CSIRO PUBLISHING

Marine & Freshwater Research

Volume 51, 2000

A journal for the publication of original contributions
in physical oceanography, marine chemistry,
marine and estuarine biology and limnology

www.publish.csiro.au/journals/mfr

All enquiries and manuscripts should be directed to
Marine and Freshwater Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood
Vic. 3066
Australia
Telephone: 61 3 9662 7618
Facsimile: 61 3 9662 7611
Email: ann.grant@publish.csiro.au

CSIRO AUSTRALIA

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

Academy of Science

Mar. Freshwater Res., 2000, **51**, 35–42

Age, growth and maturity of a New Zealand endemic shark (*Mustelus lenticulatus*) estimated from vertebral bands

Malcolm P. Francis and Caoimhghin Ó Maolagáin

National Institute of Water and Atmospheric Research, PO Box 14901, Wellington, New Zealand.
email: m.francis@niwa.cri.nz

Abstract. Rig (*Mustelus lenticulatus*) specimens were aged by counting growth bands in whole vertebrae that were illuminated laterally with fibre-optic lights. Bands were counted by two readers who used information on the diameter of the vertebrae of new-born young and 1-year-old juveniles to identify the inner bands. The greatest estimated age was 12.1 years for a female of 137 cm total length, but few rig were more than 8 years old. For west coast South Island (WCSI) rig, there was no significant difference in growth rates of males and females. After pooling both sexes, there was no significant difference in growth rates between WCSI and east coast South Island (ECSI) rig. The combined WCSI and ECSI von Bertalanffy growth curve was $L_t = 147.2\ (1 - e^{-0.119[t + 2.35]})$. This curve agreed well with growth curves derived from length–frequency data, but validation of the ageing technique is still required. WCSI males mature at ~85 cm and 5–6 years, and females at ~100 cm and 7–8 years. ECSI rig probably mature at similar lengths and ages. Tagged rig have been recaptured after nearly 14 years at liberty. Longevity probably exceeds 15 years, and may exceed 20 years.

Extra keywords: vertebrae, longevity.

Introduction

Mustelus lenticulatus Phillipps, 1932 (family Triakidae) is a small shark that is endemic to New Zealand, the Kermadec Islands and Norfolk Island in the south-west Pacific Ocean. In New Zealand the species is known as rig, and it is fished commercially throughout the country. Commercial landings increased rapidly during the 1970s and early 1980s to peak at 3800 t in 1983 (Francis 1998). Declining catches and catch rates, and high exploitation rates, indicated that rig stocks were being overfished. In 1986, when a Quota Management System was introduced, total quotas were set conservatively to promote stock rebuilding. During the period 1992–93 to 1996–97 landings averaged about 1750 t per year (Francis 1998). Recreational landings of rig (estimated from fishing diary surveys) were only about 100 t per year in 1991–94 (Francis 1998).

Estimates of rig growth rate, age at maturity, and longevity are required for stock assessment. Many shark species have been aged by reference to growth bands laid down on their vertebral centra (Cailliet 1990), and this approach has proven successful in at least six other species of *Mustelus* (Tanaka and Mizue 1979; Wang and Chen 1982; Taniuchi *et al*. 1983; Yudin and Cailliet 1990; Moulton *et al*. 1992; Yamaguchi *et al*. 1996, 1998; Goosen and Smale 1997). Techniques used for visualizing the vertebral bands in *Mustelus* include decalcification of thick sections followed by staining with Mayer's haematoxylin, alizarin staining of whole vertebrae, and X-radiography of thick sections. Our early attempts to age New Zealand rig using various stains on whole and sectioned vertebrae, and X-radiography of thick sections, revealed diffuse vertebral rings that could not be reliably interpreted. We therefore resorted to indirect methods (length–frequency analysis and tag–recapture analysis) to generate growth curves (Francis and Francis 1992). However, indirect methods do not allow individual sharks to be aged, which precludes the precise estimation of longevity and age at maturity, and prevents determination of population age structure, year class strength and age-specific fecundity.

In this study we revisited the problem of obtaining direct age estimates for rig, and developed a simple technique for visualizing growth bands using oblique lighting of whole vertebral centra. We applied this ageing technique to samples of vertebrae collected from two rig stocks, derived age-based growth curves, and estimated age at maturity and longevity.

Methods

Most vertebrae were collected from rig caught by the 30 m research trawler *Kaharoa* during trawl surveys off west coast South Island (WCSI) and east coast South Island (ECSI) in 1993–1995 (Fig. 1, Table 1). These two locations represent two different rig stocks (Francis 1988; Annala

