and Morris (1986) and Caton (1991, p. 263). The records cover each half-month that fish were caught, from 1963 (soon after the commercial fishery began) to 1992, for the three regions: South Australia, New South Wales and Western Australia. In our analyses we exclude data since 1992 because of keen targeting by Australian fishers on large 3-year-old (and older) fish for the Japanese sashimi market or to fatten in tuna farms for this market (i.e. few one- and two-year-olds are caught). This length selection (*i*) may distort the mode of 3 year olds, leading to a false impression about recent changes in length-at-age and (*ii*) gives no information about cohort growth increments from one age to another.

Not all fish caught were measured for length, but all were weighed in bulk, and the length–frequency samples were scaled up during the collection process so as to estimate the length–frequency distribution of the whole fishery. However, the scaling up introduces sampling problems into the analysis, and in particular makes hypothesis testing difficult because parameter estimates appear to be more accurate than they actually are. Moreover, the scaling was performed in two stages: first, a sample that was measured was scaled by the weight of fish caught by the sampled boat; and secondly, catches from sampled boats were scaled by the weight of the entire catch of the fishery in a particular half-monthly sampling period, so as to allow for boats that were not sampled. Also, very few samples were taken in some sampling periods in which little fishing activity took place, and results for these periods were inferred from other periods.

These problems prevent hypothesis tests from being statistically valid if only the scaled-up data are available. Approximate standard errors for parameter estimates can be calculated from the smoothness of the length–frequency histograms: a smooth histogram is considered to be fairly precise, and produces small standard errors, whereas a rough histogram is subject to much uncertainty and produces large standard errors. Fournier *et al.* (1990) used this approach in their hypothesis tests. However, given the two-stage nature of the scaling, such tests and standard errors can be only a rough guide.

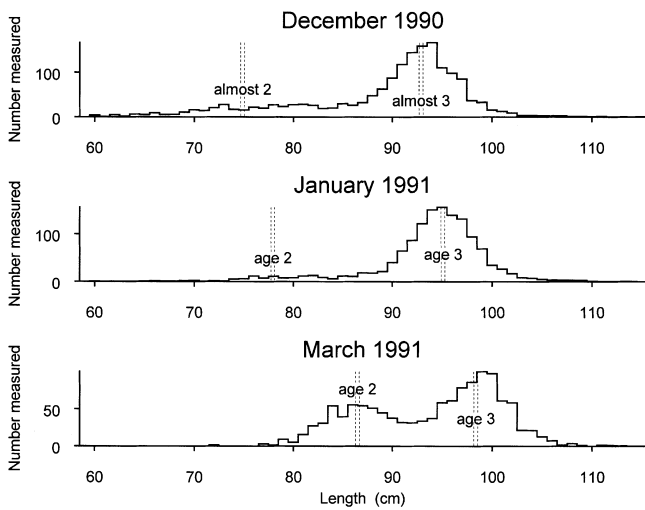
In principle, statistically valid hypothesis tests could be constructed from length–frequency sample records by including in the analysis only those fish whose lengths had been measured. We did not take this approach because (*a*) the data entry and collation resources were not available and (*b*) a return to the raw data would have discarded information on catch sizes.

We adopted a compromise, and calculated a weighting factor for each half-monthly accumulated sample. The weighting factors ensured that growth parameter estimates were based on data from the sampling periods in which most fish were measured, not those periods for which length distributions had been inferred from sampling in other periods. Calculation of weighting factors is described in Appendix 1.

In our analysis we test only for trends over the history of the fishery, and for these tests we assume that data were collected independently in each year; we do not test hypotheses within a single year and region. As a rough guide, we calculate approximate standard errors from the smoothness of the histograms, as described above. Below, we will refer to an accumulated, scaled-up, half-monthly data set for a particular geographical region as simply a ‘sample’.

### *Method of modal analysis*

Peaks in the length–frequency histogram shift to the right as the fishing season progresses (Fig. 1). We interpret this shift as growth of the fish: our method assumes that fish grow smoothly through the fishing season, and it calculates the mean length of each age group at each time (shown on Fig. 1). In some cases the graph may be distorted by, for example, management- or market-imposed minimum size limits.



**Fig. 1.** Shifts of the peaks in a length–frequency histogram over a fishing year in South Australia. Dotted double lines, mean lengths of 2-year-old and 3-year-old fish, which increase as the fish grow.

Mixtures of normal distributions were fitted to the observed length frequencies by the method of maximum likelihood. The means of the normal distributions were made to increase through the year to allow for growth of each age-class. The maximum-likelihood procedure is described in detail in Appendix 2.

Each fishing year in each region was analysed separately, so that the estimates of mean lengths in different years were unrelated. All samples in the historical database were analysed, except for some years in which very few fish were caught in a region.

For each region, limiting times for distinguishing one fishing year from another were determined prior to analysis, to enable the separate analysis of each fishing year (Table 1). In South Australia and New South Wales, limits were clear-cut, since fishing took place for only part of the calendar year (mainly December to May for the former and October to January for the latter). In Western Australia fishing often continued throughout the calendar year, and the limits in Table 1 are only approximate; the actual limits were decided individually for each fishing year, according to when catches were lowest and when new recruits began to enter the fishery.

The advantage of modelling growth over a fishing year, as opposed to analysing single samples individually, is increased precision: the

total number of parameters in the model is reduced and each parameter is estimated more accurately. Also, in the estimation of parameters for a particular age-class, each sample is automatically weighted by the number of fish measured in the age-class: estimates of mean lengths for an age-class mainly come from the samples in which the most fish of that age were measured.

In addition to the fitted mean lengths from the model, empirical means were calculated from the model’s classification of lengths into age-classes: the exact procedure for the calculations is described in Appendix 2. The motivation for the empirical means was a wish for values that represented the observed lengths in a sample as closely as possible, so that notably high or low mean lengths were not the result of lack of fit of the growth model to the data.

