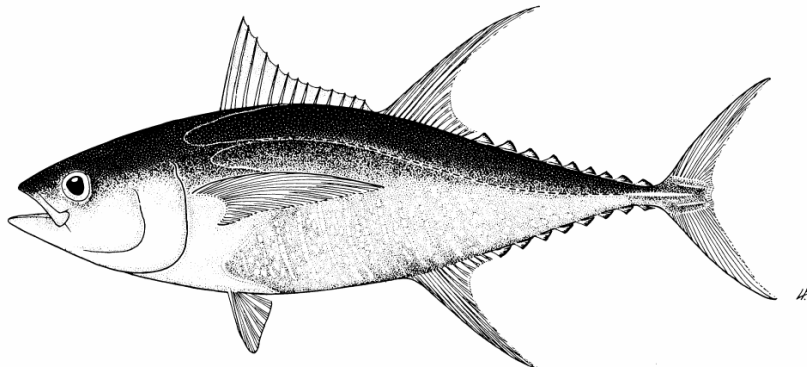


Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters



S.D. Bishop, M. P. Francis & C. Duffy

National Institute of Water and Atmospheric Research, New Zealand.
Ministry of Fisheries, New Zealand

July 2004

EXECUTIVE SUMMARY

Bishop, S.D.; Francis, M.P.; Duffy, C. (2004). Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters.

New Zealand Fisheries Assessment Report 2004/??. 35 p.

Shortfin mako sharks were aged by counting growth bands in sectioned vertebrae collected from recreational fishing competitions and the tuna longline fishery. Replicate counts were made from images taken under reflected light. No systematic ageing bias was present within or between readers and count precision was high. Growth is rapid in early years and quickly declines. Vertebral data showed that males and females grow at similar rates until age 7–9 years, after which the relative growth of males declines. Von Bertalanffy growth parameters were: male $L_{\infty} = 302.16$ cm fork length (FL), $K = 0.0524$ and $t_0 = -9.04$ years; female $L_{\infty} = 732.41$ cm FL, $K = 0.0154$ and $t_0 = -10.79$ years. MULTIFAN analysis of length-frequency data from the tuna longline fishery estimated substantially faster growth than that derived from vertebral ages. MULTIFAN growth rates were considered reliable up to age 2–3 years, and thereafter vertebral ages were more reliable. Longevity estimates based on the maximum ages from vertebral band counts were 29 and 28 years for males and females respectively. Natural mortality estimates calculated from Hoenig's (1983) equation were 0.14 for males and 0.15 for females. Ages at 50% maturity determined by probit analysis of paired age and maturity data were 6.9 years for males and 19.1 years for females. Indirect age at maturity estimates from conversion of length at maturity data were 8–9 years for males and 20–21 years for females. Median maturity in males corresponded with the age at which male growth rate declined.

The shortfin mako is a large, slow-growing, and late-maturing species with high longevity and low natural mortality. Comparison of growth curves reported here with overseas studies suggest that there are no regional differences in growth rates. Stock size and structure are unknown for this species internationally, and management should be of a precautionary nature.

1 INTRODUCTION

The shortfin mako shark (*Isurus oxyrinchus*) is a large pelagic predator occurring worldwide in tropical and temperate waters (Last & Stevens 1994; Compagno 2001). Sexual dimorphism occurs, with females reaching lengths up to 362 cm fork length (FL) and males about 250 cm FL (Bigelow & Schroeder 1948; Pratt & Casey 1983)¹. Shortfin makos are targeted recreationally, and are frequently caught as bycatch on tuna longliners operating within New Zealand's Exclusive Economic Zone. Bycatch of shortfin makos by pelagic tuna longlines has increased since the 1993–94 fishing year due to the expansion of the tuna longline fishery (Francis 1998; Ayers et al. in press). Reported commercial landings of shortfin makos were 200–300 t in 2000–01 and 2001–02, but catch estimates based on landings by observed vessels indicate that the tuna longline fishery caught about 700 t and 340 t respectively in the same two years (Ayers et al. in press).

Recreational fishing began in 1915, and has been popular ever since. Most recreational fishing competitions in New Zealand now place minimum weight limits of around 40 kg on sharks, and this has reduced the number of small shortfin makos being landed (Francis 1998). Furthermore, since 1987 a considerable increase in the popularity of tag-and-release has progressively reduced the number of shortfin makos landed in New Zealand and overseas (Casey & Kohler 1992; Francis 1998). Francis (1998) estimated the annual catch of shortfin makos by big game fishing clubs at around 500–750 individuals per year from 1977 to 1985, and around 200–450 individuals per year from 1987 to 1996. However, this decline in catches may not be entirely due to changed regulations and fishing practices, and could be a sign of declining populations.

Little is known about the biological productivity of the shortfin mako in New Zealand waters and a thorough understanding of population demographics is needed to properly assess the impacts of recreational and commercial fishing on shortfin mako stocks. Age estimation is essential to stock assessment and management of New Zealand stocks as it allows the calculation of growth rates, age at maturity, longevity and natural mortality (Cailliet et al. 1983; Campana 2001; Natanson et al. 2002).

Previous studies on shortfin mako have used bands deposited in vertebrae to estimate age. Assuming annual band deposition, the greatest age reported is 23 years (Pratt & Casey 1983). Natural mortality has not yet been estimated for this species. Little is known about the reproductive cycle and there are few records of pregnant females worldwide (Mollet et al. 2000) with only one from New Zealand (Duffy & Francis 2001). Fecundity is highly variable and can range from 4 to 25 young which are born at about 60–65 cm (Mollet et al. 2000; Duffy & Francis 2001). In a companion study, length at maturity was estimated to be 180–185 cm for males and 275–285 cm for females (Francis & Duffy in prep).

Age and growth of shortfin makos have not been studied in New Zealand waters before. This study, funded by the Ministry of Fisheries under project TUN2002/01, had the following objectives:

1. Determine age and growth of the shortfin mako shark in New Zealand waters using vertebral samples.
2. Conduct MULTIFAN analysis of length-frequency data.

¹ All reported length measurements have been converted to fork length (FL) for consistency and comparison. Conversion equations of length measurements are given in Appendix A.

3. Estimate longevity and natural mortality.
4. Estimate age at maturity.

2 METHODS

2.1 Age and growth

2.1.1 Data collection

Vertebral samples, and length, weight, and reproductive data were obtained from two principal sources: recreational gamefishing competitions and Ministry of Fisheries (MFish) observers aboard tuna longliners. Samples were obtained from North Island recreational gamefishing competitions during the summers of 2001–02 and 2002–03 (Appendix B). Additional vertebral samples collected by CD and MPF from earlier competitions (back to 1994) were also made available for this study. MFish observers collected samples between April 2002 and August 2003 from between the Kermadec and Snares islands, but most came from off Fiordland. A total of 95 vertebral samples were collected from competitions and 170 from MFish observers, giving a total of 265 samples. Samples included both sexes and encompassed a wide length range of 100–347 cm. Embryonic samples were also used to determine length at birth and the birth band radius (Section 2.1.3).

For competition-caught sharks, a block of 4–6 vertebrae was removed for ageing from underneath the first dorsal fin. Vertebral samples were collected by MFish observers from the same region where possible, but when the shark was commercially valuable vertebral samples were taken from immediately behind the head (to avoid damaging the carcass). Because vertebrae were collected from different regions of the vertebral column, whole vertebral columns were removed from small (173 cm), medium (210 cm), and large (238 cm) sharks to determine whether the number of growth rings was consistent throughout the column over the size/age range.

2.1.2 Sectioning and reading protocol

A single section ca. 0.6 mm thick was cut from a vertebra from each shark for age determination. Whole centra were cut in half along the frontal plane using a 600 grit diamond blade, bronze embedded circular saw. Excess material was then trimmed off the edge of one of the halves using a Hillquist diamond lapping wheel saw arm to get a 3 mm thick ‘bow tie’ section. Lastly, one half of the section was gradually ground down using the Hillquist lapping diamond cup wheel until the section was 0.6 mm thick. Owing to the concentric nature of the growth rings in shortfin mako vertebrae, each triangular half of the ‘bow tie’ section contains the same number of rings and thus counts only need to be performed on one half. The final grinding of one half of the ‘bow-tie’ section allowed retention of the focus (centre of the vertebra), which is essential to obtain accurate measurements of the birth band radius and vertebral radius. Sections were stored in 70% ethanol.

Vertebral sections were photographed under reflected light while submerged in 70% ethanol. Reading followed the validated porbeagle shark (*Lamna nasus*) ageing method of

Natanson et al. (2002). This technique has also provided reliable counts for shortfin mako sharks (L. Natanson, Narragansett Laboratory, National Marine Fisheries Service, Rhode Island, USA, unpublished data). The primary reader (SDB) was trained by L. Natanson, and the second reader (CD) was trained by the primary reader. Band counts were made on images on screen. Counts excluded the birth band (Fig. 1), which represents age zero. Alternating pairs of light and dark bands were assumed to represent one year of growth (see Discussion), so only dark (translucent) bands were counted. Each section was read twice by the primary reader and once by the second reader. Bands were counted without knowledge of the fish length or sex. Counts that disagreed by three or more years between readers were read a second time. If counts did not agree to an ‘acceptable’² level after the second count, the sample was classified as unreadable and discarded.

2.1.3 Centrum analysis

Validation of the innermost growth increment or birth band was achieved by comparing the mean distance from the outer edge of the birth band to the focus in 256 sections, with the vertebral radii of six embryonic sharks. To ensure that the structure (vertebra) used for ageing grows in unison with the organism, regression analysis was used to compare vertebral radius with individual fork length.

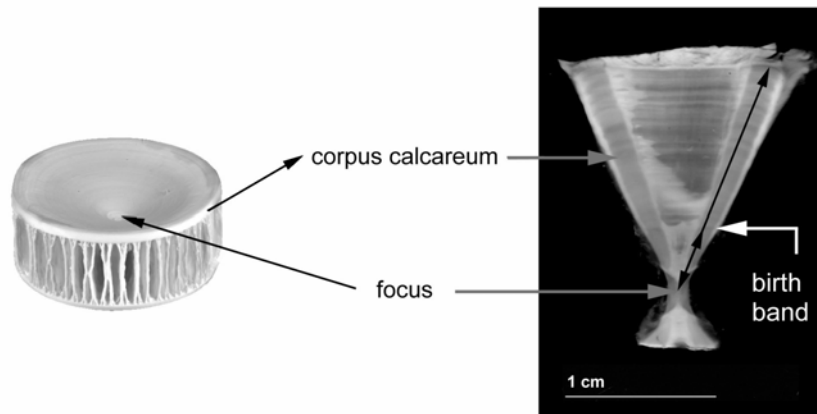


Figure 1: Diagram illustrating the locations of the focus, corpus calcareum and birth band on a whole centrum (left) and a half bow-tie section (right). Black arrows on the vertebral section show where measurements of vertebral radius (long arrow), and birth band radius (short arrow) were taken.

2.1.4 Bias and precision

Both within- and between-reader biases were controlled as much as possible via continual correspondence with reading laboratories overseas (primarily NMFS Laboratory, Narragansett, RI, USA) to ensure counts were consistent with the validated reading method. Within- and between-reader bias were determined by age-bias plots where the ages from one reading are plotted against another.

² Most counts agreed to within two years but agreement within 3–4 years was considered acceptable in fish aged 14 years and above.

To estimate precision, Beamish & Fournier (1981) suggested the use of average percent error (APE). Chang (1982) supported the use of this method and also suggested the use of a coefficient of variation (CV). Precision was measured by calculation of both an APE and CV value for each set of age comparisons, and an overall index (average across all sections) of APE and CV.

2.1.5 Theoretical birth date

Duffy & Francis (2001) reviewed evidence for the timing of parturition (birth) of mako sharks in New Zealand waters. The evidence consisted of length measurements of juvenile (0+) mako sharks caught between December and August, a pregnant female carrying full-term embryos in early February (the only pregnant female so far recorded from New Zealand), and several presumed post-partum females caught in January–February. Duffy & Francis concluded that parturition is extended, possibly year-round, but that it peaks in late winter–spring.