10.1071/MF99012 1323-1650/00/010035

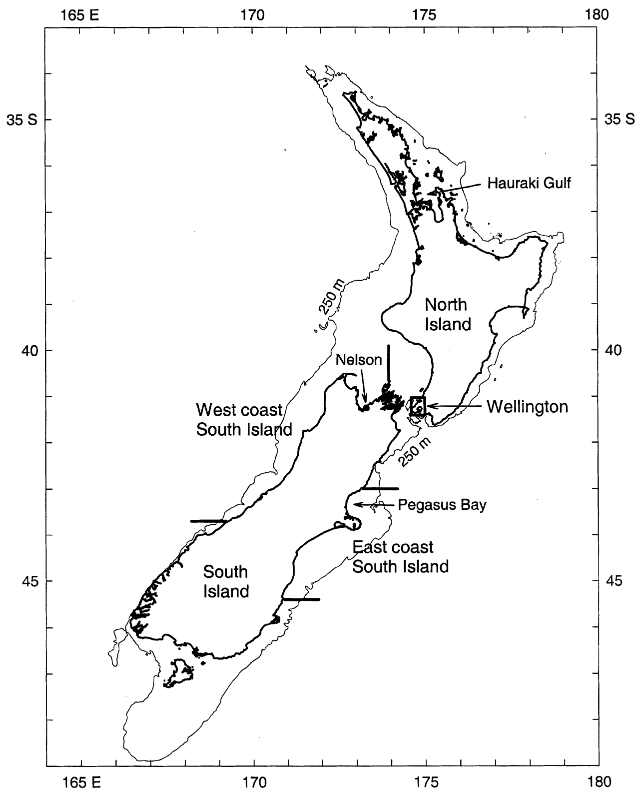

Fig. 1. Map of New Zealand showing the sampling locations (delineated by bold lines and box) and other localities mentioned in the text.

et al. 1998). Small samples of vertebrae were also collected from rig caught by set nets near Wellington in 1993–95 (Fig. 1, Table 1).

For each rig, a block of 3–10 of the largest vertebrae was removed from between the first dorsal fin and the pelvic fins, and was frozen. The largest vertebrae were used for ageing because it was anticipated that they would show the greatest band spacing and therefore resolution. Officer *et al.* (1996) reported significantly higher band counts in large thoracic vertebrae than in small cervical and precaudal vertebrae for *Mustelus antarcticus* and *Galeorhinus galeus*.

Vertebral samples were labelled with capture location, total length (TL, to the centimetre below actual length) and sex. In the laboratory, vertebrae were thawed and trimmed of neural and haemal arches and muscle and connective tissue. Individual centra were then separated and immersed in 42 g L^{-1} sodium hypochlorite until all the muscle and connective tissue had been removed (about one hour). Excessive soaking tended to dissolve the centra and made the articulating surfaces brittle and crumbly. After overnight soaking in fresh water, vertebrae were air-dried for one week.

A variety of techniques were tested for visualizing the vertebral growth bands. These included silver nitrate and alizarin staining of whole and sectioned vertebrae, obtaining X ray images of half centra and thick sections, and examination of thick sections under transmitted and reflected light. None of these techniques revealed clear vertebral bands. The bleaching process used to clean the vertebrae enhanced the three-dimensional structure of bands on the articulating faces of the vertebrae (by etching away the weakly calcified cartilage). These surface bands, and internal variations in vertebral density, were visualized by oblique lateral illumination with fibre-optic light sources (Fig. 2). By moving the light source above and below the rim of the articulating face, it was possible to view the bands with both transmitted and reflected light. This method was simple, effective, and less time-consuming than sectioning, and was used to age all the vertebrae.

Vertebral bands were counted by two readers. Both readers carried out an initial training exercise by counting bands on a subsample of the vertebrae while knowing the size and sex of the rig. The two readers then counted bands on all vertebrae without knowing the size and sex. Reader 1 used information on the diameter of the vertebrae of new-born young and 1-year-old juveniles to locate the inner band(s). New-born and 1-year old rig were identified from their lengths (the first two length modes are distinct in length–frequency distributions from Hauraki Gulf and Pegasus Bay (Fig. 1) (Francis and Francis 1992)). Reader 2 counted all vertebrae ‘blind’, but found it difficult to determine the location and number of bands in the centra of small (<60 cm) rig. Reader 2 then carried out a second reading of all vertebrae using the same technique as Reader 1. Hereinafter the single reading carried out by Reader 1 is referred to as R_1, and the first and second readings by Reader 2 as $R_{2,1}$ and $R_{2,2}$ respectively. Band counts were assessed for ageing bias and precision by using age-bias plots, and plots of the coefficient of variation (CV) against age, as recommended by Campana *et al.* (1995).

Vertebral bands were used to produce age estimates for each rig. The theoretical birthday was defined as 1 September, on the basis of birth of young during spring (Francis and Francis 1992). As in most viviparous sharks, rig lay down a ‘birth band’ on their vertebrae soon after birth. We counted the hyper-mineralized bands which are probably laid down during winter, as in *Mustelus antarcticus* (Officer *et al.* 1997). Thus, the time of band deposition approximately coincides with the theoretical birthday. Therefore, the age assigned to each rig was the band count minus one for the birth band, plus the fraction of the year elapsed between 1 September and the sampling date.

Band counts from readings R_1 and $R_{2,2}$ were similar, so the mean of the two age estimates was taken as the final age estimate for each rig. Growth curves were fitted to subsets of the length-at-age data using the von Bertalanffy growth model: $L_t = L_\infty(1-e^{-K[t-t_0]})$, where L_t is the expected length at age t years, L_∞ is the asymptotic maximum length, K is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length. Tests were made for significant differences between growth curves for *(a)* the two sexes at WCSI (samples from the other

Table 1. Rig sample collection details, and numbers of vertebrae aged by sex and area

Area	Sampling dates	Method	Females	Males	Total
West coast South Island	April 1994, March–April 1995	Bottom trawl	63	110	173
East coast South Island	May–June 1993, May–June 1994	Bottom trawl	37	34	71
Wellington	Oct. 1993–Feb. 1994, Dec. 1994–Feb. 1995	Set net	16	50	66
Total			116	194	310