In the next section we have chosen to present some fitted means and some empirical means, even though the differences are mostly less than a centimetre. We prefer the fitted mean when sampling problems necessitate an estimate based largely on data from other times of the year, and the empirical mean when there appears to be any lack of fit of the growth model. Comparisons of different years requires means from the same time of year, so the times at which estimates are most reliable cannot always be used.

The number of age-classes modelled in a regional fishery in a year was chosen to ensure that every obvious mode in every sample was allocated to an age-class. Additional age-classes were included to account for larger fish that were not covered by the obvious modes; these classes contributed information on numbers of older fish caught, but no growth information was inferred from them.

Ages were assigned to the age-classes mainly by conventional wisdom of the relationship between length and age of southern bluefin tuna (see, for example, Kirkwood 1983, pp. 1407–8, and Gunn *et al.* 1995). To help resolve doubts that were present, it was seen as reasonable to assume that (a) fish of the same age in different regions would be of similar lengths; and (b) there would be a sensible growth pattern connecting one year to the next.

The birthday of a fish was assumed to fall on 1 January. In Western Australia and South Australia this date fell early in the fishing year, so that fish were younger than their assigned age for a small part of the fishing year. For example, in South Australia in 1990–91, records began in December 1990, and fish assigned age 2 for this fishing year did not become age 2 until January 1991. In New South Wales most of the fishing took place late in the calendar year, so that for some of the fishing year fish were older than their assigned age: in 1980–81 samples were taken between October 1980 and January 1981, and fish assigned age 1 for this year became age 2 in January 1981.

The assignment of ages to length groups was checked by comparison with available data from tagging experiments on southern bluefin

**Table 1. Limiting times and reference times for fishing years in the three regions of the Australian southern bluefin tuna fishery**

Limiting times for Western Australia are only approximate, since they varied between years. The common reference time is for comparing mean lengths between different years, and the growth reference times are for comparing growth within a year to other years

Western Australia	Fishing year	2nd half November to 1st half November
	Common reference	1st half March
South Australia	Fishing year	1st half October to 2nd half September
	Common reference	1st half March
	Growth reference	1st half January to 2nd half March
New South Wales	Fishing year	1st half June to 2nd half May
	Common reference	1st half December
	Growth reference	2nd half October to 1st half January

tuna, the most reliable of which come from 1983–84. Other years in which significant numbers of fish were tagged were 1966–1970, 1974, 1977, 1978 and 1980. For example, a fish may have been tagged in South Australia with a length that indicated it was one year old. It may have been recaptured two years later in New South Wales. Its length could then be checked to see if it was consistent with that of a three-year-old fish in New South Wales that year.

#### Subsequent analysis

A common reference time of year was decided for each region, so that mean lengths of fish in different years could be accurately compared. Two growth reference times, as far apart as possible within the fishing year, were also selected so that apparent growth within a year could be compared to other years. The three reference times (Table 1) had to be times at which, in most years, all age classes were being fished. In some years, mean lengths at the reference times had to be interpolated from results before and after. In a few cases it was impossible to determine mean lengths at one or more of the reference times.

Length-at-age trends over the history of the fishery were analysed by regression analysis. Growth rate trends were also analysed by regression analysis of the cohort length increment between different ages (e.g. one-year-olds versus three-year-olds two years later). We concentrated on South Australia, where the most information on growth was available.

The age composition of catches was summarized for each region by the total catch from each age-class over the fishing year. To gauge the relative importance of each age-class to the fishery, catches were converted from number to weight of fish. The weight of a fish was assumed to be proportional to its length raised to the power  $\lambda = 2.9058$ , as recommended by Robins (1963). To cope with the spread of lengths within an age-class, we used the Taylor series approximation

$$E(x^\lambda) \approx \mu^\lambda + \frac{1}{2} \lambda(\lambda - 1) \mu^{\lambda-2} \sigma^2,$$

where  $E$  is mathematical expectation,  $x$  is fish length, and  $\mu$  and  $\sigma^2$  are the mean length and variance of the age-class.

## Results

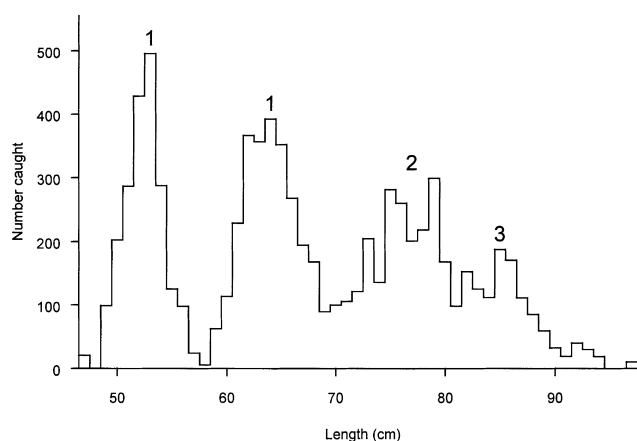
### Ages identified

Ages assigned to the fish were generally in the following ranges: Western Australia, ages 0–2; South Australia, ages 1–4; New South Wales, ages 0–3. Fish older than these ages were sometimes present, especially in New South Wales during the early 1980s, but in most cases it was impossible to accurately assign ages to them. In Western Australia, problems of data quality and infrequency of sampling precluded analysis in 1979 and 1992.

### One-year-old fish in Western Australia

Two or more groups of one-year-old fish were identified in many fishing years in Western Australia. These groups had to be assigned the same age to achieve consistency with results from South Australia. Early in the Western Australian fishing year, fish of similar length to one-year-old fish in South Australia had to be one year old, not two. Later in the season, fish had to be one year old, rather than zero, because they were almost as large as two-year-old fish at the start of the new fishing year in South Australia, shortly afterwards: fish were assumed to migrate from Western Australia to South Australia, as indicated by tagging evidence.

In February 1986, for example, one group of one-year-old fish was centred on a length of 52 cm, and one on 65 cm (Fig. 2). The multiple groups were not observed to persist to two years of age, so the smaller groups apparently ‘catch up’ with the larger ones by then; however, this conjecture needs to be verified by tagging and otolith examination. However, the catch numbers in the lower modes are small, especially after 1969, the start of the Western Australian fishery. Presumably, the lower mode migrates from Western Australia after the close of the South Australian fishing season.