We extended the dataset of juvenile makos used by Duffy & Francis (2001) to include recent years, and to cover the full 12-month cycle (Fig. 2). Presumed 0+ sharks were identified subjectively from Fig. 2 and a linear regression fitted through the data. There was a clear increase in fork length from October onwards, suggesting growth of a cohort of sharks. Few sharks small enough to be new-born were caught after January, indicating that births are concentrated in spring. We therefore selected 1 October as the theoretical birth date for New Zealand mako sharks.

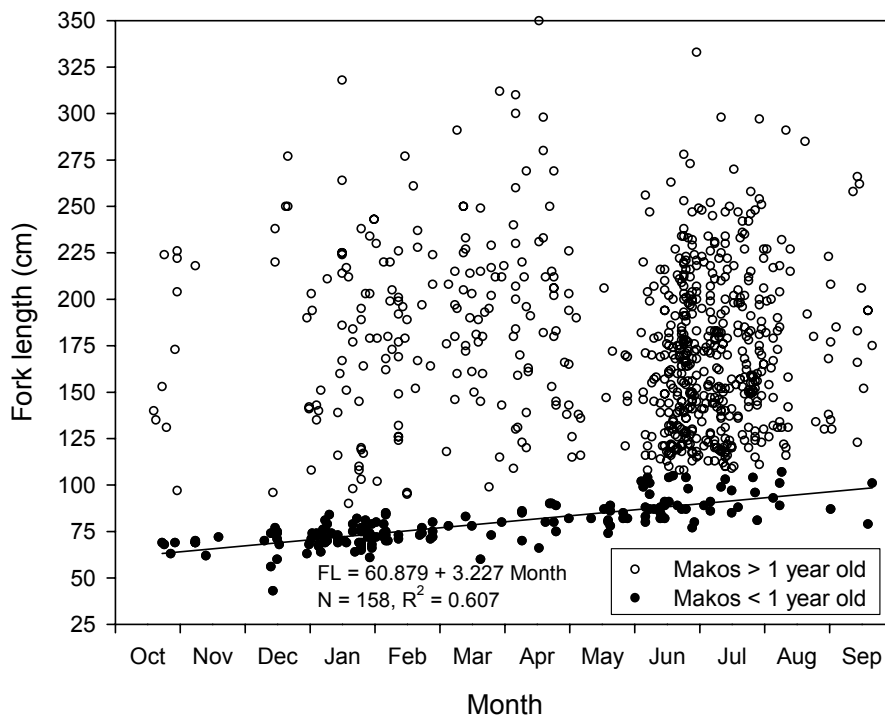


Figure 2: Relationship between fork length and capture date for shortfin mako sharks (both sexes and all years combined) measured by observers aboard tuna longline vessels in the northern fishery, 1993–2002. Presumed 0+ makos are shown as solid dots with fitted linear regression. Data for an observer who rounded many lengths to the nearest 10 cm were excluded.

2.1.6 Growth curves

Counts of growth bands were used as estimates of age, assuming one band is deposited annually. Because individual sharks were collected at different times of the year, age estimates were adjusted for time of capture relative to the theoretical birth date by adding the fraction of a year elapsed between 1 October and the date of capture to the band count.

Using SigmaPlot® software, growth curves were fitted to length-at-age data for each sex 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 (von Bertalanffy 1938; Francis & Ó Maolagáin 2000). Age standardised randomisation tests were made for significant differences between the male and female growth curves, as described by Francis & Ó Maolagáin (2000).

2.2 MULTIFAN analysis of length-frequency data

MFish scientific observers have been collecting mako shark length-frequency data aboard tuna longline vessels since 1993. Some data collected before then were excluded because some observers did not reliably distinguish between porbeagle and mako sharks. The longline fishery operates in two main regions: along east and west coasts of South Island (the southern fishery) and along the north-east coast of North Island (the northern fishery) (Francis et al. 2000; 2001). The northern fishery operates year-round, and fishing effort has been increasing steadily since 1997 due to an increase in domestic fishing vessels. The southern fishery is carried out mainly during April–July by chartered Japanese longliners. Observer coverage of the northern fishery has been low (fewer than 8% of hooks observed per year), whereas the coverage of the southern fishery has been high (usually 100% of hooks from Japanese vessels) (Francis et al. 2001; Ayers et al. in press).

Most mako shark length-frequency data from the northern fishery were collected during June–August, but sample sizes were small to moderate even when sexes were pooled (Fig. 3). Pooling was considered valid because mako growth curves from New Zealand and overseas indicate that growth is practically identical for both sexes until an age of about 7–9 years (see Fig. 9). In the southern fishery, the number of makos measured by observers was only about half the number measured in the northern fishery, and was considered too small for analysis. We decided not to combine data from both fisheries, because although tagging data indicate that mako sharks are capable of migrating large distances, previous work on another pelagic shark, the porbeagle, revealed substantial spatial variation in the modal lengths of juvenile age classes (Francis & Stevens 2000). For the present study, only the data from the northern fishery were analysed, and they were truncated to retain only sharks shorter than 275 cm (larger sharks were rare in the samples; Fig. 3). Data were grouped into two seasons: winter (June–August, 5 years) and summer (January–April, 1 year), and 5 cm length intervals for analysis (Fig. 3).

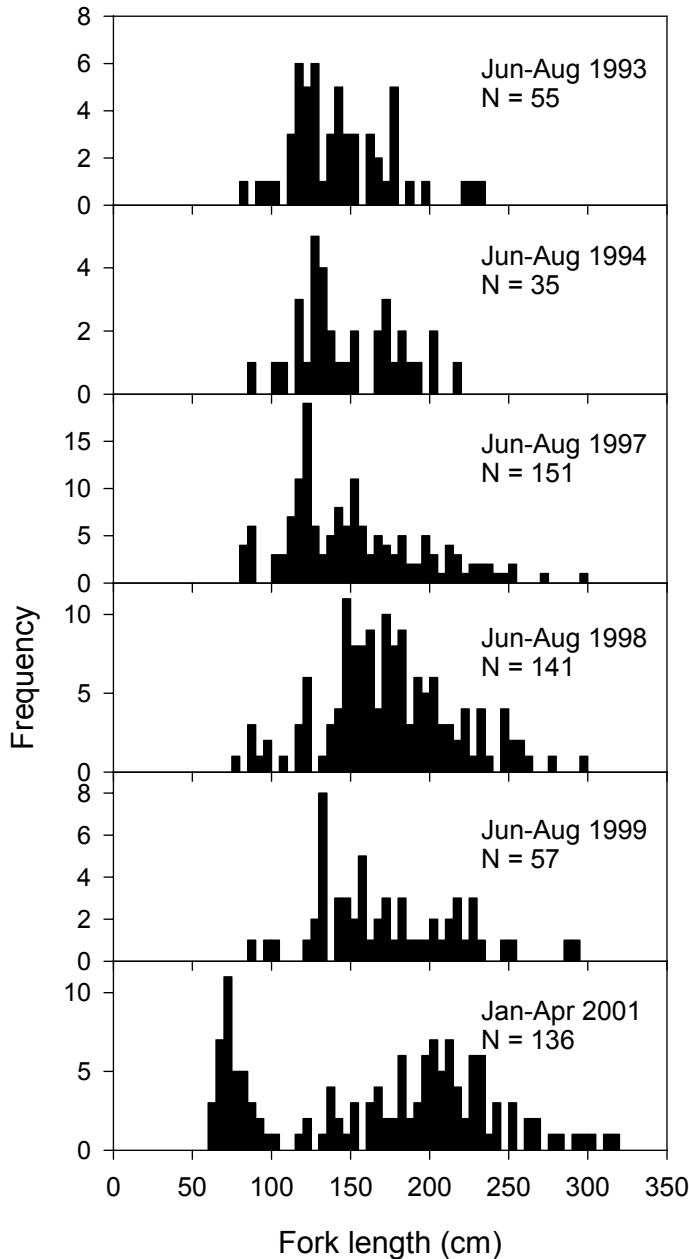


Figure 3: Length-frequency distributions for mako sharks (both sexes combined) collected from the northern tuna longline fishery in winter (June–August) and summer (January–April). Lengths are grouped into 5 cm intervals. No data were available for some years. Data for 2002 were not included because most were collected by an observer who rounded many lengths to the nearest 10 cm. These data sets were truncated at 275 cm for use in MULTIFAN analyses.

Von Bertalanffy growth curves were fitted to the distributions using the MULTIFAN model (Fournier et al. 1990). This model analyses multiple length-frequency distributions simultaneously, and uses a maximum likelihood method to estimate the number of age classes represented by the data, the proportions of fish in each age class, and the von Bertalanffy growth parameters L_{∞} and K . The main assumptions of the MULTIFAN model are: (1) the lengths of the fish in each age class are normally distributed around their mean

length; (2) the mean lengths-at-age lie on or near a von Bertalanffy growth curve; and (3) the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age (Fournier et al. 1990). The growth parameters were estimated by conducting a systematic search across a parameter space of plausible K values and age classes. Constraints were placed on the mean lengths of some age classes with distinct modal peaks to prevent MULTIFAN searching outside the realistic parameter range (Fournier et al. 1990).

For each of the identified age classes, MULTIFAN estimates the ratio of the last to first length standard deviations (S_R), and the geometric mean of the first and last standard deviations (S_A). The MULTIFAN model was fitted for two different growth hypotheses: (a) constant length standard deviation for all age classes (fitted by setting $S_R = 1$ and estimating S_A); and (b) variable length standard deviation across age classes (fitted by estimating both S_A and S_R). The constant standard deviation hypothesis was fitted to the data first, followed by the addition of the parameter for variable standard deviation. Seasonal growth parameters (amplitude and phase) were then added to both the constant and variable standard deviation models. The seasonal form of the von Bertalanffy equation is:

$$L_t = L_\infty \left(1 - e^{-K \left(t - t_0 + \left(\frac{\phi_1}{2\pi} \sin \left(2\pi \left(\left(\frac{12t+1}{12} \right) - \phi_2 \right) \right) \right) \right)} \right)$$

where ϕ_1 and ϕ_2 describe the amplitude and phase of the seasonal component, respectively. The time of maximum growth is $12\phi_2 - 1$ months after 1 January.

For each combination of K , number of age classes, and growth hypothesis, the maximum log-likelihood (λ) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the increase in λ is distributed as a χ^2 distribution with degrees of freedom equal to the number of additional parameters. Following Fournier et al. (1990), a significance level of 0.10 was used for testing whether there was any gain in introducing an additional age class in the length-frequency analyses. The tests for improvement resulting from the addition of the parameters for variable standard deviation and seasonal growth were carried out with a significance level of 0.05.

The von Bertalanffy growth parameter t_0 was estimated from the equation:

$$t_0 = t_1 - a_1$$

where a_1 is the age estimated by MULTIFAN (in years since zero length) of the youngest age class at the time it first appeared in the length-frequency samples, and t_1 is the time elapsed in years between the theoretical birth date and the first appearance of the youngest year class in the samples.

2.3 Longevity and natural mortality

Longevity was estimated directly from the oldest individual in the sample. However this probably underestimates actual longevity because maximum age in a fished population is likely to be lower than in an unfished population, and because our sample size was not large enough to include the oldest individuals in the population.

The natural mortality rate (M) was estimated using Hoenig's (1983) equation which is based on the observed empirical relationship between M and the maximum age (longevity)

in the population. Hoenig examined this relationship in fishes, cetaceans and molluscs. He found a significant negative relationship between these variables in fishes, described by the following equation:

$$\text{Log}_e M = 1.46 - 1.01[\text{Log}_e(t_{\max})]$$

where t_{\max} is the maximum age in the population, and M is the natural mortality rate.

2.4 Age at maturity

Age at maturity was estimated directly using paired age and maturity data collected at shark fishing competitions. The length and degree of calcification of claspers were used as the primary indicators of male maturity, and uterus width was used as the primary indicator of female maturity. Age at maturity was also estimated indirectly by converting estimates of median length at maturity (Francis & Duffy in prep) to age at maturity using our von Bertalanffy growth equations.

The median age at maturity, and its 95% confidence limits, were determined by probit analysis. Probit analysis assumes that the 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, and 95% confidence limits were estimated by bootstrapping. The presence or absence of overlap between the 95% confidence limits for the two sexes was used to determine whether males and females mature at different ages.

