An ageing methodology, growth parameters and estimates of mortality for hake (*Merluccius australis*) from around the South Island, New Zealand

Peter L. Horn

National Institute of Water and Atmospheric Research Ltd, PO Box 893, Nelson, New Zealand.

Abstract. A method is described to determine the age of hake by counting zones in sectioned otoliths. The technique was validated to age 1 years from the progression of modes in length–frequency distributions, and for ages 2 years onwards by examining the state of otolith margins from fish sampled regularly over a one-year period. von Bertalanffy growth parameters are estimated for hake on the Campbell Plateau and Stewart–Snares shelf, on the Chatham Rise, and off the west coast of the South Island. Hake grow rapidly for about five years, but growth is slight after about 12 years. Female fish have a significantly faster rate of growth than males. A value for M of 0·20–0·25 is proposed. Differences in growth rates and population age distributions imply that there are at least two stocks of hake in New Zealand waters, with fish off the west coast of the South Island being distinct from those on the Campbell Plateau and Chatham Rise.

Introduction

Hake, *Merluccius australis* (Hutton, 1872), is common throughout New Zealand waters south of latitude 40°S, in depths of 200–800 m. The same species also occurs off the southern coasts of Australia and South America, and around the Falkland Islands, and similar species from the same genus occur in most other temperate regions of the Atlantic and eastern Pacific Oceans.

Most of the New Zealand commercial catch is taken off the west coast of the South Island (WCSI), on the Chatham Rise, and to the north and east of Auckland Island on the Campbell Plateau (Fig. 1). Some target fishing for hake has occurred in all these areas (Patchell 1981; Colman and Vignaux 1992), but most of the landings have been a by-catch of other fisheries, particularly those targeting hoki (*Macruronus novaezelandiae*). Total annual landings since 1989 have varied between 7400 and 14 800 t (Annala and Sullivan 1996). Most hake taken commercially range between 65 and 140 cm total length.

Ageing of New Zealand hake was first reported by Wyszynski (1986), who examined cross-sectioned otoliths in an unvalidated study. He aged 20 fish from a narrow size range (51–81 cm total length), 17 of which were male, and concluded that hake were about 55 cm long at age 3 years and that the oldest fish in the sample were aged 8 years. Colman *et al.* (1991) calculated growth parameters from cross-sectioned otoliths collected in 1976 from the Chatham Rise and WCSI. No fish were aged younger than 5 years and the authors acknowledged that this produced unrealistic estimates of t_0 and L_∞. Colman and Vignaux (1992) aged otoliths collected off WCSI in 1989 and 1990. Fish as young as 2 years were present in this sample, and the resulting von Bertalanffy parameters were more realistic than those from the previous study. Neither of these studies validated the ageing method.

A study of *Merluccius australis* off southern Chile examined cross-sectioned otoliths from fish 45–155 cm long (Ojeda and Aguayo 1986). The authors showed that females grew faster than males, and the maximum recorded age for both sexes was 30 years, though few fish were older than 24 years. An examination of otolith margins indicated that the zonation pattern was probably an annual phenomenon, although the proportions of otoliths with hyaline margins ranged only between 8% and 40% in monthly samples over a one-year period.
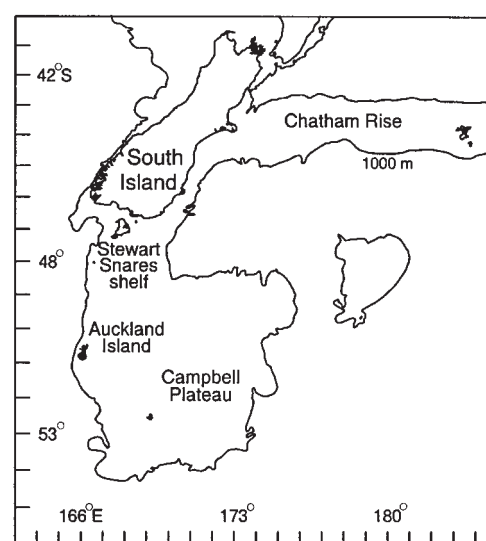

Fig. 1. Area around the South Island of New Zealand, showing locations mentioned in the text and the 1000-m isobath.

Although the interpretation of merluccid otoliths has often been controversial, validated ageing techniques have been developed for numerous *Merluccius* species (see Alheit and Pitcher 1995). A variety of preparation methods have been used: whole unmodified otoliths, whole otoliths immersed in some clearing liquid, burned otolith cross-sections, and thin sections. Whole otoliths are not always useful for determining ages of old, slow-growing hakes owing to the narrowness of growth zones formed late in life. Most successful studies have used cross-sections or thin sections through the dorso-ventral axis of the otolith.

Hake supports a relatively important fishery in New Zealand waters, and accurate growth parameters are fundamental to the sound management of hake stocks. The present study aimed to develop a standardized and validated method to age hake from otoliths by interpreting patterns of early otolith growth and determining how many growth zones are laid down annually in otoliths of juvenile and mature fish. Growth parameters for hake from the three main New Zealand fishing areas could then be calculated, and estimates of instantaneous mortality derived, for use in the stock assessment of this species.

Materials and methods

Ages of fish are given in years and fractions of years. 'Age class' refers to fish of any age within a particular whole year; for example, age class 3+ means fish at least 3·0 but less than 4·0 years old. 'Year class' refers to the year in which the fish were spawned.

Otoliths (sagittae) of hake from around the South Island have been collected from commercial and research landings since 1989. Total length (TL, rounded to the nearest centimetre below actual length) and sex were recorded for all fish from which otoliths were taken.