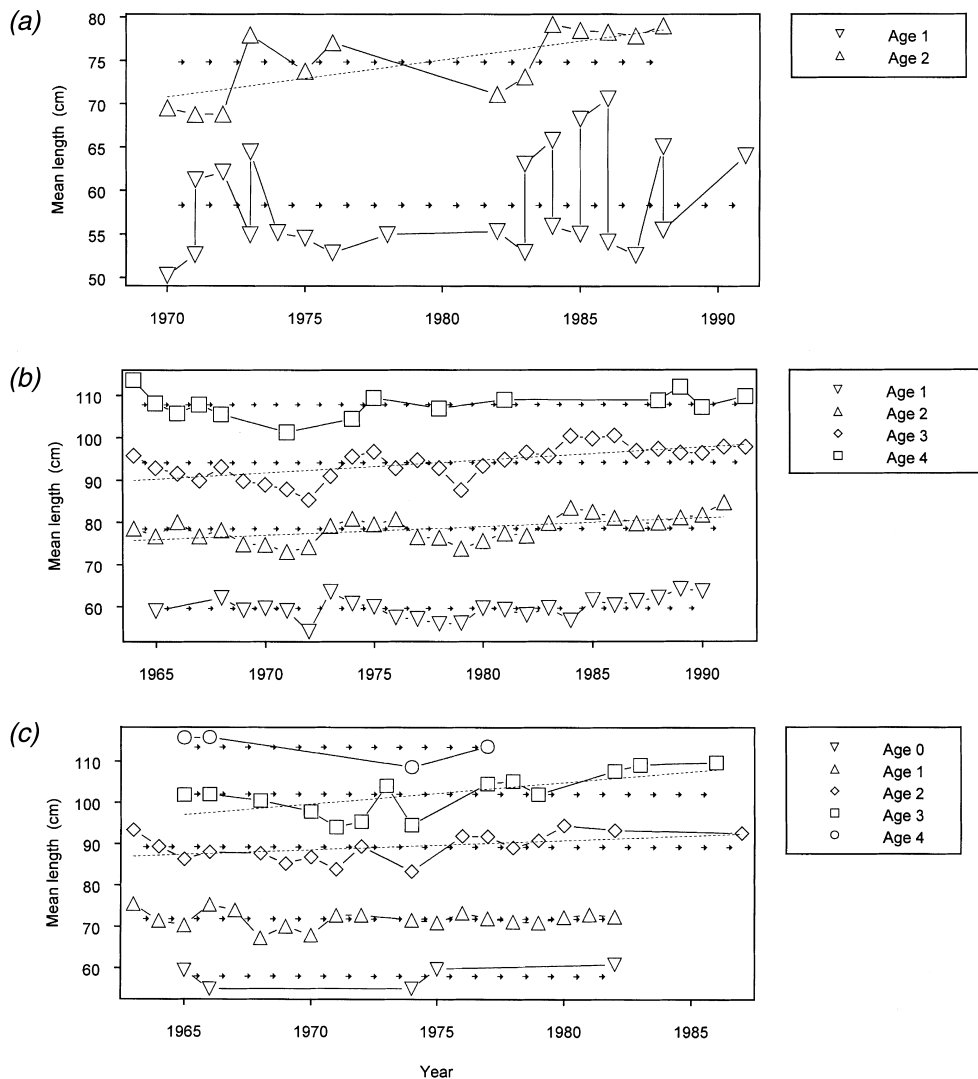
**Fig. 2.** Length–frequency histogram from the Western Australian fishery for February 1986, showing multiple groups of 1-year-old fish. Ages corresponding to each peak are indicated.

### Mean length-at-age

The mean length of each age-class at the common reference time of year (Fig. 3) varied substantially between years (Table 2). Most information is available in South Australia, but even there four-year-old fish were present in fewer years and in smaller numbers than younger fish. In New South Wales there is little information on fish aged zero, or more than three. In some years in Western Australia, especially around 1980, infrequency of sampling meant that mean lengths at the common reference time could not be estimated accurately; estimates for these years are not plotted or listed.

The Western Australian fishery not only contained multiple groups of one-year-old fish, but also obviously contained smaller fish than those caught, which were not targeted by fishers. Owing to these factors only the average length is listed in Table 2. Little information is available for fish aged  $>2$ , and fish aged 0 were usually not present in the Western Australian fishery at this time of year.

Two- and three-year-old southern bluefin tuna, at a given time of year, became larger over the history of the fishery. Results of statistical tests and regression coefficients are listed in Table 3. As remarked above, targeting by fishing operators renders data for age 1 unreliable.



**Fig. 3.** Mean lengths for modes in the fisheries of (a) Western Australia, 1st half of March, (b) South Australia, 1st half of March, and (c) New South Wales, 1st half of December, at the common reference times of year listed in Table 1. Dotted lines, statistically significant trends in mean length over the history of the fisheries. Arrows, level of the average over all seasons. In New South Wales, fish of assumed age 4 were present in more years than are shown, but were often indistinguishable from older fish.

*Growth from one age to another*

The amount of apparent growth of a cohort from age 1 to age 3 also increased significantly over the decades in both the South Australian and New South Wales fisheries (Table 4, Figs 4a, 4c).

For the South Australian fishery a quadratic regression fitted significantly better than a linear one ( $F_{1, 21} = 6.95$ ,  $P < 0.05$ ): the fitted amount of growth increased from 26 cm for the 1964 cohort to 37 cm for the 1981 cohort, and then fell back to 35 cm for the 1989 cohort (Fig. 4a). However, there are insufficient data to allow determination of whether the decrease in growth is real. From this evidence we conclude that growth increments between ages 1 and 3 years steadied in the late 1980s.

We also tested apparent growth from age 2 to age 3 in the South Australian fishery, these being the age-classes least likely to be influenced by migration. In this case a linear fit was significant (Fig. 4b, Table 4), but an additional quadratic term was not ( $F_{1, 25} = 3.66$ ,  $P \approx 0.07$ ).