3 RESULTS

3.1 Age and growth

3.1.1 Centrum analysis

Birth band radius (BR) measurements from vertebral samples ($n = 265$) of free-swimming shortfin makos were compared with the vertebral radius (VR) of six embryonic shortfin makos. The VR of embryonic shortfin makos was 3.9–4.6 mm with a mean of 4.3 mm ($SE \pm 0.11$ mm). BR for the vertebral sections was 4.0–5.7 mm with a mean value of 4.9 mm ($SE \pm 0.02$ mm).

The relationship between FL and VR was slightly curvilinear indicating allometric growth, so data were log transformed to allow linear regression. There was no significant difference in the FL–VR relationship between sexes (analysis of covariance: slope $P = 0.81$, intercept $P = 0.80$) so data were pooled for the regression. The linear regression revealed a highly significant relationship between FL and VR which accounted for 99% of the variation in the data ($P = 0.0001$) (Fig. 4). The FL–VR relationship shows that FL increases in proportion to VR in a predictable way described by the equation:

$$\text{Log}_{10} FL = 0.850 \times \text{Log}_{10} VR + 1.275$$

Vertebral measurements of MFish observer samples were not included in regression analysis because the variation in anatomical collection sites (anterior or middle of column) produced inconsistencies in VR measurements.

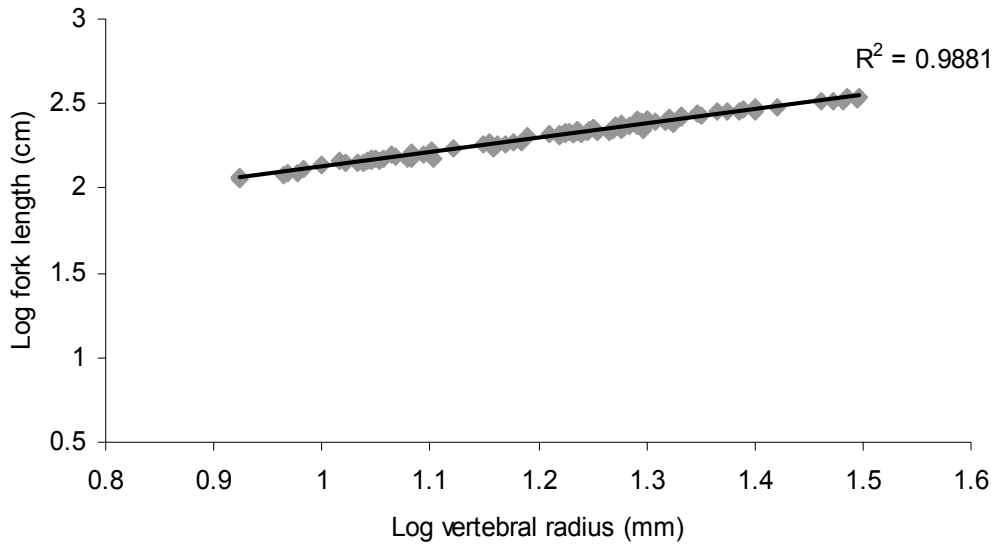


Figure 4: Log fork length versus log vertebral radius for competition shortfin mako vertebrae (sexes combined).

Sections from the anterior (vertebrae 0–10), middle (vertebrae 45–55) and posterior (vertebrae 100–110) regions of columns varied in size yet possessed identical banding patterns (Fig. 5). The middle sections were the largest, exhibiting the clearest band deposition and thus were the easiest to interpret in all three sharks. Sections from all three regions gave consistent counts throughout the column (Table 1). The maximum difference in counts between vertebral regions was one year.

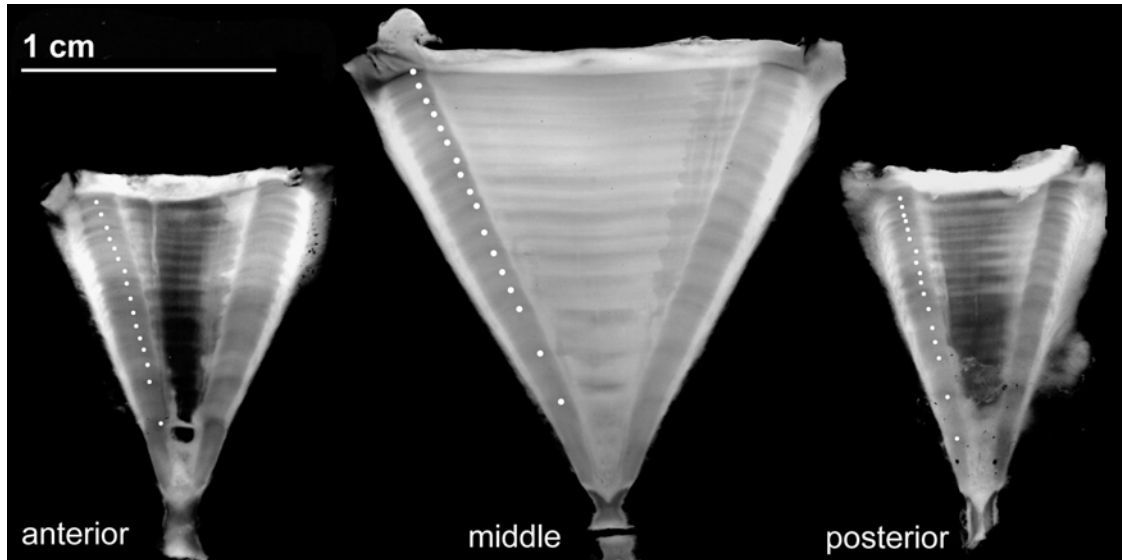


Figure 5: Anterior, middle and posterior sections from the large (238 cm female) shortfin mako illustrating similarity in band deposition and disparity in shape and size of vertebrae throughout an entire column. White dots represent annual growth bands (including birth band).

Table 1: Band counts (age in years) for vertebrae removed from anterior, middle and posterior regions of the vertebral columns from three sharks of different sizes.

Shark size	Region of vertebral column		
	Anterior	Middle	Posterior
Small (173 cm FL)	5	5	4
Medium (210 cm FL)	9	9	8
Large (238 cm FL)	15	16	16

3.1.2 *Bias and precision*

Comparison of band counts with overseas ageing laboratories showed no substantial bias between trainer and trainee (Fig. 6). Ageing precision was moderate (APE index = 6.6%; CV index = 9.3%).

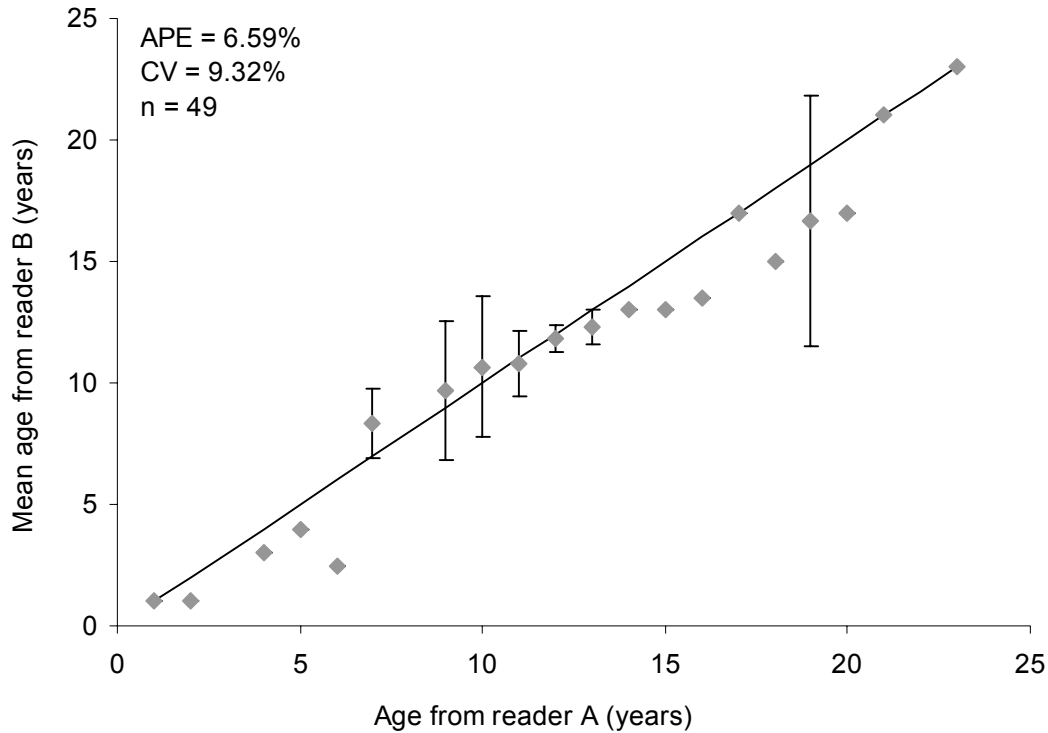


Figure 6: Age-bias graph comparing vertebral counts from two independent readers. Error bars represent the 95% confidence interval (CI) for the mean age assigned by reader B (trainee) to all fish assigned a given age by reader A (trainer). Where error bars are not shown, sample size was too small ($n \leq 3$). Precision indices of APE and CV and the line of equivalence are also presented.

From the 265 vertebral samples sectioned, 9 sections were discarded as unreadable giving a final sample size of 256 shortfin makos for age analysis (145 males, 111 females). The primary reader and second reader will be referred to as reader 1 (R1) and reader 2 (R2) respectively. For the within-reader comparisons, the two sets of age determinations will be referred to as count 1 (C1) and count 2 (C2) respectively.

Age estimates exhibited close agreement, with no systematic bias within or between readers (Fig. 7). Precision was high (within-reader APE index = 5.3%, CV index = 7.5%; between-reader APE index = 6.5, CV index = 9.2%).

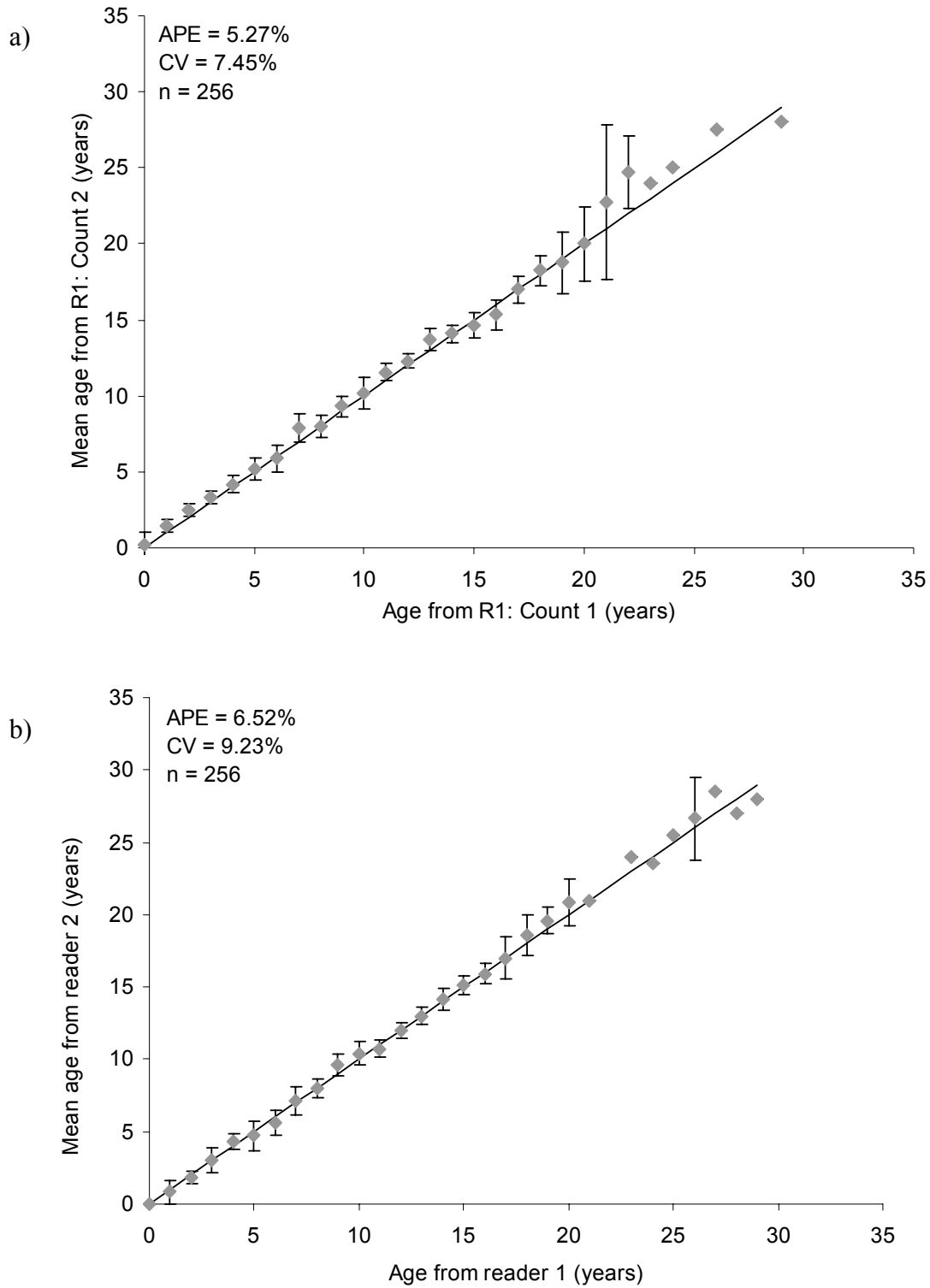


Figure 7: Age-bias plots for a) within-reader bias, error bars represent 95% confidence interval (CI) for the mean age of count 2 for all individuals assigned a given age in count 1; (b) between-reader bias, error bars represent the 95% CI for the mean age assigned by reader 2 to all individuals assigned a given age by reader 1.