All otoliths were examined in cross-section prepared in one of two ways. Initially, whole otoliths were broken across the dorsoventral axis, one broken surface was ground smooth on a rotary grinder, and the half-otoliths were baked in an oven until amber-coloured (270°C for about 4 min). Later preparations were made by baking whole otoliths in an oven until amber-coloured, embedding them in clear epoxy resin (Araldite K142), and cutting each otolith along the dorsoventral axis through the nucleus with a rotary diamond-edged saw. The latter method was preferred as it produced uniformly flat cross-sections with unchipped edges. The prepared otolith cross-section was coated in paraffin oil, illuminated by reflected light with an incident angle of about 30°, and examined under a binocular microscope (×30). A pattern of dark-brown (translucent) and light-brown (opaque) zones was apparent. Subsequently in this paper, 'zone' refers to the paired structure of one opaque band inside one translucent band. The number of complete zones (i.e. zones with at least some opaque material outside them) was counted. The zonation pattern was generally clearest on the ventral side of the otolith cross-section, so most counts were made in this area. Fish length and sex were unknown to the single otolith reader.

To convert zone counts to estimates of age, it was necessary to validate the ageing method by determining when and how frequently the zones were laid down. Seven otolith samples collected between April 1992 and June 1993 from the Campbell Plateau and Stewart–Snares shelf were selected to examine changes in otolith margin characteristics (Table 1). Otolith margins were classified as either translucent or opaque, and the number of complete zones was counted. About 15% of otoliths had a marginal state too indistinct to classify confidently, although a zone count could still be made. The proportion of otoliths with indistinct margins in a sample did not

Table 1. Details of length–frequency and otolith samples examined to determine otolith marginal state (Samples 1–7) and to provide additional data for calculating growth parameters (Samples 8–14)

Areas: CS, Campbell Plateau and Stewart–Snares shelf; CH, Chatham Rise; WC, west coast of South Island. *n*, otolith sample size; *N*, length–frequency sample size used to calculate age–frequency

Sample No.	Area	n	N	Sampling period
1	CS	164	—	20.iv.92 to 18.v.92
2	CS	198	—	11.vi.92 to 28.vii.92
3	CS	192	—	16.ix.92 to 12.x.92
4	CS	235	377	22.xi.92 to 20.xii.92
5	CS	92	—	10.ii.93 to 27.ii.93
6	CS	145	—	20.iii.93 to 30.iv.93
7	CS	160	—	3.v.93 to 2.vi.93
8	CS	114	121	20.x.89 to 12.xi.89
9	CS	374	669	26.xi.91 to 21.xii.91
10	CS	278	551	20.xi.93 to 19.xii.93
11	CH	339	746	26.xi.89 to 17.xii.89
12	CH	437	523	30.xii.92 to 5.ii.93
13	WC	450	3497	1.vii.92 to 30.ix.92
14	WC	299	3780	12.vii.93 to 22.ix.93

appear to be related to time of year. The month of collection was unknown to the otolith reader.

Validation of the ageing technique for adult fish was also attempted by examining the age structures from samples collected during trawl surveys of the Campbell Plateau in October–November 1989 and November–December 1991 and 1993 (Table 1) to see whether strong and weak year classes moved logically through. The year of collection was known to the otolith reader. For each year, the age distribution of hake in the survey area was constructed from the length–frequency distribution (scaled to represent the whole population in the survey area) and the otolith readings in the following manner: $A_t = \sum_x (L_x p_{tx})$, where A_t is the estimated proportion of fish of age class t in the survey area, L_x is the proportion of fish of length x in the length–frequency distribution, and p_{tx} is the proportion of aged fish of length x that were age t. The length strata, x, were in 5-cm groupings (i.e. 50–54 cm, 55–59 cm, etc.) up to 89 cm for males and 114 cm for females. All remaining fish were grouped into a single length stratum (i.e. 90+ cm for males, 115+ cm for females).

The growth rate of the 0+ age class (i.e. fish less than about 25 cm TL) was examined by plotting length modes of hake caught during a series of trawl surveys off the north-west of the South Island in 1982–83. The information was derived by Colman *et al.* (1991) from samples of small hake caught on the trawl meshes, presumably as the net was retrieved through mid water. Because the fish were generally bent around mesh netting in the trawl wings, rather than being caught in the codend, they were seldom recorded in the formal length–frequency samples.

Length–frequency histograms from research trawl surveys of the inshore WCSI often exhibit one or two distinct modes less than 55 cm, which were initially assumed to represent separate year classes of juvenile hake. Examining otoliths of fish from these length modes enabled the pattern of early growth of the otolith to be determined and helped to define the growth rate of juveniles.

To assess the within-reader reproducibility of the results, 114 otoliths (from Sample 4 in Table 1) representing a range of ages, both sexes, and both clear and unclear otoliths were read twice. Because the year of collection of each sample was known to the reader, and some strong year classes were apparent, it was necessary to examine the possibility that age structures had been biased by this knowledge. Sixty otoliths ranging in age

from 10 to 16 years were selected from Samples 4, 8 and 9 in Table 1 (20 per sample), jumbled, and reread.

von Bertalanffy growth curves were fitted to the age–length data by a non-linear least-squares regression procedure (Ralston and Jennrich 1978). Separate equations were derived for each sex from each of the three main fishing areas.

Results

Interpretation of early growth

Plotted length modes from surveys off the WCSI exhibit two clear diagonal groups of points (Fig. 2). Fitting a linear regression to the right-hand group of points indicates that hake have a length near zero about August, close to the known spawning season in August–September. There is also a clear indication that they are about 10–15 cm long by early April and reach a length of 20–25 cm one year after spawning.