*Growth within a fishing year*

The apparent rate of growth within a fishing year varied substantially between years. For the South Australian fishery, increases in mean length from the first half of January to the second half of March for ages 1, 2 and 3 are plotted in Fig. 5. The increases are summarized in Table 5. Growth rates of two- and three-year-old fish in the same year were significantly correlated (correlation coefficient  $r = 0.551$ , 24 obser-

**Table 2. Statistics of the mean length corresponding to each age at the reference times of year listed in Table 1**

Av., average; s.d. standard deviation (calculated between years, and unrelated to the spread of fish lengths within the same sample); Min., minimum; Max., maximum. Multiple modes of age 1 in Western Australia are grouped together. In Western Australia some statistics were not considered meaningful because of multiple modes and the presence of small modes that were not always targeted by fishing operators

State	Age	Av. (cm)	s.d. (cm)	Min. (cm)	Max. (cm)
South Australia	1	59.6	2.6	54 (1972)	64 (1989)
	2	78.4	3.0	73 (1971)	85 (1991)
	3	94.1	3.9	85 (1972)	100 (1986)
	4	107.8	3.1	101 (1971)	112 (1989)
New South Wales	1	71.8	2.1	67 (1968)	75 (1966)
	2	89.2	3.4	83 (1974)	94 (1980)
	3	102.0	5.2	94 (1971)	109 (1983)
Western Australia	1	58.3	—	—	—
	2	74.8	4.1	68 (1972)	80 (1986)

**Table 3. Statistical tests and regressions of mean length-at-age**  
Mean length =  $a + b$  (year - 1960)

State	Age	<i>F</i>	df	<i>P</i>	<i>R</i> <sup>2</sup>	<i>a</i> (cm)	<i>b</i> (cm year <sup>-1</sup> )
South Australia	1	2.50	1, 22	> 0.1	—	—	—
	2	11.24	1, 26	< 0.01	0.302	74.9	0.201
	3	19.44	1, 27	< 0.001	0.419	88.7	0.298
	4	0.66	1, 12	> 0.1	—	—	—
New South Wales	1	0.015	1, 17	> 0.1	—	—	—
	2	3.99	1, 15	≈ 0.06	0.210	86.3	0.226
	3	9.00	1, 12	< 0.05	0.429	94.4	0.523
Western Australia	2	10.17	1, 11	< 0.01	0.480	66.5	0.429

vations, *t*-test,  $P < 0.01$ ). Growth rates of one-year-old fish were not significantly correlated with either two- or three-year-old fish ( $r = -0.114$  with 18 observations and  $r = -0.069$  with 14 observations respectively).

The New South Wales and Western Australian fisheries provided much less information on growth within a fishing year than the South Australian fishery; in New South Wales the fishing season was shorter, and in Western Australia growth was often confounded with migration and targeting by fishers, as mentioned above. However, fish appeared to grow less rapidly in New South Wales than in South Australia and Western Australia.

We compare growth between fish in New South Wales and South Australia for the 14 seasons where information is sufficient. In New South Wales, the mean length of fish becoming 2 years of age during the fishing season increased by an average of 2.32 cm (s.d. 1.90 cm), over the 2½-month period between the second half of October and the first half of January. For corresponding seasons in South Australia, the average growth increment of age-2 fish over the same length of time, between the first half of January and the

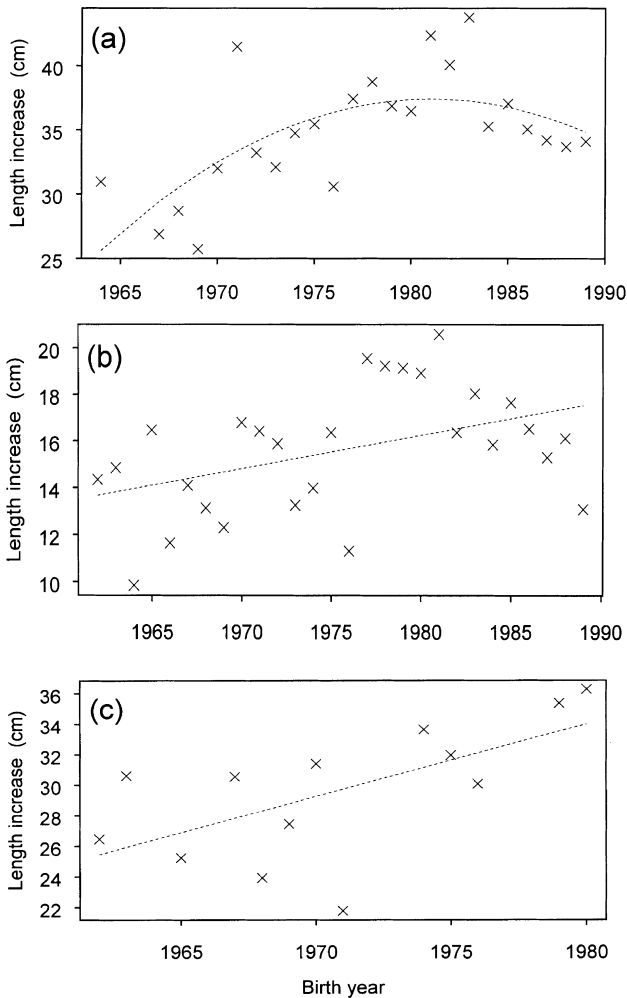
second half of March, was 5.98 cm (s.d. 2.75 cm). In 13 of 14 seasons (the exception being 1978–79) the estimated growth increment for South Australia was greater than that for New South Wales (binomial test,  $P < 0.002$ ).

We regard results in all three fisheries for 1982–84 as less reliable than results for other periods, because of problems with data quality: histograms of the data are not as smooth as in other years, and there is lack of agreement between successive sampling periods.