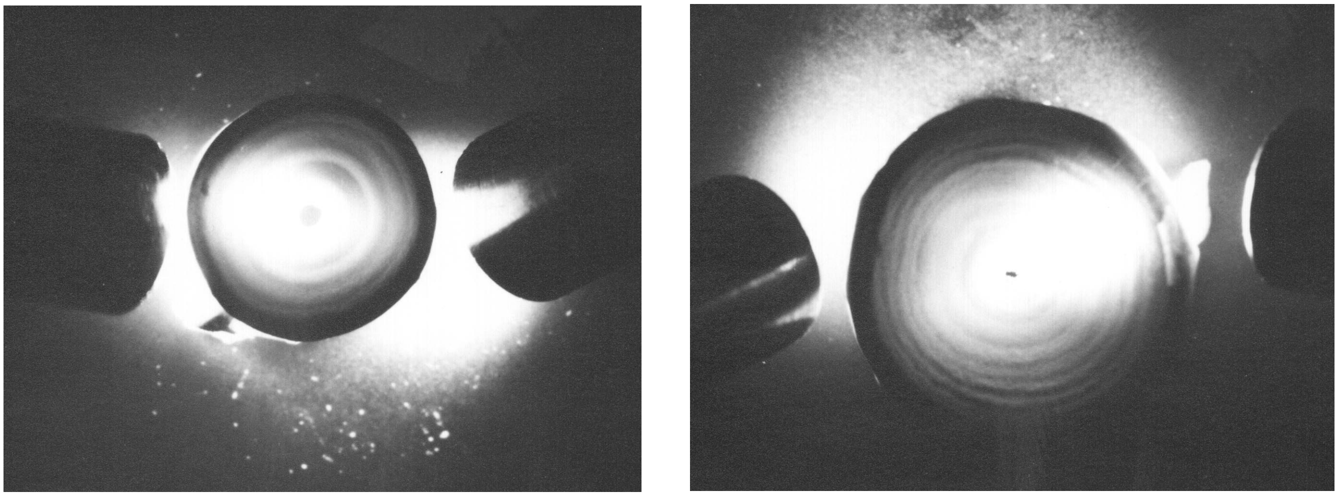

Fig. 2. Vertebral centra illuminated laterally by two fibre-optic sources. *(left)* male rig (72 cm total length) from west coast South Island with 4 bands; centrum diameter 6.5 mm. *(right)* female (97 cm) from west coast South Island with 8 bands; centrum diameter 9.3 mm.

areas were too small for testing by sex), and *(b)* WCSI and ECSI rig. We initially used Kimura's (1980) curve-fitting procedure and likelihood ratio test (see also Cerrato 1990). However, Kimura's method assumes that the residuals from fitting the von Bertalanffy growth model are normally distributed with constant variance. Inspection of diagnostic plots showed that data were normally distributed, but that the variance increased with age. This probably does not unduly affect the curve-fitting, but it may cause problems for the tests.

We therefore applied an age-standardized randomization test (Cox and Hinkley 1974). For each of 1000 simulated data sets, selected randomly with replacement from the original data, rig were allocated randomly to each subgroup (i.e. the two sexes or the two areas). The null distribution was generated by calculating, for each data set, the difference between the residual sum of squares obtained from fitting the full data (via Kimura's method) and that obtained by fitting the subgroups (again via Kimura's method) (A. Dunn, NIWA, personal communication). The probability that growth curves fitted separately to the two subgroups represented an improvement over fitting a single growth curve to the pooled data was determined by comparing the actual difference in residual sum of squares with the simulated null distribution. In conducting the randomization test, we randomly selected rig *within each age class*. This preserved the age structure of the different subgroups, and allowed a more accurate comparison. For this purpose, we rounded the mean age estimates to the nearest 0.5 years before carrying out the test.

Validation of the vertebral ageing technique by marginal increment analysis was not possible, because the samples from each stock were collected during a short period each year. However, verification of the ageing technique (Cailliet 1990) was attempted by comparing the overall growth curve based on length-at-age data (sexes and areas combined) with growth curves obtained previously for rig from length–frequency data (Francis and Francis 1992). The overall length-at-age growth curve was also compared with growth curves based on vertebral bands reported in the literature for other *Mustelus* species (Wang and Chen 1982; Yudin and Cailliet 1990; Moulton *et al.* 1992; Goosen and Smale 1997; Yamaguchi *et al.* 1998).

Length at maturity was determined for samples of rig caught during trawl surveys of WCSI in March–April 1994, 1995 and 1997. The rig were classified on a three-stage maturity scale, adapted from Francis and Mace (1980):

Immature. Males – claspers do not extend beyond posterior edge of pelvic fins. Females – ovarian eggs small (pinhead-sized) and white (no vitellogenesis).

Maturing. Males – claspers extend beyond posterior edge of pelvic fins, but are soft and uncalcified. Females – ovarian eggs medium (pinhead- to pea-sized) with some vitellogenesis producing a light yellow colour.

Mature. Males – claspers extend beyond posterior edge of pelvic fins and are heavily calcified, and the terminal cartilages can be splayed open. Females – ovarian eggs larger than pea-sized with active vitellogenesis producing an orange colour.

The WCSI rig that we aged were a subset of the samples used for estimating length at maturity, thus allowing direct estimation of age at maturity.