Precision was typically high across the age range for within- and between-reader comparisons, but there was a tendency for lower precision in the sharks up to 6+ years old (Fig. 8).

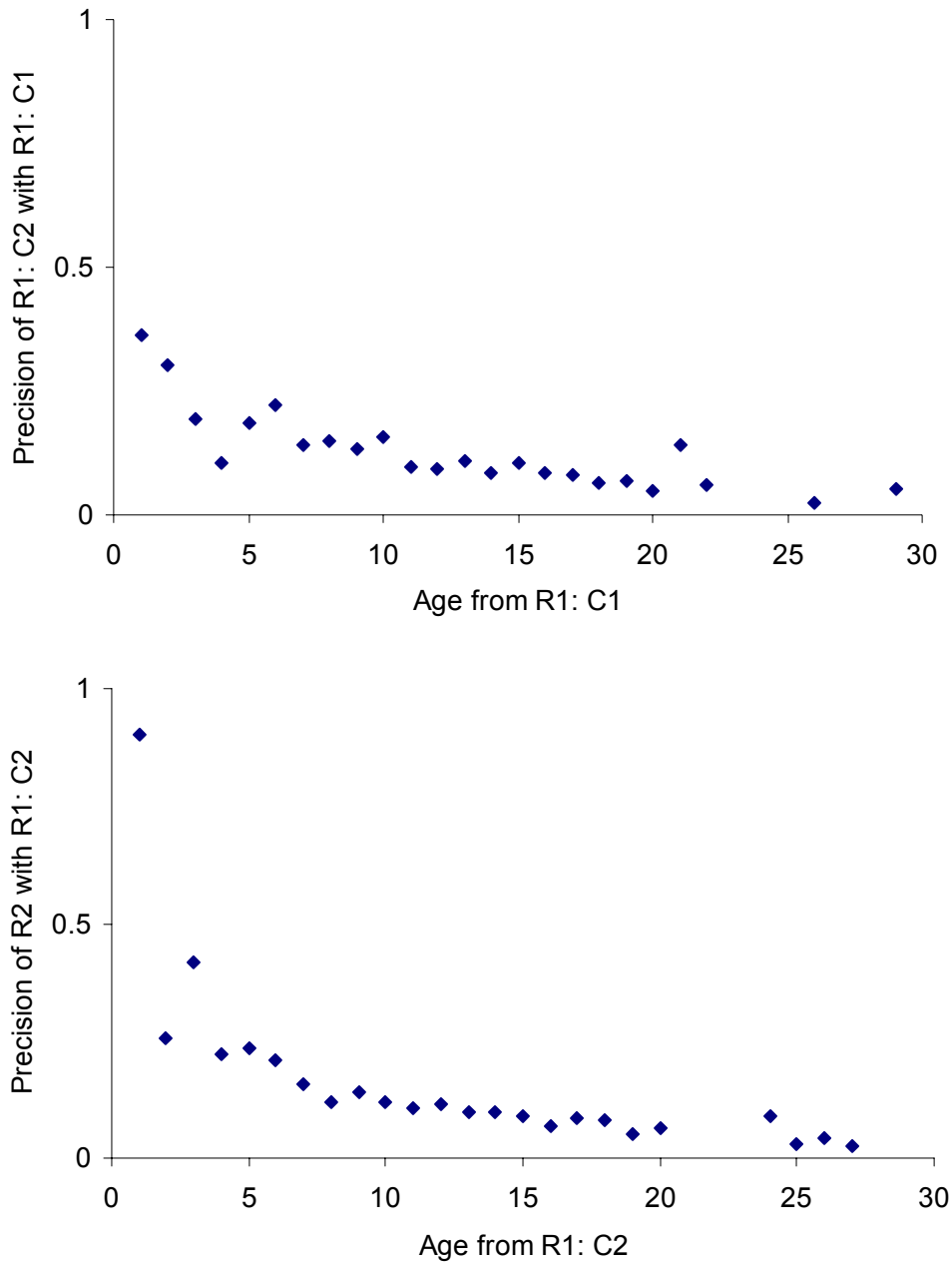


Figure 8: Precision, measured as the coefficient of variation. Plots are of the coefficient of variation of age estimates against age for a) within-reader precision; b) between-reader precision. Equations used to calculate precision estimates are given in Appendix C.

3.1.3 Growth curves

The second age determinations (C2) by the primary reader (R1) were used for fitting growth curves to the length-at-age data. Males and females grew at similar rates until

approximately age 7–9 years and 180–190 cm FL (Fig. 9). After this point, male growth rate declined relative to female growth.

An age-structured randomisation test for differences between male and female growth curves was attempted but failed to converge because of the near-linearity of the female length-at-age data. However, from observation of the curves it is clear that growth is different between the sexes (Fig. 9). Both sexes reach 200 cm at ca. 10–12 years of age; by 25 years males are ca. 250 cm and females 310 cm. Females grow longer than males: our largest female was 347 cm, and our largest male was 270 cm (Fig. 9). The latter appears to be longer than any male previously reported.

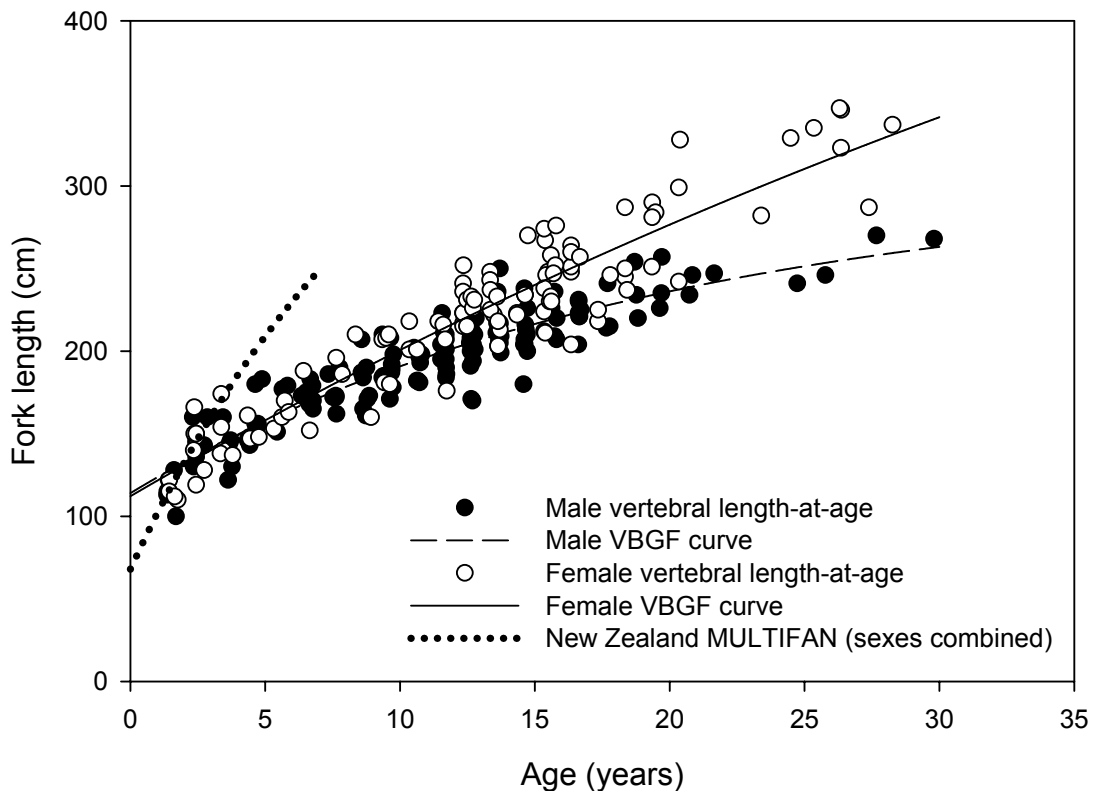


Figure 9: Von Bertalanffy growth curves produced from male and female shortfin mako vertebral data, and MULTIFAN length-frequency data.

Von Bertalanffy growth parameters were: male $L_{\infty} = 302.16$ cm, $K = 0.0524$ and $t_0 = -9.04$ years; female $L_{\infty} = 732.41$ cm, $K = 0.0154$ and $t_0 = -10.79$ years. Residual plots (Fig. 10) of the length-at-age data showed no strong patterns, although there was a slight tendency for larger residual spread in the older females (Fig. 10a). There were no clusters of negative or positive values, indicating a good fit of the models to the data.

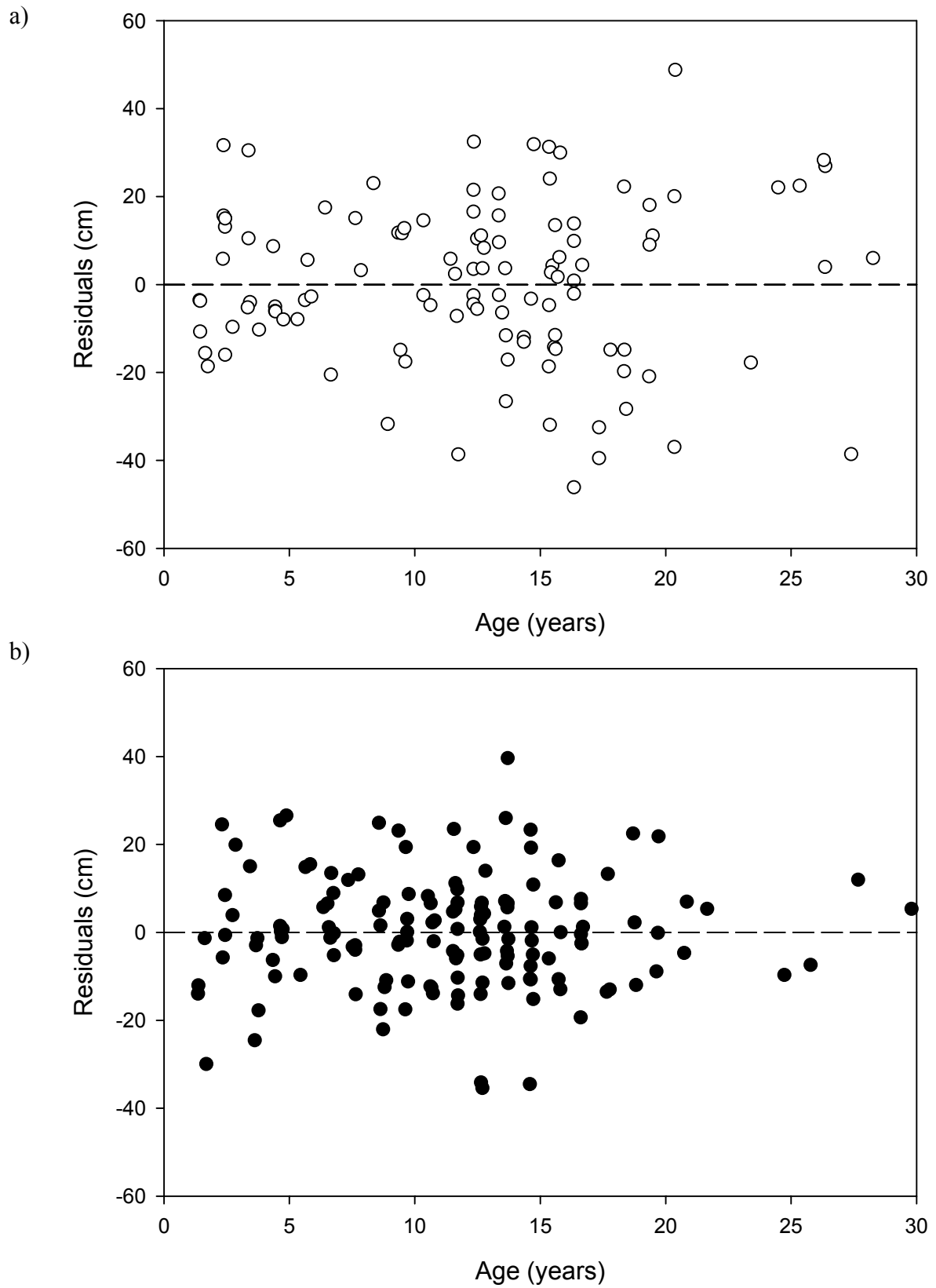


Figure 10: Residuals from the fitted von Bertalanffy growth curves versus predicted age for a) female and b) male shortfin mako sharks.