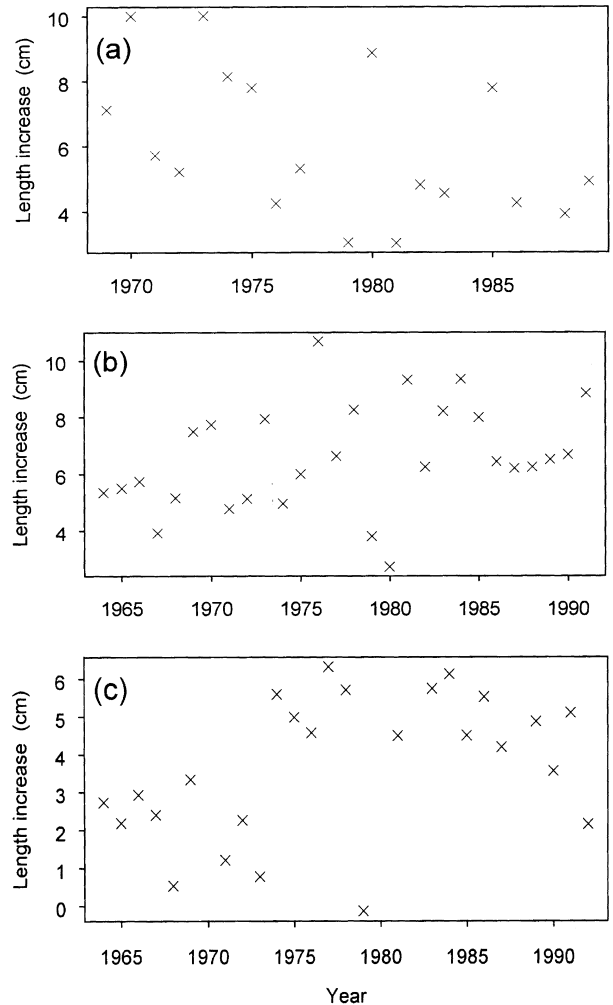
#### Age composition of catches

We emphasize age composition (Fig. 6) rather than total size of catches because calculation of the latter does not require length–frequency analysis and therefore is outside the scope of this paper; however, some remarks on total catch size may be appropriate.

The South Australian fishery was the largest of the three, except for a few years around 1970 when it was surpassed by New South Wales. Catch numbers from the South Australian and Western Australian fisheries between 1990 and 1992



**Fig. 4.** Increases in mean length of cohorts: (a) age 1 to age 3 (i.e. 2 years later), South Australian fishery in 1st half of March; (b) age 2 to age 3, South Australian fishery; (c) age 1 to age 3, New South Wales fishery in 1st half of December. Dotted curves: fitted regressions [quadratic in (a), linear in (b) and (c)]



**Fig. 5.** Increases in mean length of from 1st half of January to 2nd half of March, for (a) age 1, (b) age 2 and (c) age 3 in the South Australian fishery, showing the amount and variation of growth within a fishing year.

averaged respectively about one-fifth and one-twentieth of their peak sizes in the early 1980s. The New South Wales fishery collapsed in the mid 1980s; by 1992 significant numbers of fish were again being caught, but recovery since has been partial.

The age composition of catches differed markedly between the fishing areas. The Western Australian fishery has always been based on one-year-old fish, with some older

fish and a few fish younger than one year. The South Australian fishery has consisted mainly of fish aged from 1 to 3; however, the fishery changed in the 1980s (see below). From the late 1970s to its collapse, the New South Wales fishery was based on fish aged  $\geq 3$  (i.e. those just short of their 4th or higher birthday), with some younger fish.

Fishers in South Australia began to target larger fish in the 1980s. The proportion of 1-year-old fish by weight in the catch

**Table 4.** Statistical test of trends in the length increment from one age to another

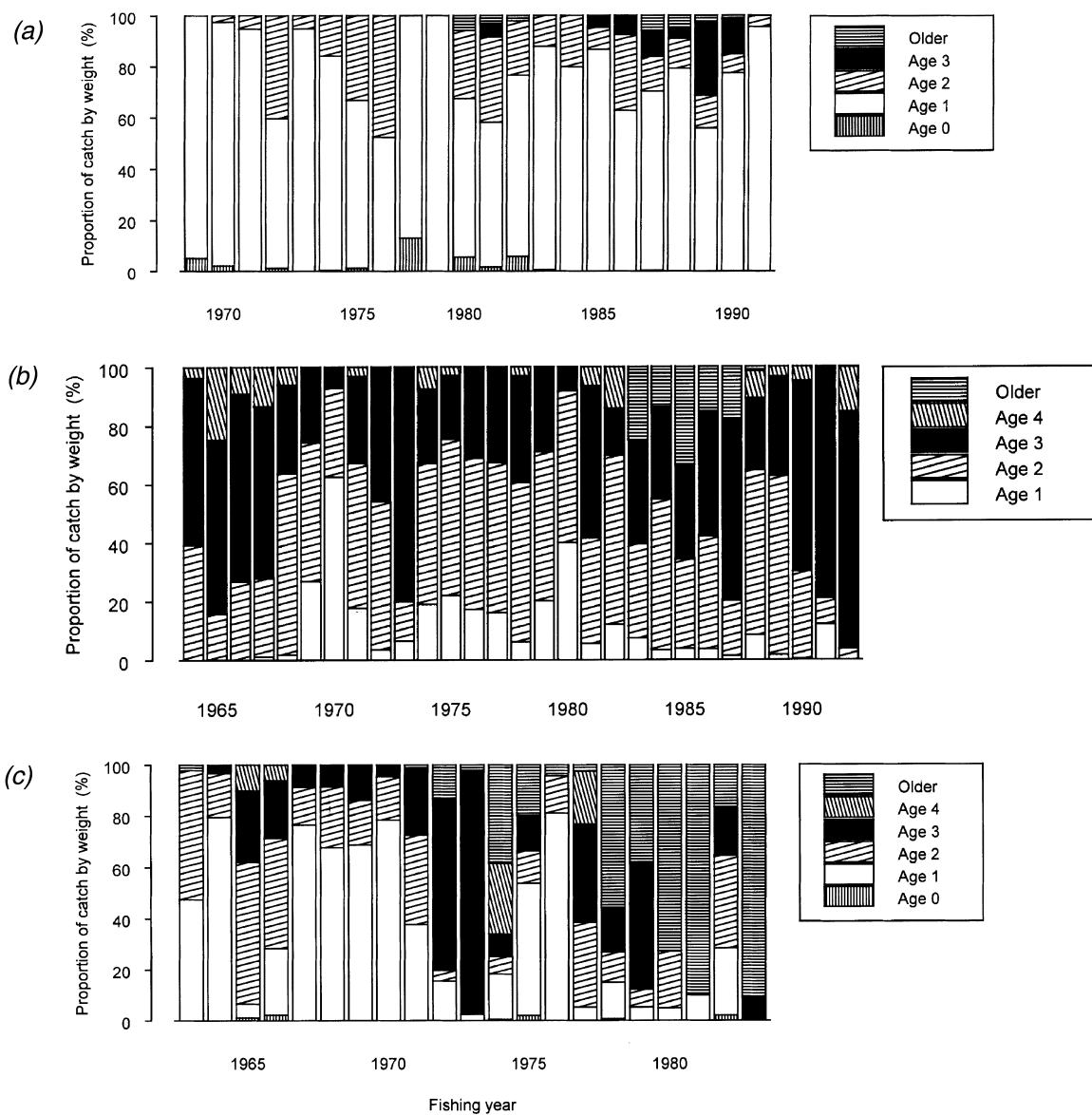
State	Ages	Degree	F	df	P	R <sup>2</sup>
South Australia	1-3	Quadratic	8.08	2, 21	<0.01	0.435
	2-3	Linear	6.77	1, 25	<0.05	0.191
New South Wales	1-3	Linear	7.14	1, 11	<0.05	0.394