A randomization procedure was used to test for between-sex differences in maturity ogives. The test statistic used was a weighted average of the differences in proportions mature at age or length (the weights were devised so that each term in the summation had equal variance):

$$S = (1/m)\sum_i w_i(p_{i1} - p_{i2}), \text{where } w_i = \sqrt{\frac{N_{i1}N_{i2}(N_i - 1)}{N_i^2 p_i(1-p_i)}}$$

and N_{ij} and p_{ij} are the number and proportion mature in the ith age/length class in the jth sample, N_i and p_i are the number and proportion mature in the ith age/length class in the combined sample, and m is the number of age/length classes included (classes for which one sample was not represented, or where $p_i = 0$ or 1, were excluded from this analysis). The randomization was done only within age/length classes and so as to preserve the class sample sizes (i.e. the p_{ij} varied between simulated data sets but the N_{ij} and p_i did not).

Maturity ogives were fitted to the length- and age-at-maturity data separately by sex by use of probit analysis (Pearson and Hartley 1962). This analysis assumes that the length or age at which a randomly selected fish reaches maturity is normally distributed. Two parameters, the mean and standard deviation of the normal distribution, were fitted. Each maturity ogive is the cumulative distribution function for the associated normal distribution. The probit function was fitted by maximum likelihood. Mean lengths at maturity, and their associated confidence limits, were corrected for downward rounding of length measurements by adding 0.5 cm.

Maturity status was not determined for ECSI rig, so their age at maturity was estimated indirectly by inserting the mean lengths at maturity for Pegasus Bay rig reported by Francis and Francis (1992) into the overall growth curve (Eqn 1 below).

Our aged rig samples were small, and rig stocks have been heavily exploited for >20 years, so the maximum age from our vertebral samples is likely to underestimate longevity. An alternative estimate of longevity was obtained from data from tagging programmes conducted in 1982–84 (Francis 1988) and 1990. For tagged rig that were at liberty for more than 7 years, the age at recapture was estimated by applying the vertebral-based growth curve derived in the present study (Eqn 1 below) to the length at tagging, and then adding the period at liberty.

Results

Vertebral length, width and depth increased from behind the chondrocranium to reach a maximum between the first dorsal fin and the origin of the pelvic fins (vertebrae numbers 32–37). Near the pelvic fin origins, vertebral length declined rapidly, marking the transition from monospondylous vertebrae to diplospondylous vertebrae.

Vertebral band counts made by R_1 and $R_{2,1}$ sometimes varied markedly, and there was a systematic bias, with R_1 counts being about 0.5 bands higher on average than those for $R_{2,1}$ over most of the age range (Fig. 3*A*). Furthermore, Reader 2's age estimates for small rig were inconsistent with ages based on length–frequency distributions (Francis and Francis 1992). Counts by R_1 and $R_{2,2}$ showed much closer agreement, with no significant bias for age classes represented by sample sizes greater than 10 (Fig. 3*B*). Ageing precision was poor for the comparison between R_1 and $R_{2,1}$, but improved substantially for the comparison between R_1 and $R_{2,2}$, with CVs usually in the range 10–15% (Fig. 4).

The greatest estimated age (mean of R_1 and $R_{2,2}$) was 12.1 years for a 137 cm female from WCSI, but few rig were more than 8 years old (Fig. 5). There was a close relationship between estimated age and total length, with no obvious outliers. For WCSI, there was no significant difference between the von Bertalanffy growth curves for males and females (P = 0.18; Fig. 5*A*). After pooling the data for both sexes, there was also no significant difference between the growth curves for WCSI and ECSI (P = 0.12; Fig. 5*B*). No test was carried out for differences between Wellington and the other two areas, because data from Wellington came from set net samples whereas data from WCSI and ECSI came from trawl samples. Both methods selectively sample the population, and probably introduce some bias into the length-at-age distributions. Such biases are likely to be different for the two methods. A growth curve was therefore fitted to just the WCSI and ECSI data (Fig. 5*B*). von Bertalanffy parameter estimates for the combined WCSI+ECSI growth curve (± s.e.) were L_∞ = 147.2 cm (± 9.2), K = 0.119 (± 0.016) and t_0 = –2.35 years (± 0.27). The corresponding growth curve was

$$L_t = 147.2(1-e^{-0.119[t+2.35]}) \qquad (1)$$

The WCSI+ECSI growth curve agreed remarkably well with growth curves derived from length–frequency data from the Hauraki Gulf and Pegasus Bay by Francis and Francis (1992) (Fig. 6). The WCSI+ECSI curve also indicated that rig growth falls within the range of growth reported for other species of *Mustelus* (Fig. 7).