3.2 MULTIFAN Length-frequency distributions

The regression in Fig. 2 indicates that 0+ juveniles grow at about 3.2 cm per month during their first year, and are 60.9 cm long on 1 October. This length is identical to the mean length of eight full-term mako embryos (range 55.5–62.5 cm) reported by Duffy & Francis (2001), and also close to the reported length at birth (ca. 70 cm total length) found in a worldwide study of mako shark reproduction (Mollet et al. 2000). Our best estimate of mean length at birth is therefore 61 cm.

The winter length-frequency distributions from the northern fishery usually had a mode between 100 cm and 130 cm, though it was not always well defined (Fig. 3). The only summer sample had a strong mode at 60–85 cm. There was little modal structure above 175 cm.

The best fit MULTIFAN model consisted of constant length standard deviation with 7 age classes and seasonal growth (Table 2). The fit of the model to the data is shown in Appendix D, and the von Bertalanffy growth curve is shown in Fig. 9.

Table 2: Von Bertalanffy growth curve parameters derived by MULTIFAN analysis of length-frequency data from the northern tuna longline fishery (data shown in Fig. 3). Seasonal growth phase is given in years since 1 January.

Sex	Number of age classes	L_{∞} (cm)	K	t_0 (years)	Seasonal amplitude	Seasonal phase (yr)
Both	7	435.0	0.097	-1.75	0.949	0.37

3.3 Longevity and natural mortality

The maximum ages based on vertebral band counts were 29 and 28 years for males and females respectively, indicating no difference in longevity between the sexes. Estimates of natural mortality as calculated by Hoenig's equation were 0.14 and 0.15 for males and females respectively.

3.4 Age at maturity

3.4.1 Direct estimates

Paired age and maturity data collected from fishing competitions showed that females matured at a much later age than males (Figs 11 and 12). There was no overlap in age of immature and mature males (but the sample size was small), and an overlap of five years in age for immature and mature females. The ages at which 50% of sharks were mature were estimated by probit analysis as 6.9 years for males (CI 6.9–6.9) and 19.1 years for females (CI 17.9–20.7) (Fig. 12). The absence of overlap between the 95% confidence limits for

the two sexes clearly showed that males and females mature at different ages. Maturity in males coincided with the age at which male growth slowed.

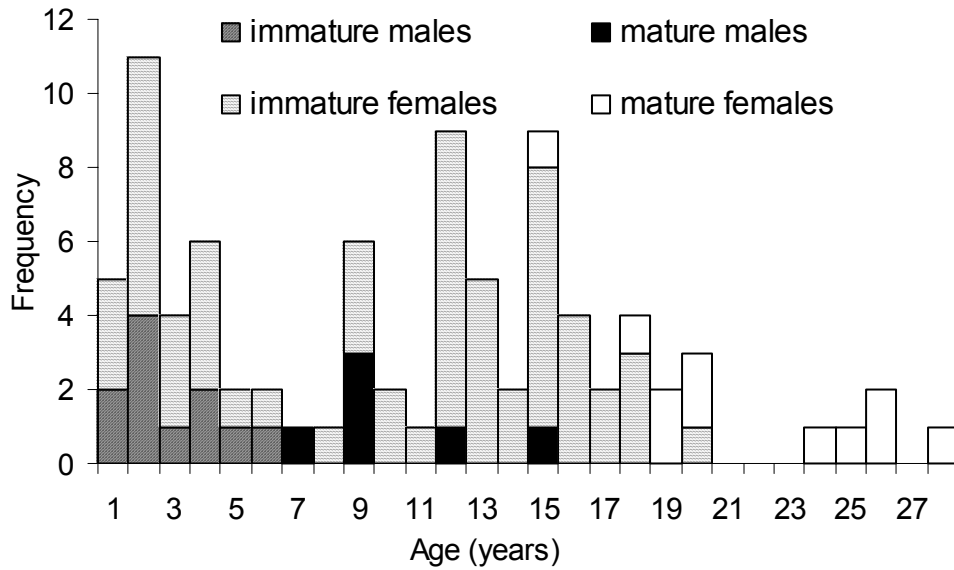


Figure 11: Age-frequency distributions of immature and mature males and females as estimated from paired age and maturity data. Immature males (n = 11), mature males (n = 6), immature females (n = 57), mature females (n = 11).

3.4.2 Indirect estimates

Indirect estimates of age at maturity were derived by conversion of length at maturity estimates of 180–185 cm and 275–285 cm for males and females respectively (Francis & Duffy in prep). Substituting these values into the von Bertalanffy growth equations produced indirect age at maturity estimates of 8–9 years for males and 20–21 years for females (Fig. 13) which are slightly higher than the direct age at maturity estimates of 6.9 and 19.1 (Figs 12 and 13).

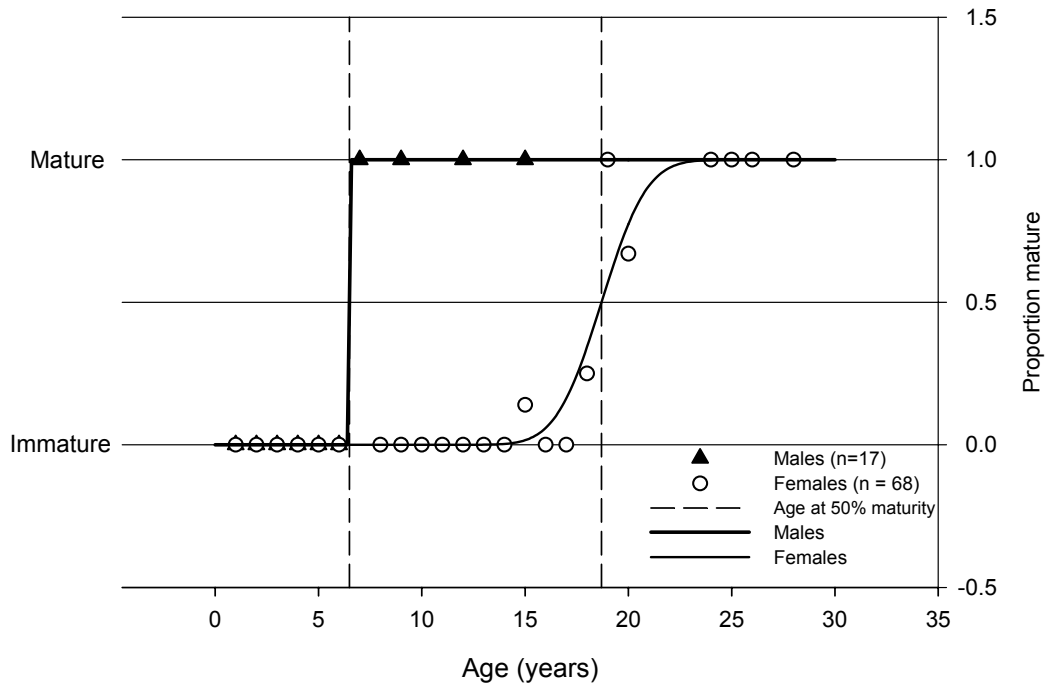


Figure 12: Direct age at maturity estimates from paired age and maturity data. Curves were fitted by probit analysis.

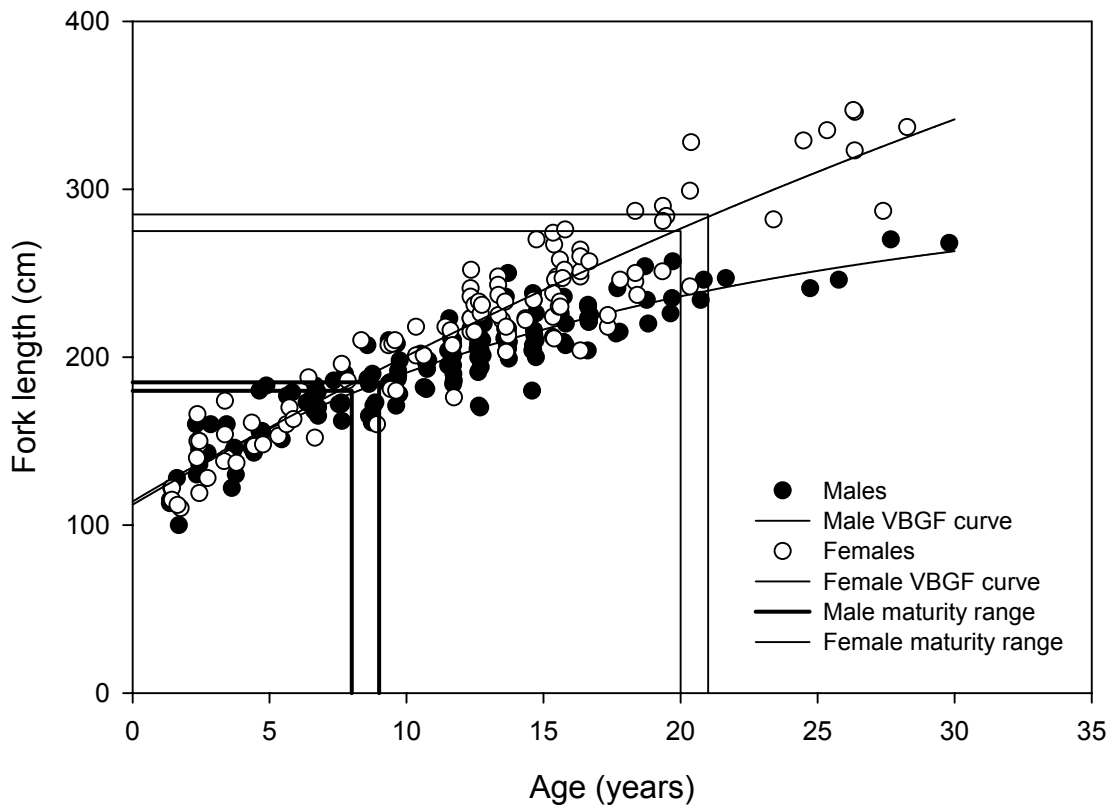


Figure 13: Indirect age at maturity estimates derived from conversion of length at maturity estimates (Francis & Duffy in prep). Ranges in length at maturity and corresponding ranges in age at maturity are 180–185 cm = 8–9 years (males) and 275–285 cm = 20–21 years (females).

4 DISCUSSION

4.1 Age determination and growth

4.1.1 *Centrum analysis*

The strong correlation between FL and VR supports the use of the vertebral centrum as a structure for ageing (see also Cailliet et al. 1983; Pratt & Casey 1983). Close agreement between the mean vertebral birth band radius of free-swimming makos, and the mean radius of embryonic shortfin makos, indicates that the birth band was identified correctly. Because identical band deposition was apparent throughout the vertebral column, vertebrae from any region of the column can be used in age analysis. However, the larger central vertebrae were easier to read because of the wider band spacing.