averaged 21% between 1970 and 1980, but declined to 5% between 1981 and 1990 and has virtually ceased since then (catches of 2-year-olds effectively ceased since 1991, Fig. 3*b*). In contrast, the proportion of fish aged  $\geq 3$  averaged 33% between 1970 and 1980, and 60% between 1981 and 1992; however, the proportion of fish aged  $\geq 4$  increased only from 1980 to 1985, and then declined again. In New South Wales the shift was earlier: the proportion of fish aged  $\geq 3$  increased from 15% prior to 1972, to 68% between 1972 and 1983.

**Table 5.** Summary of increases in mean length from the first half of January to the second half of March in the South Australian fishery s.d., calculated between years, is unrelated to the spread of fish lengths within the same sample

Age	Av. (cm)	s.d. (cm)	Min. (cm)	Max. (cm)
1	6.0	2.3	3 (1981)	10 (1973)
2	6.6	1.8	3 (1980)	11 (1976)
3	3.7	1.9	0 (1979)	6 (1974, 1977)



**Fig. 6.** Age composition of catches for each fishing year in the fisheries of (a) Western Australia, (b) South Australia, and (c) New South Wales. Limits for the fishing years are shown in Table 1. In Western Australia the limits varied slightly from year to year; the other fisheries were more seasonal, and usually no fishing took place around the limiting times. 'older': all ages greater than those that could be distinguished in a particular year.

**Table 6. Statistics of the standard deviation parameters fitted to the distributions of fish length**

A single parameter applies to each fishing-year in each region: all age-classes in all samples from the fishing year were assumed to have the same s.d. Multiple modes of age 1 in Western Australia were treated like separate age-classes

State	Av. (cm)	Min. (cm)	Max. (cm)
Western Australia	3.2	2.4	4.2
South Australia	4.2	3.3	5.4
New South Wales	4.1	3.1	5.9

#### Standard deviations and standard errors

The standard deviations of the fitted normal distributions (Table 6) generally represent the standard deviation of a whole age-class, except for the case of one-year-old fish in Western Australia where there were often several groups of this age with different means.

Rough standard errors for the parameter estimates were calculated as described above. For the means, most standard errors were <1 cm, but some were ~2 cm, and a few were in the range 5–7 cm in cases where very few fish of a certain age were measured. For the specific growth results mentioned above, the standard errors for the fitted means are all <0.4 cm, except for the value of 109 cm given for the length of three-year-old fish in New South Wales in December 1983, which is subject to a standard error of 0.49 cm. As mentioned, many of the values quoted are empirical rather than fitted means, so these standard errors are not strictly applicable, but they give a rough guide to precision. The standard errors of the standard deviation parameters were generally ~0.05 cm, but some were in the range 0.1–0.2 cm, and one was 0.6 cm.

The standard errors of age fractions of catches were usually <0.05, but some were 0.05–0.1, and a few were >0.1. Several were anomalously large because of poor data quality or lack of fit of the growth model to a sampling period in which the catch was very small. It is to be expected that age fractions will have a relatively higher standard error than the other parameters, because they are all allowed to vary independently: analysing many samples simultaneously does not increase the precision of the age fractions. However, an estimate of the total catch of an age-class over a fishing year, calculated by summing over all the samples, is subject to relatively less error than the individual age fractions.

#### Discussion

This study has quantified the patterns of variation that have occurred in the growth of juvenile southern bluefin tuna. The causes of the long-term growth trend are unknown; it could be related to environmental factors, the behaviour of the fish and/or population size. It is likely that a major cause of the steady increase in mean length of age-classes over the years

would be the reduced population size due to past fishing pressure, because it appears to be a widespread fisheries phenomenon. If sustained by further research it would constitute a vital element in understanding southern bluefin tuna bioenergetics, management strategies, the detection of the onset of overfishing or recovery from the same, and input into population models. Therefore, juvenile growth rates should continue to be monitored for the next few years, at least.

From a scientific survey, Hynd (1965) also found multiple modes in one-year-old southern bluefin tuna off Western Australia. Those and the present findings are consistent with suggestions in Farley and Davis (1998) that the fish have multiple spawnings; one in September–October and the other in February–March. There was some suggestion of multiple modes of one-year-olds off New South Wales. A possible causal mechanism for the disappearance of the multiple classes by age 2 is that fish that remain in the Western Australian fishery over winter grow faster than those that migrate eastwards, owing to higher water temperature associated with the warm tropical winter Leeuwin current (Godfrey *et al.* 1986). Another contributing mechanism might be that the Western Australian fishery may deplete the numbers in the lower mode (which could explain the small catch numbers from the three post-1969 lower modes in New South Wales). Under these hypotheses, migration would make the mean length-at-age vary geographically, increasing from west to east.