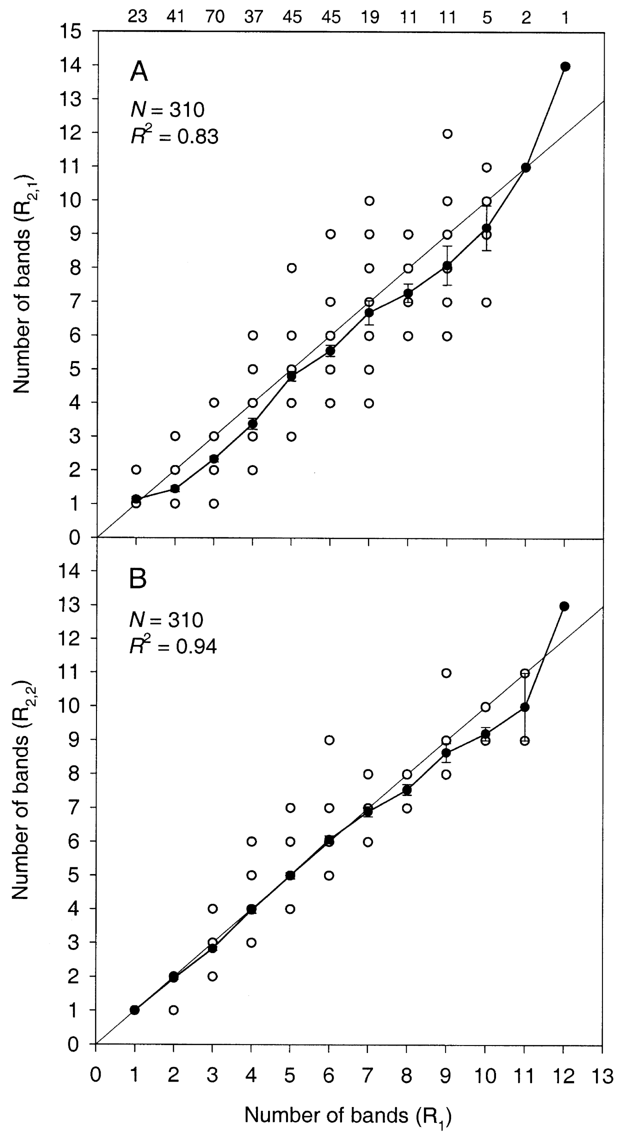

Fig. 3. Between-reader comparison of vertebral band counts for WCSI, ECSI and Wellington combined. *(A)* First count of Reader 2 *v.* Reader 1. *(B)* Second count of Reader 2 *v.* Reader 1. (○) actual count (some symbols represent more than one rig); (●) mean count of Reader 2 ± 1 s.e. Diagonal lines indicate the expected relationship. Numbers along the top axis are sample sizes for band counts made by R_1. N = total sample size.

WCSI male rig reached 50% maturity at 85.2 cm (95% confidence limits 83.9–86.4 cm) and 5.5 years (4.9–6.1 years) (Figs 8 and 9). Females matured at 99.6 cm (95.7–106.5 cm) and 7.5 years (6.3–11.4 years) (Figs 8 and 9). The female age-at-maturity ogive was poorly defined because of small sample sizes of larger fish, and this was reflected in the wide confidence interval. However, the ages at maturity estimated by inserting the mean lengths at maturity into Eqn (1) were similar to those estimated directly: 4.9 years for males and 7.1 years for females.

ECSI rig mature at about 87 cm (males) and 102 cm (females) (Francis and Francis 1992); insertion of these

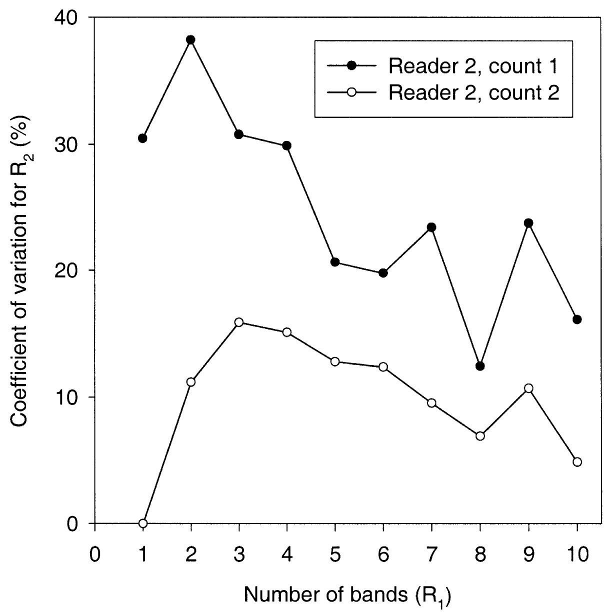

Fig. 4. Precision of rig age estimates made by Reader 2 (R_2) relative to the estimates made by Reader 1 (R_1).