4.1.2 *Bias and precision*

From personal observation during training, it was clear that age determinations improved with time because of increasing familiarity with the banding structure. Although growth bands were mostly distinct, there is still potential for sizeable error if readers are not trained in the ageing of this particular species. The use of reference collections of known age samples is also suggested as a means of assessing consistency (Campana et al. 1995). Nevertheless, our ageing precision was good, because CVs for shark ageing studies are rarely less than 10% (Campana 2001).

The only ‘known age’ shortfin mako vertebra which could be used as a reference is the single vertebra aged by bomb radiocarbon analysis (Campana et al. 2002). A ‘blind’ reading of this individual was carried out in this study as part of training and the age estimate was identical to the published bomb radiocarbon estimate of 21 years. Furthermore, the bias and precision results reported here showed that age determinations of individual readers did not drift over time, age determinations of different readers were comparable, and the precision of age determinations did not deteriorate over time.

4.1.3 *Growth curves*

The von Bertalanffy growth curves fitted the length-at-age data well with minimal spread in the residuals. The minor spread of residuals observed for large females was expected, as variability in length-at-age increases with age, especially in slow-growing species such as sharks.

Parameters reported here for the von Bertalanffy equation were poorly estimated in some cases, for example the female $L_{\infty} = 732.41$ cm. This estimate is implausible because it is much higher than the maximum reported length of 362 cm (Bigelow & Schroeder 1948). Several authors have warned against extrapolation of the von Bertalanffy growth model, particularly with reference to L_{∞} (Knight 1968, 1969; Campbell & Phillips 1972). The overestimation of L_{∞} in this case is explained by the near linearity of the data. Growth slows considerably in older individuals (Fig. 15, Section 4.3) and it is unlikely that the oldest sharks in the population were sampled (See section 4.4.1). This absence of old (greater than 29 years) individuals that would normally produce an asymptote within the range of the data has meant that the growth curve continues rising, resulting in an

unrealistically high asymptote and estimate of L_{∞} . More importantly, the growth curves fit well over the range of the observed data.

4.2 Comparison of growth estimates from vertebrae and length-frequency data

Length-frequency data predicted considerably faster growth than estimates from vertebral ages for the younger age classes (Figs. 9, 14, and 15). Our previous experience has shown that MULTIFAN growth curves are generally reliable for younger age classes, which often exhibit discernible length modes, but not for older age classes, which usually lack any modal length structure. This is because MULTIFAN underestimates the number of older age classes present in the data, and consequently overestimates the length-at-age of the older age classes (Francis & Francis 1992; Francis 1997). MULTIFAN fits seemed plausible for the first 2–4 age classes, which implies that mean length-at-age from the vertebral data was unrealistically high for the first few years. This interpretation is supported by the observation that the Y-axis intercept (112–114 cm) is much higher than the known length at birth of about 61 cm (Fig. 9).

Possible reasons for overestimating length-at-age at the left hand end of the vertebral growth curve include:

1. Sampling was biased towards larger sharks from the younger age classes. This is certainly true for competition sharks, for which there was a minimum weight limit at most fishing competitions. Scientific observers may also have preferentially sampled vertebrae from larger sharks.
2. Ageing error may have resulted in underestimation of some ages. It is sometimes easier to interpret early growth bands in old fish than it is in young fish, because the presence of older bands on the vertebrae put younger bands into perspective. Within- and between-reader age comparisons indicated lower precision in younger sharks.
3. Very small mako sharks may be rare in New Zealand waters. Juveniles may migrate southwards from tropical regions as they grow. This is supported by the observation that only one pregnant female mako shark has been recorded in New Zealand (Duffy & Francis 2001).

For sharks aged approximately 4+ and older, the vertebral growth curves are considered more reliable than the MULTIFAN growth curve, which is adversely affected by the merging of length modes. Additional samples of young sharks combined with back-calculation methods are suggested to correct the bias apparent in the left hand end of the vertebral growth curves.

4.3 Comparison with overseas studies

Age and growth of the shortfin mako shark have been reported in a range of studies using a range of techniques (Cailliet et al. 1983; Pratt & Casey 1983; Chan 2001; Campana et al. 2002). The greater maximum length of females compared with males observed in this study is consistent with other studies (Table 3) (Cailliet et al. 1983; Pratt & Casey 1983; Chan 2001). However, there are considerable differences among the ages and growth rates

estimated by those studies (Figs 14 and 15), primarily due to differences in assumed band deposition rates.

Pratt & Casey (1983) analysed length-month, length-frequency, tag-recapture and vertebral growth rates of shortfin makos in the North Atlantic Ocean. Growth rates from their vertebral ages were approximately half the rates given by the other three methods. This led to their assumption of bi-annual band deposition (two bands per year), thus resulting in significantly faster growth from their study compared with the present study and other shortfin mako studies (Figs 14 and 15). If Pratt & Casey's (1983) estimates are adjusted to assume annual periodicity, their growth curves are considerably closer to those from other studies (Fig. 14).

Pratt & Casey's (1983) length-month analysis gave an annual growth increment in the first year of 47 cm, which is higher than the annual growth increment of 39 cm for age 0+ New Zealand makos calculated from the regression in Fig. 2. This supports rapid growth in the first year, and the conclusion that mean length-at-age for the New Zealand vertebral data was unrealistically large for the first few years. Pratt & Casey's (1983) tag-recapture measurements gave a similar growth rate of approximately 40 cm.year⁻¹ but this should be interpreted with caution due to high measurement error.

Pratt & Casey (1983) assumed bi-annual deposition based solely on the agreement of the faster growth this generated with their other three methods. Attempts at validating bi-annual deposition from four tagged-recaptured shortfin makos were inconclusive, with two of the four recaptured shortfin makos supporting annual band deposition, and two supporting bi-annual band deposition.

Chan (2001) aged vertebrae of shortfin makos from New South Wales. He unsuccessfully attempted to validate the periodicity of band formation using marginal increment analysis, and arbitrarily followed Pratt & Casey's two bands per year hypothesis. Thus the curves from Chan's study also predict significantly faster growth than those from other studies (Figs 14 and 15).

Table 3: Comparison of length-at-age estimates for the shortfin mako calculated by the von Bertalanffy equation based on vertebral and length-frequency (MULTIFAN) data.

Age (yrs)	This study			Cailliet et al. (1983)	Pratt & Casey (1983)		
	Vertebral ages		MULTIFAN	Vertebral ages Both sexes	Vertebral ages		Length-month analysis
	Males	Females	Both sexes		Males	Females	Both sexes
0	114	112	68	69	69	62	71
1	124	122	102	85	122	112	118
2	133	131	133	99	162	153	149
3	141	140	161	113	192	187	
4	150	149	186	126	216	214	
5	157	158	209	138	234	236	
6	165	167	230	149		254	
7	172	176	249	159		269	
8	178	184		169		281	
9	185	192		177		291	
10	191	201		186		299	
11	196	209		193		305	
12	202	217		201		311	
13	207	225		207			
14	212	232		213			
15	216	240		219			
16	221	248		225			
17	225	255		230			
18	229	262					
19	233	269					
20	236	277					
21	240	284					
22	243	290					
23	246	297					
24	249	304					
25	251	310					
26	254	317					
27	256	323					
28	259	329					
29	261	336					
30	263	342					

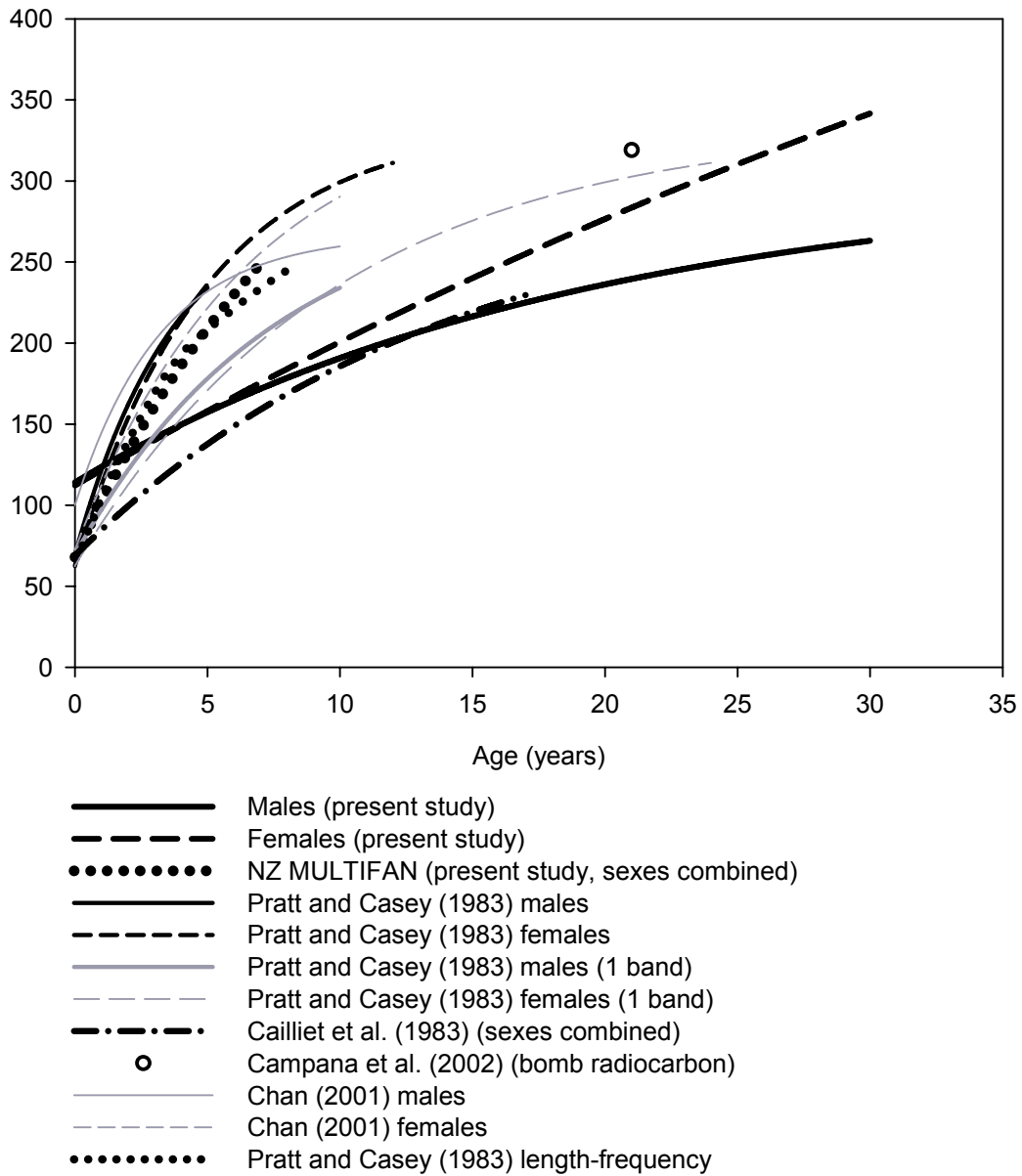


Figure 14: Comparison of New Zealand and overseas von Bertalanffy growth curves for shortfin mako sharks generated from vertebral length-at-age data and length-frequency data. The single bomb radiocarbon vertebra of Campana et al. (2002) is also included. Adjusted versions of Pratt & Casey's (1983) curves assuming 1 band per year are also given.