Length–frequency histograms from three of the inshore trawl surveys conducted in March–April off the north-west coast of the South Island exhibit peaks in the range 10–15 cm (Fig. 3). Otoliths from fish 10–18 cm long ($n = 23$) in 1994 had no complete otolith zones, as would be expected for fish of age class 0+. In the 1995 sample, otoliths from fish 24–45 cm long ($n = 31$) all had one complete zone, those from fish 10–14 cm long ($n = 7$) had no zones, and otoliths from hake 19–23 cm long ($n = 11$) had either one or no zones. Hence, in this year, the 0+ age class is bimodal. The 1+ age class is apparent in three of the histograms, with mean values of 34–37 cm. A 2+ age class is abundant in only the 1992 sample and has a mean length of about 44 cm.

Most of the individual age classes apparent in Fig. 3 have broad size ranges. For example, 0+ fish in 1994 and 1995
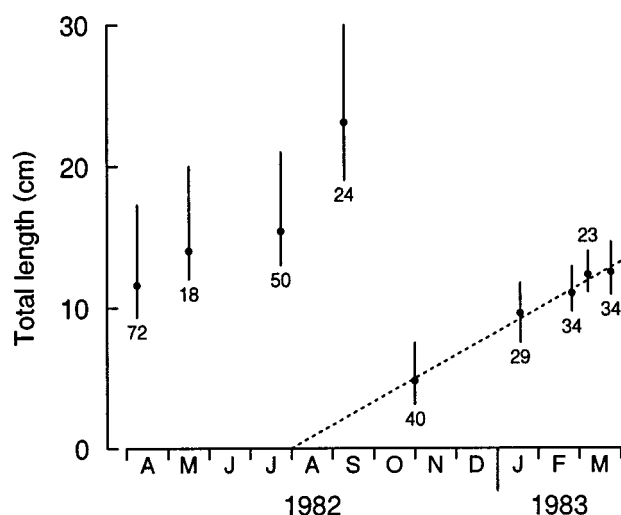

Fig. 3. Length–frequency histograms of hake (sexes combined) caught in research trawl surveys off the north-west coast of the South Island during April–May 1990, 1992, 1994 and 1995. The data have been scaled to represent the estimated number of hake in the survey area. The bottom three distributions are directly comparable, because the samples were taken by the same vessel and fishing gear. The 1990 sample was taken by a different, and probably less efficient, trawl. n, number of fish measured. Length–frequency peaks are labelled with year of spawning and age class.

range from 9 to 23 cm, and 1+ and 2+ fish have distributions 15–25 cm wide. The 1992 distribution is complicated. No otoliths are available from this survey, so it is not known whether the hake of size 20–30 cm are large 0+ or small 1+ fish.

In about half of the otoliths, a distinct translucent band was visible quite close to the nucleus but clearly inside the first annulus. The radius to this band was generally about a third to a half as long as the radius to the first annulus, indicating that the band forms when hake are about 7–12 cm long. Similar bands have been noted in other merluccids (e.g. Penttila and Dery 1988) and are often referred to as the 'pelagic zone'.

Fig. 2. Length modes of juvenile hake caught during bottom trawl surveys off the north-west of the South Island between April 1982 and March 1983. Points indicate the mean length and lines indicate the range. Sample sizes are shown adjacent to each range. The dotted line is the linear regression fitted to the right-hand group of mean points.
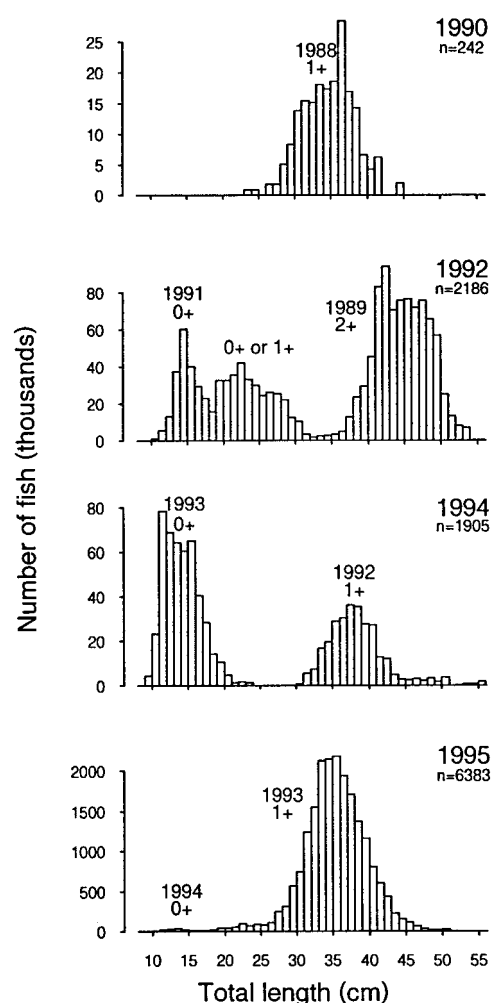
Validation