On the basis of results presented in Figs 4a and 4b, delegates to the international workshop (Anon. 1994) suggested that the growth model incorporate a linear change in growth rates from 1970 to 1980. This assumption was incorporated into yearly growth curves by Hearn (1994) to quantify the transition between the 1960s and the 1980s growth curves that were obtained from tag-return data (Anon 1994). These curves are being used to partition the catch-at-length into catch-at-age, which improves on the Kirkwood (1983) curve that only used 1960s information. Despite the improvement, this partitioning still suffers from being a knife-edge approach.

The growth-rate trends from the modal analysis are generally supported by results obtained from tagging (Hearn and Hampton 1990), which compared growth in three years in the mid 1980s with a few years in the 1970s and several in the 1960s. They are also supported by results from tagging in the 1990s (Polacheck and Preece 1998) which show that the growth rates of young juveniles in the 1990s are similar to the 1980s but are higher than those of the 1960s. The von Bertalanffy growth curves of Fournier *et al.* (1990) for southern bluefin tuna show an effect in the same direction, although less pronounced.

We compared growth increments from ages 1 to 3 years (Figs 4a, 4c) with estimates from the corresponding growth curve derived from tagging data (Anon. 1994). The 1960s curve was used for birth years up to 1967 and the 1980s curve was used for birth years 1981, 1982 and 1983. The differ-

ences between results of the two estimation methods ranged from -15% to +13%, which shows a consistency between results obtained from length–frequencies and tag–return data. It indirectly indicates a consistency between growth in South Australia and New South Wales for these ages.

We believe the difference in intra-year growth rates between South Australia and New South Wales is mainly due to a seasonal effect because there appears to be little difference in the growth increment from age 1 to age 3 between South Australia and New South Wales. Moreover, it is consistent with the tagging results of Hearn (1986), who showed that southern bluefin tuna grew much faster in summer–autumn than in winter–spring. (If all fish lived in South Australia in summer–autumn and in New South Wales in winter–spring the seasonal and spatial effects would be confounded, but this would make no practical difference to the description of fish growth.)

Seasonal growth is automatically taken into account in our method of ageing fish from length–frequency data, especially from South Australian and New South Wales catches where the fishing seasons are relatively short. The method currently used to age southern bluefin does not take seasonal growth into account, which may lead to substantial systematic errors.

The method developed for our analysis is an improvement over the previous methods because it accounts for year-to-year variation in growth. Also, in common with the MULTIFAN approach, but unlike the knife-edge partition approach (Majkowski and Hampton 1983), it allows fish in the length range normally occupied by an age-class to be assigned a different age in years when very few fish of that age are present in the fishery. For example, for South Australia in the second half of March 1973, we estimated that 14.7% by number of the fish caught were 1 year old, 0.5% were 2, 84.8% were 3 and none were 4; but a knife-edge partition mis-assigns many of the 3-year-old fish to age 2 and some to age 4. In fact the partition based on the presently used two-stanza growth curve allocates 13.6% of fish to age 1, 22.6% to age 2, 60.9% to age 3, and 2.9% to age 4.

The main advantages of length–frequency analysis over tagging and age determination from otoliths are that (a) it provides a continuous record of the species since the early 1960s, and (b) the analysis comes at little extra cost, since the length–frequency of the commercial catch is already being comprehensively monitored. Monitoring by tagging is labour intensive and will probably always be expensive; direct ageing of otoliths is also expensive. We expect both these methods to be important in the future, but it is unclear whether their routine application will be practical. Length–frequency analysis may complement direct ageing by indicating the scope of sampling that is needed to achieve accurate length–age keys.

A disadvantage of length–frequency analysis is that it is very difficult to use for old fish because individuals have dif-

ferent growth histories; for example, a 6-year-old fish that has grown quickly may be the same size as an 11-year-old fish that has grown slowly. We expect the method developed here to be applicable to fish only up to 5 years of age. Fournier *et al.* (1990) dealt with this difficulty by assuming that growth was identical in all years and that the mean lengths all lay on a single von Bertalanffy growth curve.

Australian fishers are currently targeting older southern bluefin tuna, especially 4- and 5-year-old fish for the Japanese sashimi market, either directly or via fish farms. Reliable ageing of these fish from modes will be a major challenge for scientists, because a year's growth produces less change in length at these ages. Accurate results will probably need to rely on otolith and tagging studies, and size selectivity of 3-year-olds may become a concern.

It is encouraging that there seems to be close agreement between estimates of growth rates from length–frequency modes and tag–return data. Future research may provide a model to jointly analyse length–frequency modes and tag–return data, and possibly include direct age information from otoliths.

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### Appendix 1. Weighting factors for the half-monthly samples

The weighting factors used for the half-monthly sampling data were only approximate, but ensured that estimates of growth parameters were based on data from sampling periods in which the most fish were measured. It is considered that the lengths of all fish sampled come from an identical distribution, which is only an approximation because small fish predominated in some catches and large fish in others. The weighting factor comes from the precision of the estimate of the mean length of a sample.