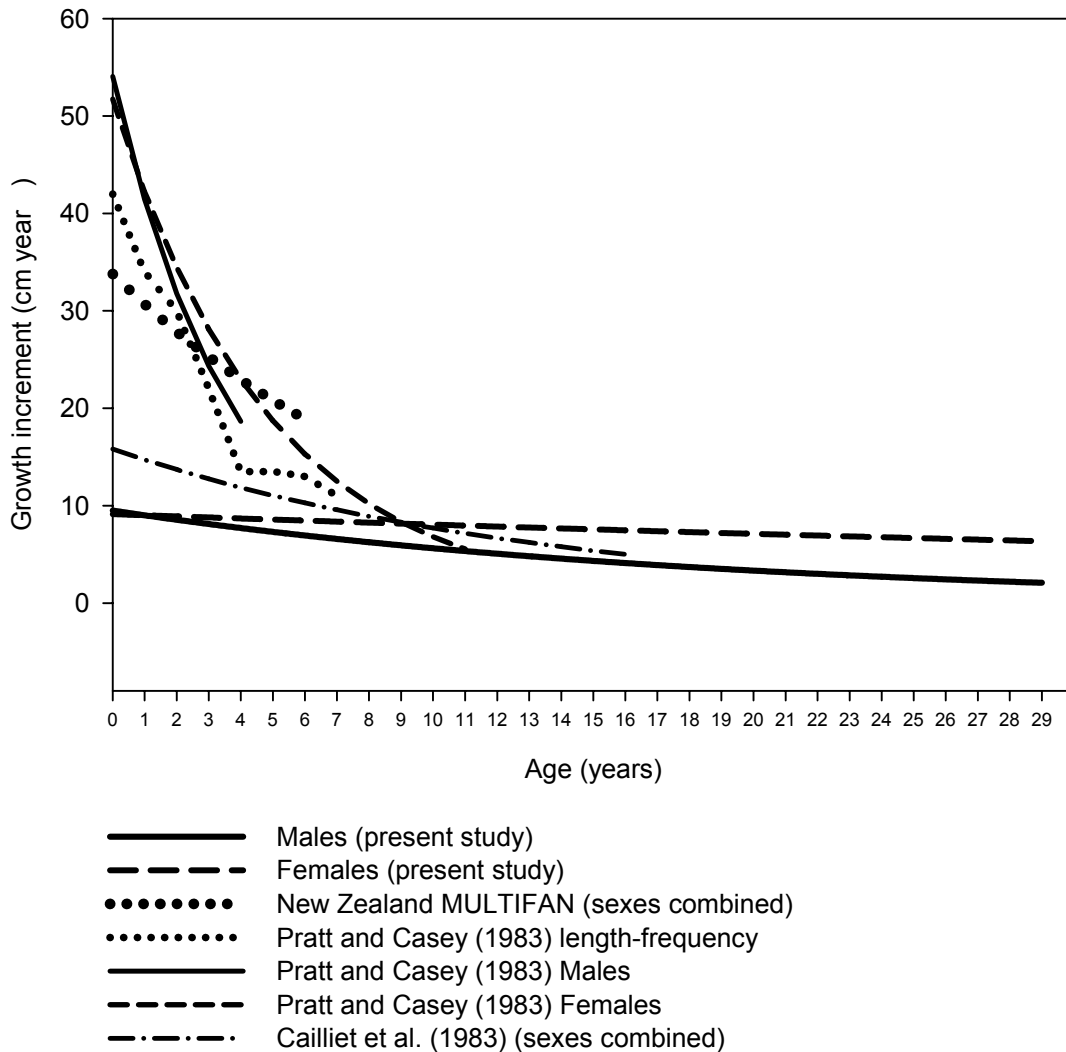


Figure 15: Comparison of the annual growth increments (centimetres per year) for shortfin makos using vertebral length-at-age data and length-frequency data.

Cailliet et al. (1983) aged vertebrae from shortfin makos from the north-east Pacific Ocean using an assumed annual deposition of growth bands. Their growth curve (for both sexes combined) is similar to ours. The New Zealand growth curves for shortfin makos (present study) are closest to unpublished data for north-west Atlantic shortfin makos and exhibit almost identical length-at-age relationships after age 10+ (L. Natanson, pers. comm.). These two studies had considerably larger sample sizes and higher maximum ages than other earlier studies. The vertebral age estimates presented here are further supported by the single bomb radiocarbon dated female specimen (Campana et al. 2002) which sits among the female vertebral age data from our study (Fig. 16).

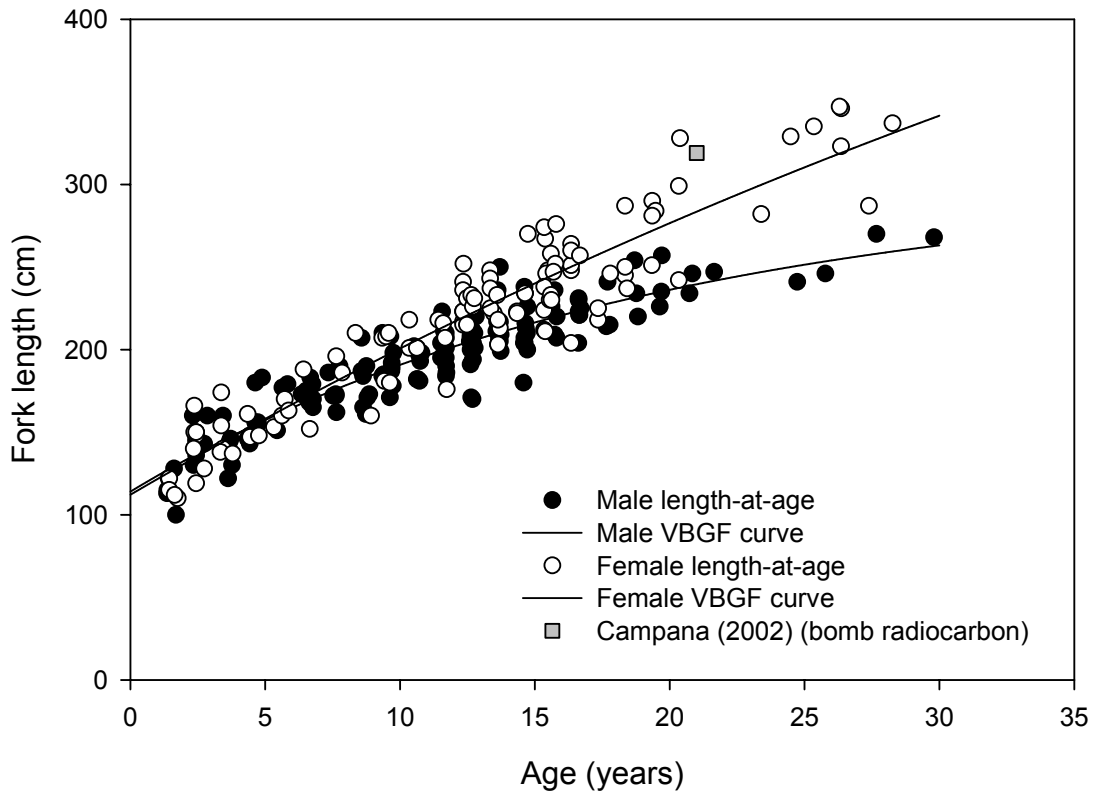


Figure 16: Von Bertalanffy growth curves from length-at-age data for shortfin makos (present study) compared with the bomb radiocarbon estimate of a north-west Atlantic female shortfin mako (Campana et al. (2002)).

Bi-annual deposition of vertebral bands has not been validated in any other elasmobranch species. Recent validation of the ageing method for porbeagle sharks (Natanson et al. 2002) and the bomb radiocarbon age estimate for a single shortfin mako vertebra strongly suggest annual periodicity of band formation in these two species. Further bomb radiocarbon work to validate the periodicity of band formation is underway (L. Natanson, pers. comm.) and will allow these estimates to be confirmed or refuted. Other validation work such as tetracycline injection of tagged sharks could also be valuable.

4.4 Longevity and natural mortality

4.4.1 Longevity

Longevity in this study (29 years) was higher than any published estimates (Table 4). The previous greatest reported age was 17 years (Cailliet et al. 1983), though if one band per year is formed on vertebrae, the 11.5 year old shark reported by Pratt & Casey (1983) would have been 23 years old. An unpublished study from the north-west Atlantic produced a maximum age only a few years older than found in this study.

Tag-recapture data sometimes provide information on longevity, based on the period for which a tagged shark is at liberty. The longest periods at liberty for tagged New Zealand makos were 5.5–6.5 years for four sharks (MFish recreational tagging database; J. Holdsworth, Blue Water Marine Research, pers. comm.). Therefore tagging data do not provide a comparable estimate of longevity, probably because of loss of tags over time.

Actual longevity is likely to be even greater than the 29 years suggested above; the probability of catching the oldest individual in a population is low because old individuals represent a small proportion of the population and are likely to be the most difficult to capture and land (Hoenig 1983). There appears to be a relationship between sample size and the estimate of longevity (Table 4). As sample size increases so will the probability of sampling the older individuals in a population, thus increasing longevity estimates. Other factors that might affect estimates of longevity include ageing technique and error, fishing history (high fishing mortality can reduce the proportion of old sharks in the population, or even remove them altogether), and inter-stock differences.

Table 4: Maximum ages reported for shortfin makos. All ages are based on annual periodicity of band deposition. Bracketed values are the reported ages from studies which assumed bi-annual band deposition.

Maximum age	Sample size	Location	Author
17	44	NE Pacific	Cailliet et al. (1983)
20 (10)	76	Australia	Chan (2001)
23 (11.5)	109	NW Atlantic	Pratt & Casey (1983)
29	256	New Zealand	This study

4.4.2 Natural mortality

The coefficient of natural mortality is one of the most difficult parameters to estimate in fish population dynamics. The relationship between natural mortality and longevity proposed by Hoenig (1983) is based on the observation that individuals live longer when natural mortality is low. Therefore if longevity is underestimated, which is common with small samples from fished populations, then mortality will be overestimated. Hoenig (1983) noted that a limitation of his technique was that it did not incorporate sample size. Our sample size was not large enough to ensure that the oldest makos were included, so our estimates of M are probably too high.

4.5 Age at maturity

Differences in growth rates calculated using different assumed band deposition rates have led to debate about the age at maturity in the shortfin mako. Furthermore, our limited knowledge of the reproductive biology of this species within New Zealand waters and worldwide complicates age at maturity estimates. In this study, direct and indirect estimates of median age at maturity were similar. Growth curves from our study and from

the north-west Atlantic (L. Natanson, unpublished data) were similar, indicating little regional variability in growth rates. Similarly, length at maturity is similar in New Zealand and elsewhere, except perhaps for females from South Africa which may mature at a shorter length (Cliff et al. 1990; Francis & Duffy in prep). It therefore seems that makos worldwide may mature at similar ages.

4.6 Conclusions

Shortfin makos are large sharks with rapid growth in the first few years of life, followed by slow growth. Growth rates for the two sexes diverge as males mature, with male growth slowing compared with females. Age at maturity is very late, particularly for females, and longevity is moderately long (longer than reported in any previous studies), resulting in a low natural mortality rate. This combination of population parameters, coupled with a very low annual fecundity (Mollet et al. 2000), means that the productivity of shortfin makos is very low.

4.7 Acknowledgements

We thank the Ministry of Fisheries for funding this study under research project TUN2002/01, and providing access to data collected by observers. Lynda Griggs (NIWA) assisted with data extracts and interpretation, and Chris Francis (NIWA) carried out the probit analyses. Lisa Natanson provided invaluable training and advice in the ageing of mako shark vertebrae, and access to unpublished data.

4.8 References

- Ayers, D.; Francis, M.P.; Griggs, L.H.; Baird, S.J. (in press). Fish bycatch in New Zealand tuna longline fisheries, 2000-01 and 2001-02. *New Zealand Fisheries Assessment Report*.
- Beamish, R.J.; Fournier, D.A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 982-983.
- Bigelow, H.B.; Schroeder, W.C. (1948). Fishes of the Western North Atlantic. Part 1. Lancelets, cyclostomes, sharks. *Memoir of the Sears Foundation for Marine Research 1*: 59-546.
- Cailliet, G.M.; Martin, L.K.; Harvey, J.T.; Kusher, D.; Welden, B.A. (1983). Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. *NOAA Technical Report NMFS 8*: 179-188.
- Campana, S.E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59: 197-242.
- Campana, S.E.; Annand, M.C.; McMillan, J.I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* 124: 131-138.
- Campana, S.E.; Natanson, L.J.; Myklevoll, S. (2002). Bomb dating and age determination of large pelagic sharks. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 450-455.
- Campbell, N.A.; Phillips, B.F. (1972). The von Bertalanffy growth curve and its application to capture-recapture data in fisheries biology. *Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer* 34: 295-299.
- Casey, J.G.; Kohler, N.E. (1992). Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic. *Australian Journal of Marine and Freshwater Research* 43: 45-60.
- Chan, R.W.K. (2001). Biological studies on sharks caught off the coast of New South Wales. Ph.D. Thesis. University of New South Wales. 323 p.
- Chang, W.Y.B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1208-1210.
- Cliff, G.; Dudley, S.F.J.; Davis, B. (1990). Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). *South African Journal of Marine Science* 9: 115-126.