It was generally possible to determine whether an otolith margin was translucent or opaque. Some interpretations for older fish were complicated because of the narrowness of the margin, and the diffuse early growth zones in some young otoliths were sometimes difficult to classify. Percentages of otoliths with translucent margins, for each sample separated into three groups of age classes (2+ to 6+, 7+ to 12+, >12+), are shown in Fig. 4. It is apparent that translucent material is initially laid down about May, that most otoliths have a translucent margin in mid winter, and that most fish are again laying down opaque material by October. These data support the hypothesis that one opaque and one translucent band (i.e. one complete zone) are laid down annually in the otoliths of hake.
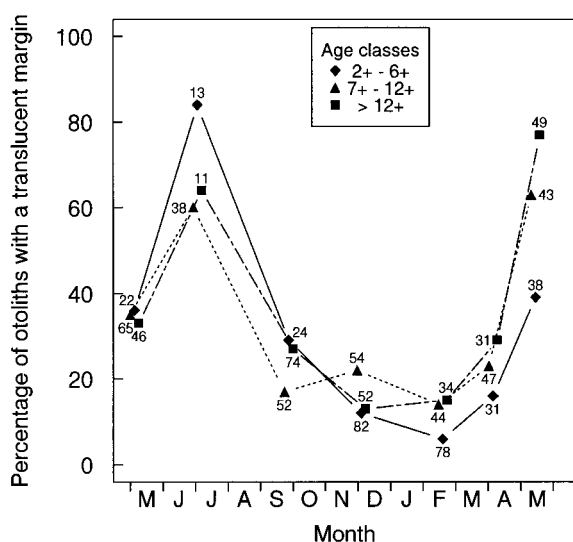

Fig. 4. Seasonal change in the percentage of otoliths with a translucent margin, over the period May 1992 to May 1993. Numbers adjacent to symbols denote sample size for the three age-class groupings (i.e. 2+ to 6+, 7+ to 12+, >12+).

Hake spawn about August–September off WCSI and during late spring and early summer on the western Chatham Rise and the north-western Campbell Plateau (Colman 1995). Hence, a 'birthday' of 1 October was chosen. As the translucent part of a zone appears to be complete by late winter (August–September), fish are about 1 year old on completion of the first translucent band. Hence, the number of complete zones, plus a correction for the time elapsed between 1 October and the date of sampling, was taken as the age of the fish.

Errors would result if no account was taken of the variable timing of zone completion. Consequently, margins of otoliths collected during September to December were

subjectively graded as either wide or narrow, though this was difficult at times because of the narrow zones on otoliths of older fish. Since the new opaque material appears to start forming about 1 September, fish caught after this time and showing n complete zones and a wide margin were assigned to the same age class as those with $n + 1$ zones and a narrow margin.

Further support for the ageing method was derived by examining the progression of a strong year class through estimated age distributions from the Campbell Plateau (Fig. 5). The 1979 year class was abundant as 10-year-old fish in 1989 and progressed through the set of samples to be age 14 in 1993. However, some moderately strong year classes do not appear to progress between years, e.g. 13+ males in 1989 and 9+ males in 1992.

Growth parameters

von Bertalanffy growth-curve parameters (with asymptotic 95% confidence intervals) calculated from the otolith readings of fish from the Campbell Plateau, Chatham Rise and WCSI are given in Table 2. Time of sampling, and hence part-year growth, is incorporated in this analysis. All samples (except for the 1993 Chatham Rise and WCSI collections) have few fish younger than 4 years, so t_0 is poorly defined. Also, young fish that are caught may not be
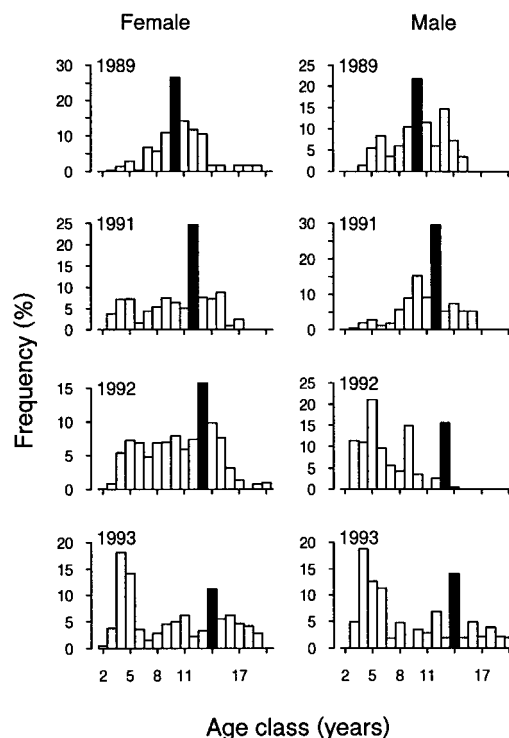

Fig. 5. Calculated age distributions, by sex, for the total catch from trawl surveys of the Campbell Plateau in 1989 and 1991–93. Dark bars indicate the strong 1979 year class. See Table 1 for sample sizes.

Table 2. **von Bertalanffy parameters (with 95% confidence intervals) for hake from the Campbell Plateau (CP), Chatham Rise (CR) and off the west coast of the South Island (WC)**

Parameters are shown for a dataset comprising otolith readings only and for a dataset combining all otolith readings ≥3 years and length-based estimates of juvenile growth

Sex	Area	n	L_∞(cm)	k	t_0(years)
			Otolith data only		
Female	CP	1086	122·3 (119·0–125·6)	0·134 (0·119–0·150)	−1·56 (−2·06 to −1·07)
	CR	393	123·9 (119·1–128·7)	0·135 (0·117–0·153)	−1·13 (−1·56 to −0·68)
	WC	365	110·6 (105·9–115·5)	0·146 (0·119–0·174)	−1·94 (−2·73 to −1·15)
Male	CP	550	97·6 (95·0–100·2)	0·161 (0·135–0·188)	−2·34 (−3·21 to −1·47)
	CR	345	93·1 (91·1–95·1)	0·207 (0·183–0·230)	−1·02 (−1·40 to −0·64)
	WC	331	84·5 (83·0–85·9)	0·265 (0·228–0·302)	−0·67 (−1·25 to −0·09)
			Otolith and length-based data		
Female	CP	1383	115·5 (114·3–116·8)	0·185 (0·177–0·192)	−0·18 (−0·25 to −0·10)
	CR	656	116·1 (113·9–118·3)	0·181 (0·170–0·192)	−0·21 (−0·29 to −0·12)
	WC	637	111·1 (109·0–113·2)	0·194 (0·182–0·207)	−0·16 (−0·25 to −0·07)
Male	CP	849	92·5 (91·6–93·4)	0·259 (0·249–0·269)	−0·06 (−0·11 to 0·00)
	CR	601	88·8 (87·8–89·8)	0·294 (0·281–0·307)	0·00 (−0·05 to 0·05)
	WC	625	83·5 (82·7–84·3)	0·308 (0·294–0·322)	0·00 (−0·05 to 0·06)