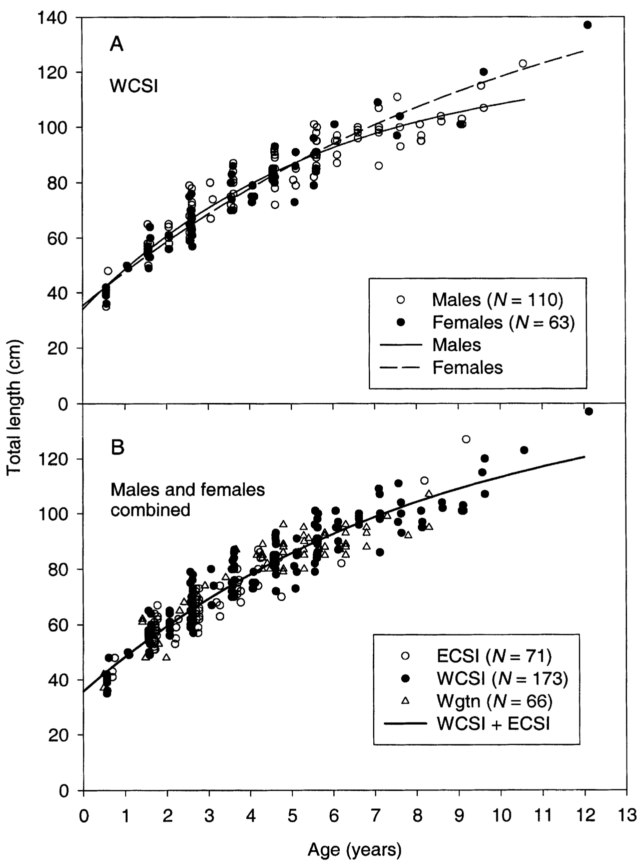

Fig. 5. Rig length-at-age, based on the mean of R_1 and $R_{2,2}$ age estimates. *(A)* WCSI, sexes separate, with fitted von Bertalanffy growth curves. *(B)* WCSI, ECSI and Wellington, sexes combined, with von Bertalanffy growth curve fitted to the combined WCSI and ECSI data. *N* = sample size.

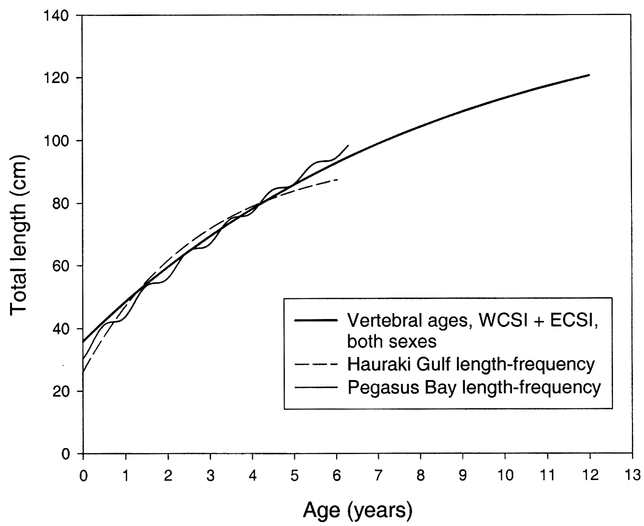

Fig. 6. Comparison of growth curves derived from vertebral ages (present study, Eqn (1)), and length–frequency data from Hauraki Gulf and Pegasus Bay (Francis and Francis 1992).

values into Eqn (1) gives estimated ages at maturity of 5.2 years (males) and 7.6 years (females). Thus length and age at maturity are similar for both WCSI and ECSI stocks.

Seven tagged rig were recaptured after 7.7–13.8 years at liberty (Table 2). Their estimated ages at tagging were between 4.0 and 6.4 years, and four out of the five males were already mature when tagged. The estimated ages of these rig when recaptured were 12.9–19.5 years (Table 2). On the basis of these results, longevity of rig probably exceeds 15 years, and may exceed 20 years.

Discussion

In the absence of ancillary information, identification of the birth and one-year bands on rig vertebrae was difficult. Data on the diameter of the vertebrae at birth and at an age of one year were obtained from new-born young and presumed one-year-old juveniles (determined from their lengths). With this information, both readers obtained similar band counts with no apparent between-reader bias, and low CVs.

The remarkable consistency between the WCSI+ECSI growth curve generated here and growth curves based on length–frequency data from Hauraki Gulf and Pegasus Bay has been noted. Vertebral bands have been validated or verified in four other species of *Mustelus*, including seven populations of *M. manazo* (Tanaka and Mizue 1979; Wang and Chen 1982; Taniuchi *et al.* 1983; Moulton *et al.* 1992; Goosen and Smale 1997; Officer *et al.* 1997; Yamaguchi *et al.* 1998). In two other species of *Mustelus*, the band pattern was consistent with annual deposition, but the number and spacing of samples used for centrum edge validation were insufficient to provide definitive validation (Yudin and Cailliet 1990). These results suggest that the bands we counted in rig vertebrae are deposited annually, but validation is still required.

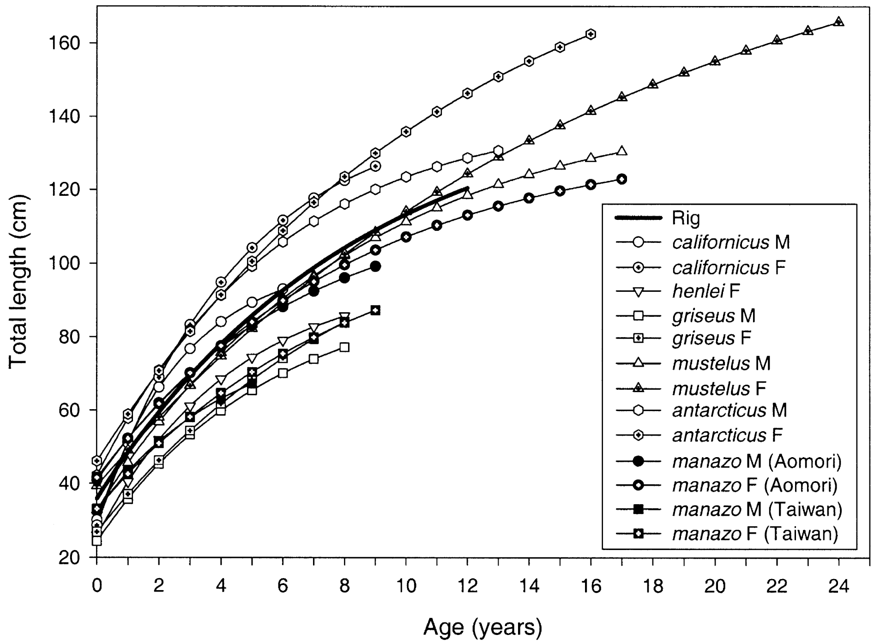

Fig. 7. Comparison of rig growth curve (present study, Eqn (1)), with growth curves reported in the literature for other species of *Mustelus*. M, males; F, females. For *M. manazo*, only the two populations showing the most extreme growth (Aomori in northern Japan, and Taiwan) are shown. Sources are given in the text.