Suppose a half-monthly accumulated sample is constructed from catches from  $k$  boats, and that boat  $i$  caught  $n_i$  fish (judging from the weight of the catch), of which  $m_i$  fish were measured. Let  $y_{ij}$  ( $j = 1, \dots, m_i$ ) be the measured lengths. Then the overall mean is

$$Y = (1/n) \sum_{i=1}^k (n_i/m_i) \sum_{j=1}^{m_i} y_{ij},$$

where  $n = \sum_{i=1}^k n_i$ . Its variance is

$$\text{var}(Y) = (\sigma^2/n^2) \sum_{i=1}^k n_i^2/m_i,$$

where  $\sigma^2$  is the variance of fish length. Let  $N$  be the scaled-up estimate of the total number of fish caught in the half-month. If this were the true number of fish measured then  $\text{var}(Y)$  would equal  $\sigma^2/N$ . The weighting factor is then the ratio of these variances,

$$(N/n^2) \sum_{i=1}^k n_i^2/m_i.$$

### Appendix 2. Details of maximum likelihood estimation

Length–frequency samples taken in the same region and fishing year were analysed together. A half-monthly sample was modelled by a mixture of normal distributions, the standard deviations of which were constrained to be equal. The notation is similar to that of Fournier *et al.* (1990). The likelihood for a single length measurement  $x$  in sample number  $\alpha$  is

$$(2\pi)^{-1/2} \sigma^{-1} \sum_{j=1}^J p_{j\alpha} \exp \left\{ -1/2 (x - \mu_{j\alpha})^2 / \sigma^2 \right\} \quad (\text{A1})$$

where  $J$  is the number of age-classes,  $p_{j\alpha}$  ( $j = 1, \dots, J$ ) are the age fractions for the classes in sample  $\alpha$ ,  $\mu_{j\alpha}$  are the mean lengths of the age-classes, and  $\sigma$  is the common standard deviation. The sample index  $\alpha$  varies from 1, the first sample in the fishing year, to  $A$ , the last sample in the year.

Strictly, the likelihood (A1) should be integrated over the 1-cm interval into which the length is classified, of which  $x$  is the midpoint. However, in common with Fournier *et al.* (1990), for our main analysis we approximated the integral by the point-likelihood value (A1), since the interval width of 1 cm was small compared with the standard deviations, which were typically about 4 cm. The advantages of this approximation were that computation time was greatly reduced, and that transformation of the data was made easy, enabling the fitting of, for example, log-normal distributions instead of normal distributions if required. In a preliminary analysis on some of the data using the correct integrated likelihood, results were practically indistinguishable from those of the approximated likelihood.

Forms of standard deviation other than a constant were tried for some samples. These forms included the single-parameter relationships of making the standard deviation proportional to the mean length (which would spread out the length distributions of older fish), and making the standard deviation inversely proportional to the mean length (which would result in a greater spread of lengths in younger fish than in older fish). In addition, we tried the two-parameter linear func-

tion of mean length used by Schnute and Fournier (1980) and Fournier *et al.* (1990). None of these models fitted the data any better than the model with constant standard deviations; the single-parameter models clearly failed to match the observed length distributions for either small fish or large fish, and the two-parameter model slowed numerical convergence and appeared to be an over-parameterization.

Transformation of the lengths was also considered, so that, for example, the distributions fitted may be log-normal instead of normal, but was also not pursued. There was little evidence that the length distributions were skew, and the ordinary normal distributions fitted as well as any other.

The analysis involved estimating all the means  $\mu_{j\alpha}$  and age fractions  $p_{j\alpha}$ , and the standard deviation  $\sigma$ . The means were made to increase with time, so that in most cases values for  $\mu_{j1}$  and  $\mu_{jA}$  specified all of them. Parameters corresponding to different values of  $j$  were defined independently.

In most cases a straight line fitted the growth of an age-class over a single fishing year sufficiently well. Departures from linearity were dealt with by fitting separate straight lines to different parts of the year, so that three  $\mu_{j\alpha}$  values had to be specified at different times during the year. For years in which multiple groups of fish of the same age were present, a separate line was fitted to each one. In some cases all samples with substantial numbers of a particular age-class were collected within a short space of time; then the mean for the age-class was made constant, and was specified by the value of  $\mu_{j1}$ .

The age fractions  $p_{j\alpha}$  were all estimated separately (except for the constraint that they had to sum to one for each sample), which added a large number of parameters to the model. In a two-stage estimation procedure, for each  $\alpha$  the  $p_{1\alpha}, \dots, p_{J\alpha}$  were calculated conditional on the values for  $\mu_{1\alpha}, \dots, \mu_{J\alpha}$  and  $\sigma$ . Another advantage of separately estimating the age fractions was that age fractions that were converging to zero could be set to zero and thereafter left out of the model; this happened when no fish of a certain age were present in a sample.

The modal analysis used a computer program written in Fortran. Code was written to evaluate the log-likelihood and its first and second derivatives with respect to the parameters, and the IMSL routine DUMIAH, which is based on the Newton optimization method, was used to maximize the log-likelihood. Estimation of age fractions at each step in the IMSL routine was programmed separately by the Newton method; the constraint that the fractions sum to one was handled by a Lagrange multiplier.

The final parameter estimates were used to calculate empirical mean lengths for each age-class in each sample. These means, denoted  $\tilde{\mu}_{j\alpha}$  for age-class  $j$  in sample  $\alpha$ , were the mean lengths for the sample, conditional on the classification into age-classes produced by the analysis. They were defined by

$$\tilde{\mu}_{j\alpha} = \left( \sum_{i=1}^{I_\alpha} f_{i\alpha} e_{ij\alpha} x_{i\alpha} \right) / \left( \sum_{i=1}^{I_\alpha} f_{i\alpha} e_{ij\alpha} \right),$$

where  $x_{i\alpha}$  ( $i = 1, \dots, I_\alpha$ ) are the lengths measured in the sample,  $f_{i\alpha}$  is the number of fish of length  $x_{i\alpha}$ , and  $e_{ij\alpha}$  is the probability that a fish of length  $x_{i\alpha}$  is classified into age-class  $j$ :

$$e_{ij\alpha} = P_{i\alpha} q_j / \left( \sum_{k=1}^J P_{k\alpha} q_k \right),$$

where

$$q_j = \sigma^{-1} \exp \{ -(x_{i\alpha} - \mu_{j\alpha})^2 / (2\sigma^2) \}.$$

If a length  $x_{i\alpha}$  is close to the mean of an age-class,  $e_{ij\alpha}$  will usually be close to one for that class and zero for the other classes, while if the length is midway between two classes  $e_{ij\alpha}$  may be close to  $1/2$  for those classes and zero for the rest.