- Compagno, L.J.V. (2001). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. *FAO Species Catalogue for Fishery Purposes* 1, vol. 2. 269 p.
- Duffy, C.; Francis, M.P. (2001). Evidence of summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* 35: 319-324.
- Fournier, D.A.; Sibert, J.R.; Majkowski, J.; Hampton, J. (1990). MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). *Canadian Journal of Fisheries and Aquatic Sciences* 47: 301-317.
- Francis, M.P. (1997). Spatial and temporal variation in the growth rate of elephantfish (*Callorhynchus milii*). *New Zealand Journal of Marine and Freshwater Research* 31: 9-23.
- Francis, M.P. (1998). New Zealand shark fisheries: development, size and management. *Marine and Freshwater Research* 49: 579-591.
- Francis, M.P.; Francis, R.I.C.C. (1992). Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). *Australian Journal of Marine and Freshwater Research* 43: 1157-1176.
- Francis, M.P.; Stevens, J.D. (2000). Reproduction, embryonic development and growth of the porbeagle shark, *Lamna nasus*, in the south-west Pacific Ocean. *Fishery Bulletin* 98: 41-63.
- Francis, M.P.; Ó Maolagáin, C. (2000). Age, growth and maturity of a New Zealand endemic shark (*Mustelus lenticulatus*) estimated from vertebral bands. *Marine and Freshwater Research* 51: 35-42.
- Francis, M.P.; Duffy, C. (in prep). Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus* and *Prionace glauca*) from New Zealand. *Fishery Bulletin*.
- Francis, M.P.; Griggs, L.H.; Baird, S.J. (2001). Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine and Freshwater Research* 52: 165-178.
- Francis, M.P.; Griggs, L.H.; Baird, S.J.; Murray, T.E.; Dean, H.A. (2000). Fish bycatch in New Zealand tuna longline fisheries, 1988-89 to 1997-98. *NIWA Technical Report* 76. 79 p.
- Hoening, J.M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* 81: 898-903.
- Knight, W. (1968). Asymptotic growth: an example of nonsense disguised as mathematics. *Journal of the Fisheries Research Board of Canada* 25: 1303-1307.

- Knight, W. (1969). A formulation of the von Bertalanffy growth curve when the growth rate is roughly constant. *Journal of the Fisheries Research Board of Canada* 26: 3069-3072.
- Last, P.R.; Stevens, J.D. (1994). Sharks and rays of Australia. CSIRO, Hobart. 513 p.
- Mollet, H.F.; Cliff, G.; Pratt, H.L.; Stevens, J.D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin* 98: 299-318.
- Natanson, L.J.; Mello, J.J.; Campana, S.E. (2002). Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin* 100: 266-278.
- Pratt, H.L.; Casey, J.G. (1983). Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1944-1957.
- von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws II). *Human Biology* 10: 181-213.

4.9 Appendices

Appendix A: Conversion equations of length measurements

Fisheries laboratories working in the north-west Atlantic take measurements of total length (TL) and fork length (FL) over the curve of the body (OTB) as opposed to the straight line (caliper) method used in most other parts of the world, including New Zealand. For this reason it was necessary to convert lengths to a common standard (straight line FL) for comparison and consistency. The following equations were used for this:

$$FL = 0.9682 \times FL(OTB) + 0.9731$$

Source: Competition sharks measured during the present study.

$$FL(OTB) = 0.929 \times TL(OTB) - 1.931$$

Source: Pratt & Casey (1983).

$$FL = 0.9184TL - 2.078$$

Source: Competition sharks measured during the present study.

Appendix B: List of fishing competitions sampled in the North Island

Competition	Club	Location
Coruba Megafish	Hawkes Bay Sports Fishing Club	Napier
Raglan one-base	Waikato Boating & Sportfishing Club	Raglan
Whitianga one-base	Mercury Bay Ocean Sports	Whitianga
New Plymouth one-base	New Plymouth Sportfishing and Underwater Club	New Plymouth
Castlepoint SuperFish	Wairarapa Sports Fishing Club Inc	Castlepoint
Plimmerton Shark Hunt	Plimmerton Boating Club Inc	Plimmerton

Appendix C: Precision equations

Equations for estimating precision, as summarised by Campana et al. (1995). Average percent error (APE) is a measure of precision recommended by Beamish & Fournier (1981) and is defined as:

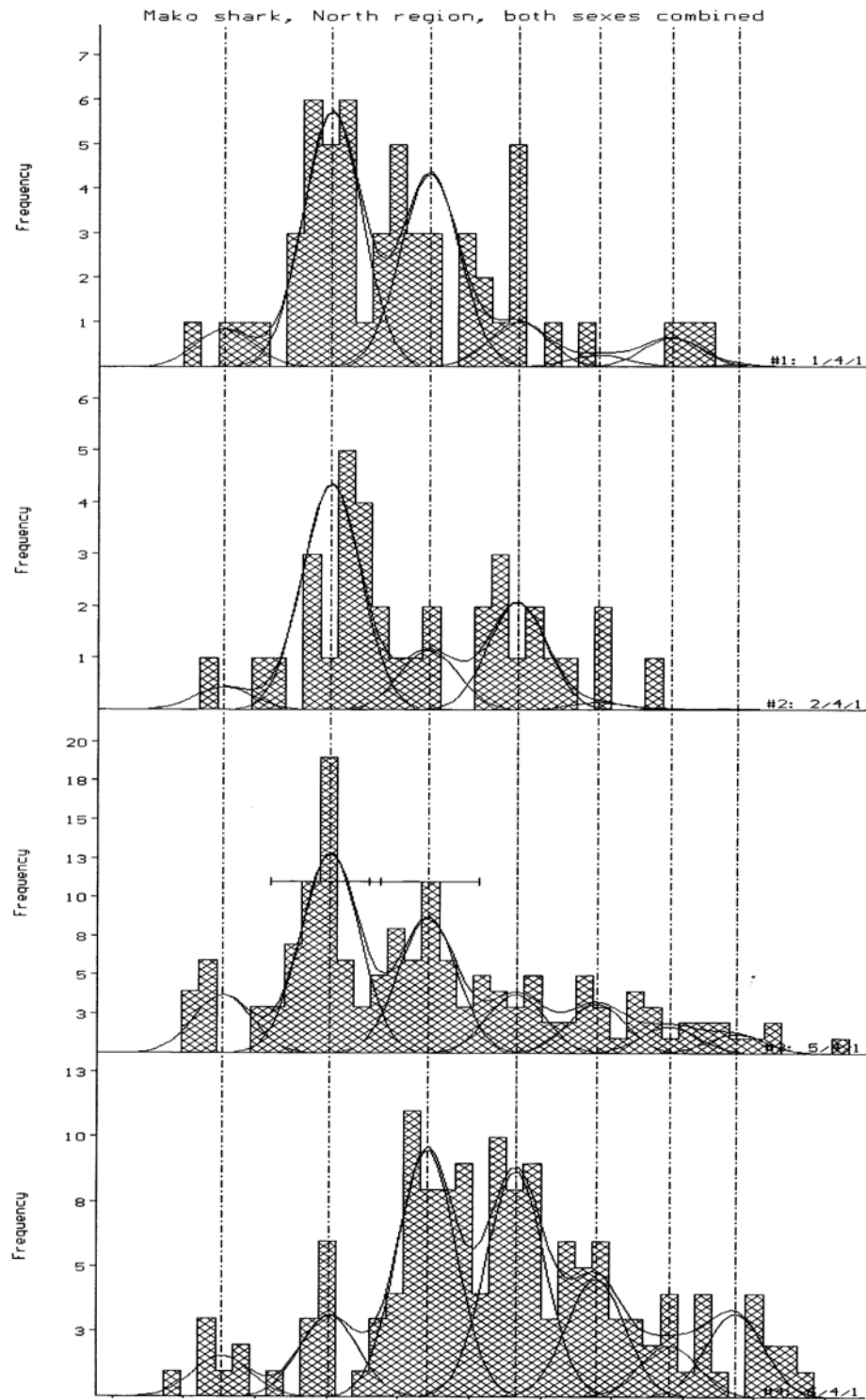
$$APE_j = 100 \times \frac{1}{R} \sum_{i=1}^R \frac{(X_{ij} - X_j)}{X_j}$$

where X_{ij} is the i th age determination of the j th fish, X_j is the mean age of the j th fish, and R is the number of times each fish is aged. When APE_j is averaged across many fish, it becomes an index of average percent error. Chang (1982) agreed that APE is a substantial improvement over old methods but suggested that the standard deviation be used in the above equation rather than the absolute deviation from the mean age. The resulting equation produces an estimate of the co-efficient of variation (CV), expressed as the ratio of the standard deviation to the mean, and can be written as:

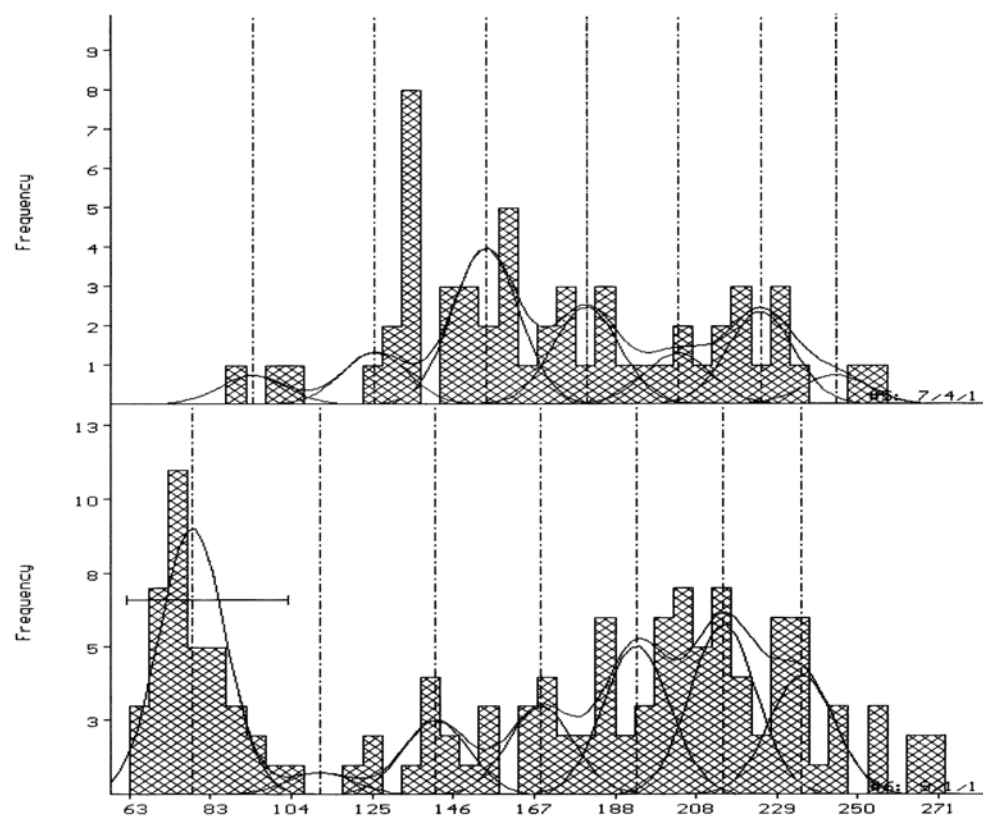
$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - X_j)^2}{R - 1}}}{X_j}$$

The above equation is a CV estimate for a single fish (j th fish). As with the first equation, it can be averaged across fish to produce a mean CV. Both equations produce similar values however, the latter is statistically more rigorous and thus more flexible. The CV index is approximately 1.4 times greater than the APE index (Campana 2001).

Appendix D: Length-frequency distributions



Appendix D: 1993–1994 and 1997–1998 length-frequency distributions for mako sharks collected from the northern tuna longline fishery showing the fit of the best MULTIFAN model containing seven age classes and seasonal growth. Horizontal bars above some modes indicate constraints placed on the mean lengths of those modes. See Fig. 3 for details of sampling periods and sample size. (Continued.)



Appendix D (cont.): 1999–2001 length-frequency distributions.