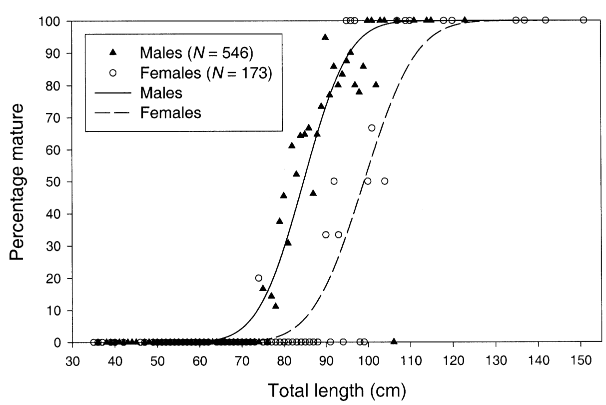

Fig. 8. Percentage maturity by length for WCSI rig collected in March–April 1994, 1995 and 1997. Curves were fitted by probit analysis. N = sample size.

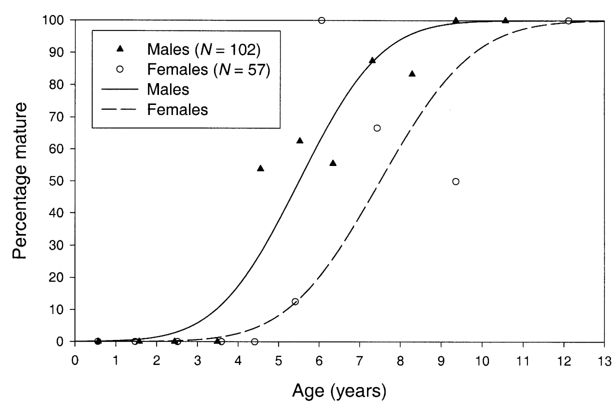

Fig. 9. Percentage maturity by age class for a subset of the WCSI rig shown in Fig. 8. Curves were fitted by probit analysis. N = sample size.

Although no significant difference in the growth curves of male and female WCSI rig was found, we cannot discount the possibility that the two sexes do have different growth rates; in other species of *Mustelus*, differences only become apparent in older, mature sharks (Francis and Francis 1992; Moulton *et al*. 1992; Yamaguchi *et al*. 1996, 1998; Goosen and Smale 1997), and our WCSI samples contained few rig older than eight years. Furthermore, tagging data for WCSI and ECSI rig (combined) revealed significantly higher growth rates for female rig than male rig (Francis and Francis 1992).

Studies on other *Mustelus* species suggest that females tend to live longer than males (Fig. 7; Francis and Francis 1992; Moulton *et al*. 1992; Yamaguchi *et al*. 1996, 1998; Goosen and Smale 1997). Female rig grow considerably larger than male rig (maximum recorded lengths are 151 cm for females and 126 cm for males (Francis 1997)), but further work is required to determine whether they live longer than males, grow faster than males, or both. Of interest in this respect is that the tagged rig that was at liberty for the longest period (13.8 years), and which produced our greatest estimate of longevity (19.5 years), was a male (Table 2).

Table 2. Estimated age at recapture of tagged rig that were at liberty more than seven years

Tagging area	Total length at tagging (cm)	Estimated age at tagging (years)	Sex	Maturity status at tagging	Period at liberty (years)	Estimated age at recapture (years)
WCSI	78	4.0	M	Mature	8.9	12.9
WCSI	82	4.5	M	Maturing	9.0	13.5
WCSI	92	5.9	M	Mature	7.7	13.6
ECSI	87	5.2	F	Unknown	9.1	14.3
ECSI	79	4.1	F	Unknown	10.9	15.0
WCSI	95	6.4	M	Mature	9.1	15.5
WCSI	91	5.7	M	Mature	13.8	19.5

Francis and Mace (1980) sampled rig caught in set nets at the northern end of the range of the WCSI stock, near Nelson (Fig. 1). Their samples contained no immature males, and they concluded that males mature at <82 cm, and females at ~85 cm. The present study indicates that WCSI males mature at ~85 cm and females at ~100 cm. The differences between the two studies may have resulted from *(a)* small sample sizes for females in the present study, *(b)* the greater geographic range sampled in the present study, and the possible presence of distinct sub-stocks within the overall stock range or *(c)* a concentration of mature animals among small size classes of rig near Nelson, where mating occurs (Francis and Mace 1980). No maturity data were collected for ECSI rig in the present study, but previous estimates of the lengths at 50% maturity of 87 cm for males and 102 cm for females (Francis and Francis 1992) suggest that they mature at about the same lengths as WCSI rig.