representative of the mean size of their year class. Thus, these parameters will poorly describe the growth of juvenile hake.

To estimate population growth parameters that will be applicable over the entire life of all fish, it is necessary to add information on the growth of juveniles. Mean lengths for hake at ages 0·6, 1·6 and 2·6 years, as determined from modes in length–frequency distributions collected off WCSI, are 13, 35 and 44 cm TL, respectively (from Fig. 3). A length-based dataset of 300 points was created comprising three sets of 100 points, each normally distributed with means (and coefficients of variation, CVs) at 13 (16%), 35 (10%) or 44 (10%). The chosen CVs were similar to those calculated for the distributions in Fig. 3. The length-based data were combined with observed age–length data for ages 3 and older from the three sampling areas. This is not the ideal method to incorporate juvenile growth into the model as it necessitates two assumptions: that rates of juvenile growth are comparable between sexes and between areas. The assumption concerning sexual differences is likely to be valid. Growth differences between areas are demonstrated for adult hake (see below), and though these differences may also be apparent for juveniles, they are likely to be relatively slight. Thus, von Bertalanffy parameters fitted to these combined data (see Table 2) are considered to be the best descriptors of growth for the three hake populations.

The calculated curves, raw data, and mean lengths at age (all corrected for part-year growth) for hake from the Campbell Plateau, Chatham Rise and WCSI are plotted in Fig. 6. The calculated curves fit the observed data well. In all three areas, female hake grow significantly faster and reach a larger size than males. There are no significant differences in growth rates for female hake from the Campbell Plateau and Chatham Rise, but females off WCSI grow significantly more slowly than those in the other two areas. For male

hake, the three L_∞ values calculated from the combined datasets are all significantly different, with growth being fastest on the Campbell Plateau and slowest off WCSI (see Table 2).

Male hake had a maximum age of 30 years, and females were aged to 27 years. Of all fish aged 20 years or more, 69% were male. The minimum age of the oldest 5% of fish from each area was similar between sexes, being 17 years on the Campbell Plateau, 16 years on the Chatham Rise, and 15 years off WCSI. For all areas combined, about 1% of females were older than 18 years and 1% of males were older than 20 years.

Age replication

Results of the within-reader comparisons are shown in Table 3. Of the 114 otoliths from a single sample examined twice, 60% were aged identically and 92% differed by 1 year or less. For the 60 otoliths selected from three samples and reread jumbled, 58% were aged identically and 83% differed by 1 year or less. There was no apparent bias in the ageing error over the entire age range, and error in the jumbled samples was comparable to that for the single sample.