WCSI male and female rig mature at about 5–6 and 7–8 years respectively, and ECSI rig mature at similar ages. The male age at maturity is consistent with an estimate of 5 years provided for Pegasus Bay male rig based on a growth curve derived from length–frequency data (Francis and Francis 1992). Rig from the Hauraki Gulf comprise a distinct stock, with individuals maturing at smaller sizes and younger ages (about 4 years for males and 5 years for females (Francis and Francis 1992)) than in WCSI or ECSI. Most other species of *Mustelus* mature at younger ages than rig (Francis and Francis 1992), but *M. antarcticus* from Australia (Moulton *et al*. 1992) and *M. griseus* from Taiwan (Wang and Chen 1982) both mature at 5–7 years, and *M. mustelus* from South Africa matures at 6–9 years (males) and 12–15 years (females) (Goosen and Smale 1997).

Longevity of rig probably exceeds 15 years, and possibly 20 years, thus extending the minimum longevity estimate of 12 years provided by Francis and Francis (1992). The greatest age so far reported for a species of *Mustelus* was 24 years for *M. mustelus* (Goosen and Smale 1997). In general, larger species of *Mustelus* live longer than smaller species (Fig. 7), though many literature reports probably underestimate longevity because they were based on small sample sizes taken from exploited populations (Francis and Francis 1992).

Sharks are typically considered to be long-lived and slow-growing. Although this is true for some species, others are short-lived and fast-growing. *Mustelus* species exhibit moderate to fast growth and have short to moderate life spans. Thus, even within a single genus, there is considerable diversity of growth patterns and longevity (Fig. 7). The paradigm that sharks comprise a homogeneous group characterized by slow growth and high longevity is no longer tenable and should be abandoned.

Acknowledgments

We thank our NIWA colleagues, especially Michael Stevenson, for assisting with the collection of vertebral samples and maturity data. Alistair Dunn and Chris Francis provided statistical advice and assistance with the randomization tests and probit analyses. This research was funded by the New Zealand Ministry of Fisheries under project SHA801.

References

Annala, J. H., Sullivan, K. J., O'Brien, C. J., and Iball, S. D. (Eds). (1998). Report from the Fishery Assessment Plenary, May 1998: stock assessments and yield estimates. (Ministry of Fisheries: Wellington.) 409 pp.

Cailliet, G. M. (1990). Elasmobranch age determination and verification: an updated review. *NOAA Technical Report NMFS* **90**, 157–65.

Campana, S. E., Annand, M. C., and McMillan, J. I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* **124**, 131–8.

Cerrato, R. M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1416–26.

Cox, D. R., and Hinkley, D. V. (1974). 'Theoretical Statistics.' (Chapman and Hall: London.) 511 pp.

Francis, M. P. (1988). Movement patterns of rig (*Mustelus lenticulatus*) tagged in southern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **22**, 259–72.

Francis, M. P. (1997). Rig records. *Seafood New Zealand* **5**(5), 25.

Francis, M. P. (1998). New Zealand shark fisheries: development, size and management. *Marine and Freshwater Research* **49**, 579–91.

Francis, M. P., and Francis, R. I. C. C. (1992). Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). *Australian Journal of Marine and Freshwater Research* **43**, 1157–76.

Francis, M. P., and Mace, J. T. (1980). Reproductive biology of *Mustelus lenticulatus* from Kaikoura and Nelson. New Zealand *Journal of Marine and Freshwater Research* **14**, 303–11.

Goosen, A. J. J., and Smale, M. J. (1997). A preliminary study of age and growth of the smooth-hound shark, *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science* **18**, 85–91.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**, 765–76.

Moulton, P. L., Walker, T. I., and Saddlier, S. R. (1992). Age and growth studies of gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. *Australian Journal of Marine and Freshwater Research* **43**, 1241–67.

Officer, R. A., Gason, A. S., Walker, T. I., and Clement, J. G. (1996). Sources of variation in counts of growth increments in vertebrae from gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*: implications for age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1765–77.

Officer, R. A., Day, R. W., Clement, J. G., and Brown, L. P. (1997). Captive gummy sharks, *Mustelus antarcticus*, form hypermineralised bands in their vertebrae during winter. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2677–83.

Pearson, E. S., and Hartley, H. O. (1962). 'Biometrika Tables for Statisticians.' Vol. 1. (Cambridge University Press: Cambridge.)

Tanaka, S., and Mizue, K. (1979). Studies on sharks - XV. Age and growth of Japanese dogfish *Mustelus manazo* Bleeker in the East China Sea. *Bulletin of the Japanese Society of Scientific Fisheries* **45**, 43–50.

Taniuchi, T., Kuroda, N., and Nose, Y. (1983). Age, growth, reproduction, and food habits of the star-spotted dogfish *Mustelus manazo* collected from Choshi. *Bulletin of the Japanese Society of Scientific Fisheries* **49**, 1325–34.

Wang, T.-M., and Chen, C.-T. (1982). Age and growth of smooth dogfish, *Mustelus griseus* in northwestern Taiwan waters. *Journal of the Fisheries Society of Taiwan* 9, 1–12.

Yamaguchi, A., Taniuchi, T., and Shimizu, M. (1996). Age and growth of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fisheries Science* **62**, 919–22.

Yamaguchi, A., Taniuchi, T., and Shimizu, M. (1998). Geographic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Fisheries Science* **64**, 732–9.

Yudin, K. G., and Cailliet, G. M. (1990). Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei*, sharks from central California. *Copeia* **1990**, 191–204.

Manuscript received 15 February 1999; revised and accepted 19 August 1999