Population age distributions

The estimated age distributions for four samples from the Campbell Plateau (Samples 4, 8, 9 and 10 in Table 1) are presented in Fig. 5. The distributions were quite similar for males and females in all years except 1992. In that year, there were few males in the sample and the male age distribution was based on only 40 otolith readings. The 1979 year class is dominant in all distributions. Age distributions for two samples from each of the Chatham Rise and WCSI (Samples 11–14) are given in Fig. 7. The strong 1979 year
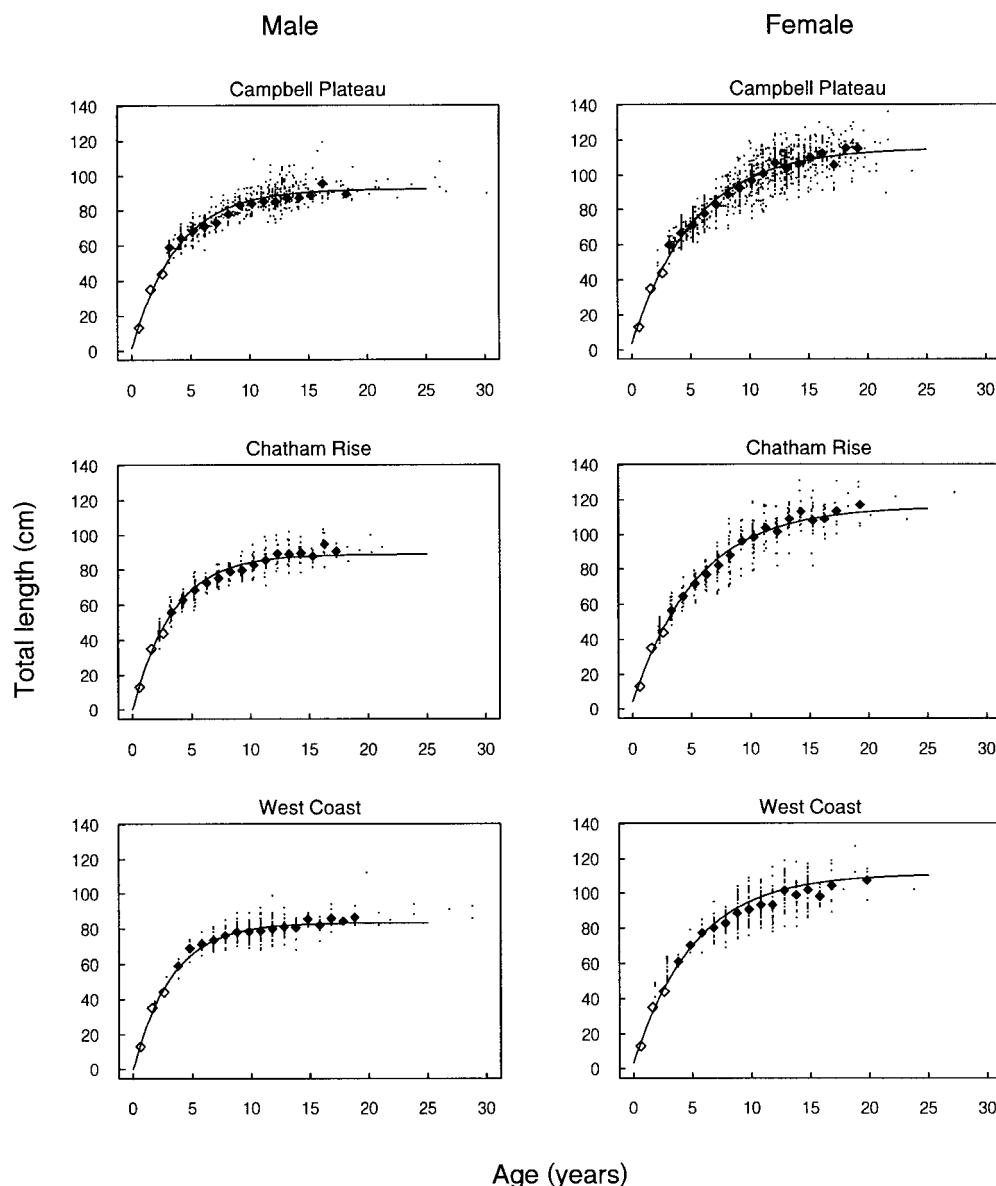
Fig. 6. Raw age–length data and calculated von Bertalanffy growth curves for hake from the Campbell Plateau, Chatham Rise and west coast of the South Island, by sex. Mean lengths at age (where $n \geq 3$ years) are plotted as closed diamonds. Open diamonds represent the estimated mean lengths at ages 0·6, 1·6 and 2·6 years, from Fig. 3.

class apparent in the Campbell Plateau distributions also appears relatively abundant on the Chatham Rise. The 1979 year class is not dominant in the WCSI population, but several relatively strong year classes spawned in the early 1980s are apparent.

The age distributions from all three areas imply that hake recruitment is variable. Juvenile length–frequency data from the WCSI (see Fig. 3) support this hypothesis. The 1994 and 1995 samples were taken from the same area by identical fishing gear, and the estimated number of age class 1+ fish in the survey area in 1995 was over 70 times greater than the estimated number of 1+ fish in 1994. Hence, the 1993 year

class spawned off WCSI is very large relative to other recently spawned year classes.

Discussion

Studies of age and growth of *Merluccius* species are numerous because of their importance as commercial fish in many areas (Pitcher and Alheit 1995). Though the interpretation of some merluccid otoliths has been controversial because of the complex nature of the early growth zones and the frequent lack of clarity of true annuli (e.g. Penttila and Dery 1988), the present study has shown

Table 3.   Within-reader comparisons of *(a)* 114 otoliths from Sample 4 in Table 1 and *(b)* 60 otoliths from Samples 4, 8 and 9 in Table 1
Age class, age class at first reading; Diff., extent by which the second reading differed from the first; Sim., percentage of fish by age class for which both readings were the same

(a)

Diff.	Age class																Total
	2	3	4	5	6	7	8	9	10	11	12	13	14	15–16	17–19	20+	
+2							1							2			3
+1		1	2			1	2	2	2	2		3	1	2	1		19
0		5	8	3	2	1	2	4	3	5	8	8	8	6	4	1	68
−1			1	1			2		3	3	1	4	1	1	1		18
−2									1				1	2			4
−3														1	1		2
Sim. (%)		83	73	75	100	50	29	67	33	50	89	53	73	43	57	100	60

(b)

Diff.	Age class							Total
	10	11	12	13	14	15	16	
+3			1					1
+2				1		1		2
+1	1	1	2	1	2	1		8
0	6	2	7	6	6	5	3	35
−1		1	1	2	2		1	7
−2		1	1		1	1	2	6
−3					1			1
Sim. (%)	86	40	58	60	50	63	50	58

that otoliths of *M. australis* can be interpreted consistently to provide estimates of age. Growth was validated to age 1 by following the progression of length modes, and from age 2 onwards by examining the state of the otolith margins. The progression of a strong 1979 year class through age–frequency distributions over a five-year period provided further evidence that the ageing method was valid.

Comparisons of the present work with previous ageing studies of *M. australis* from New Zealand (Wyszynski 1986; Colman and Vignaux 1992) suggest that all authors have been interpreting otoliths quite similarly (Fig. 8). Curves from the three studies representing growth of male hake from WCSI (Curves M2, M3 and 4) are virtually identical. However, the growth curves for Chilean *M. australis* (Ojeda
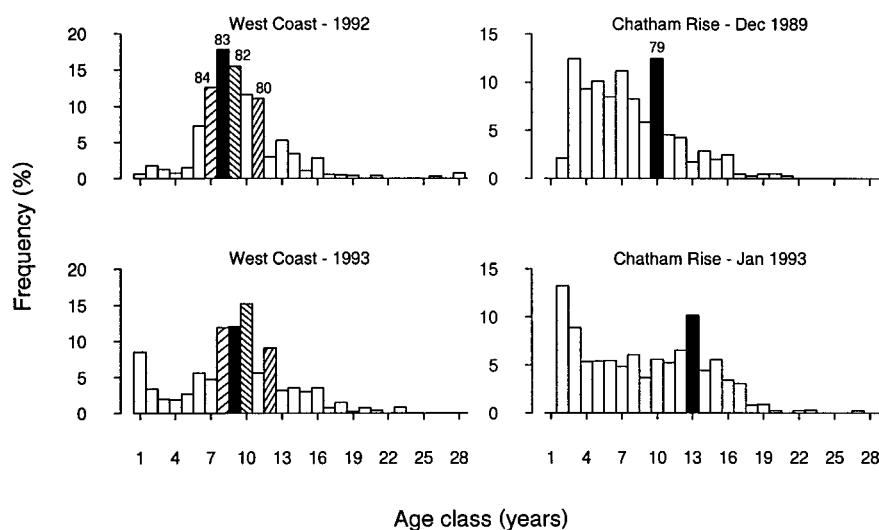

Fig. 7. Calculated age distributions for the total catch from trawl surveys of the Chatham Rise in December 1989 and January 1993 and for the commercial catch from the west coast of the South Island in winter 1992 and 1993. Year classes mentioned in the text are noted on the figure. See Table 1 for sample sizes.
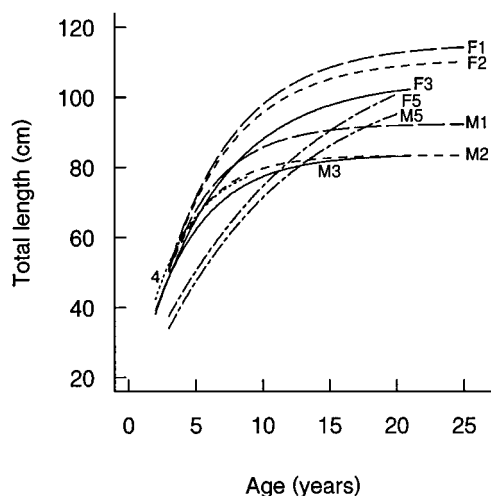
Fig. 8. Calculated von Bertalanffy growth curves for *Merluccius australis*. Curves are plotted over the range of age data used to calculate the parameters. F, female; M, male; 1, Campbell Plateau (present study); 2, WCSI (present study); 3, WCSI (Colman and Vignaux 1992); 4, WCSI (3F + 17 M; Wyszynski 1986); 5, Chile (Ojeda and Aguayo 1986).

and Aguayo 1986) are very different from those for New Zealand fish and imply either a different pattern of growth or a different interpretation of the otoliths. There is insufficient information in that paper to suggest why the differences have occurred. Wyszynski (1986) commented on the translucent band often apparent inside the first true annuli and postulated that it represented a lifestyle change as the fish shifted from a pelagic to a demersal habitat. A similar 'pelagic zone' has been noted in the otoliths of other *Merluccius* species (Penttila and Dery 1988).

Female hake are larger than males at corresponding ages, a trend noted for *M. australis* by Ojeda and Aguayo (1986) and Colman and Vignaux (1992) and general to *Merluccius* species (Pitcher and Alheit 1995). The differences in growth curves for males and females from the same area are statistically significant. The growth of both sexes is relatively rapid up to about age 4–5 but then slows markedly. Hake begin to mature sexually at age 6 at lengths of about 65 cm for males and 70 cm for females (Colman 1995). Growth by both sexes, but particularly males, is slight after about 12 years.

Merluccius australis is among the largest and most long-lived of the *Merluccius* species, but this may be due in part to a low level of exploitation relative to that of hake from other areas. Longevity may differ slightly between sexes: 69% of hake aged 20 years or older were male. Also, whereas 1% of all aged males were older than 20 years, the comparable figure for females was 18 years. Studies of merluccids generally show females to grow larger and have a similar or slightly greater longevity than do males (Alheit

and Pitcher 1995). Colman *et al.* (1991) estimated that 1% of the fish in a 1976 sample from the Chatham Rise and WCSI survived to at least 23 and 21 years for females and males, respectively, although no age compositions were presented. That study examined fish sampled before major fishery exploitation, whereas all samples examined in the present study were collected since late 1989 and following several years of fishing (although no estimates of instantaneous fishing mortality are available). The implied reduction in longevities since 1976 may be due to exploitation concentrating on the larger female fish, though this conclusion is based on relatively small changes in maximum age.

The length range of fish in juvenile year classes is very broad, being at least 10 cm for hake aged 0·6 years and up to 25 cm for fish aged 1·6 years (from Fig. 3). This suggests either an extended spawning season or a wide variation in growth rates of individual fish in a year class. An examination of otoliths showed the 0+ age class in 1995 to be bimodal. The 1992 distribution showed a similar pattern, but ages could not be verified. Time of peak spawning is known to vary between years on the Chatham Rise and WCSI (Colman 1995), and there is evidence that spawning off southern New Zealand can occur any time between August and March (Colman, personal communication). Protracted or batch spawning has been reported for several *Merluccius* species (Pitcher and Alheit 1995). It appears most likely that the broad length ranges are due to extended spawning periods that sometimes result in bimodal distributions within individual year classes, and to rapid overall juvenile growth. Bimodal distributions could also occur when times of peak spawning in consecutive years are less than 12 months apart. For example, a late spawning in 1990 may have caused the bimodal distribution in the 1992 survey sample (Fig. 3).

Year-class strengths of *M. australis* can vary considerably, as has been noted for other species of *Merluccius* (e.g. Woodbury *et al.* 1995). The 1993 year class spawned off WCSI was almost two orders of magnitude more abundant than any year class spawned in the previous five years. Population age distributions from the Campbell Plateau, Chatham Rise and WCSI indicate that recruitment is sufficiently variable to preclude a confident estimation of instantaneous total mortality (Z) from the slopes of the right-hand limbs of the catch curve. It has been suggested that cannibalism by *Merluccius* species may reduce the dominance of any exceptional year class and produce a more even pattern of recruitment to the fishery (Pitcher and Alheit 1995). The age distributions presented here do not exhibit variations in adult year-class strengths approaching two orders of magnitude, but the strengths of these year classes when they were juvenile are unknown, so smoothing of recruitment cannot be ruled out.

Estimates of instantaneous natural mortality (M) were derived from the equation $M = \log_e 100/A_{max.}$, where $A_{max.}$ is the age reached by 1% of a virgin population (Sparre *et al.* 1989). The samples aged here suggest an $A_{max.}$ value of about 20 years for male hake and 18 years for female hake, giving estimates for M of 0·23 and 0·26, respectively. However, these samples were not from virgin populations, so M may be slightly overestimated. Colman *et al.* (1991) used a similar method to produce estimates of M of 0·22 and 0·20 for males and females, respectively, from populations that had been only lightly exploited. It seems likely that M for hake is in the range 0·20–0·25.

Several methods have been used to differentiate hake stocks around the world, e.g. analyses of distribution patterns, growth, morphometrics, immunobiology, genetics and reproductive biology (Alheit and Pitcher 1995). The results from the present age and growth study provide some insights into the possible stock structure of New Zealand hake. Hake from the WCSI have significantly slower growth rates than fish from the Campbell Plateau or Chatham Rise, and growth rates for males differ between the Chatham Rise and the Campbell Plateau. Populations from the last two areas both exhibit a strong 1979 year class, which is not apparent in the WCSI samples. A comparison of the estimated age distributions from the Campbell Plateau and Chatham Rise show younger age classes to be better represented on the Chatham Rise, particularly age classes 2+ and 3+ in summer 1992–93 and age classes 3+ to 8+ in 1989. Hence, it is likely that there are at least two separate stocks of hake in New Zealand waters, with WCSI fish being clearly distinct from the rest. The Chatham Rise and Campbell Plateau populations could also be separate stocks, despite their comparable female growth rates, as differences are apparent in their population age structures and clearly defined spawning grounds are present in both areas.

Acknowledgments

References

Alheit, J., and Pitcher, T. J. (Eds) (1995). 'Hake: Biology, Fisheries and Markets.' (Chapman and Hall: London.) 478 pp.

Annala, J. H., and Sullivan, K. J. (1996). Report from the Fishery Assessment Plenary, April–May 1996: stock assessments and yield estimates. 308 pp. (Unpublished report available from NIWA library, Wellington.)

Colman, J. A. (1995). Biology and fisheries of New Zealand hake (*M. australis*). In 'Hake: Biology, Fisheries and Markets'. (Eds J. Alheit and T. J. Pitcher.) pp. 365–88. (Chapman and Hall: London.)

Colman, J. A., and Vignaux, M. (1992). Assessment of hake (*Merluccius australis*) for the 1992–93 fishing year. NZ Fisheries Assessment Research Document No. 92/17. 23 pp. (Unpublished report available from NIWA library, Wellington.)

Colman, J. A., Stocker, M., and Pikitch, E. (1991). Assessment of hake (*Merluccius australis*) stocks for the 1991–92 fishing year. NZ Fisheries Assessment Research Document No. 91/14. 29 pp. (Unpublished report available from NIWA library, Wellington.)

Ojeda, V., and Aguayo, M. (1986). Edad y crecimiento de merluza del sur (*Merluccius australis*) (Gadiformes–Merlucciidae). *Investigación Pesquera (Chile)* **33**, 47–59.

Patchell, G. J. (1981). The Westland hake fishery. NZ Fisheries Research Division Occasional Publication No. 31. 18 pp.

Penttila, J., and Dery, L. M. (Eds) (1988). Age determination methods for northwest Atlantic species. NOAA Technical Report NMFS 72. 135 pp.

Pitcher, T. J., and Alheit, J. (1995). What makes a hake? A review of the critical biological features that sustain global hake fisheries. In 'Hake: Biology, Fisheries and Markets'. (Eds J. Alheit and T. J. Pitcher.) pp. 1–14. (Chapman and Hall: London.)

Ralston, M. L., and Jennrich, R. I. (1978). DUD, a derivative-free algorithm for nonlinear least squares. *Technometrics* **20**, 7–14.

Sparre, P., Ursin, E., and Venema, S. C. (1989). Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fisheries Technical Paper No. 306. 337 pp.

Woodbury, D., Hollowed, A. B., and Pearce, J. A. (1995). Interannual variation in growth rates and back-calculated spawn dates of juvenile Pacific hake (*Merluccius productus*). In 'Recent Developments in Fish Otolith Research'. (Eds D. H. Secor, J. M. Dean and S. E. Campana.) pp. 481–96. (University of South Carolina Press: Columbia, SC.)

Wyszynski, M. (1986). Attempt to determine the applicability of various bony elements for estimation of age and growth of hake *Merluccius australis* (Merluccidae) from New Zealand waters. *Reports of the Sea Fisheries Institute, Gdynia* **21**, 62–88.