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from the New Zealand Exclusive Economic Zone**

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## EXECUTIVE SUMMARY

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Age and growth, longevity, natural mortality, and age-at-maturity estimates for blue sharks in the New Zealand Exclusive Economic Zone (EEZ) were derived from 428 whole and X-radiographs of sectioned vertebral centra and other biological data collected from commercial and recreational catches. This study was funded by the New Zealand Ministry of Fisheries under research project TUN2002-01 Objective 1.

Vertebral reading precision was fair within-reader (IAPE = 5.99; mean c.v. = 8.47%), and compares favourably between-readers with overseas studies (IAPE = 9.02; mean c.v. = 12.76%). There was no evidence of bias within-reader; however there was some evidence of a difference in interpretation between-readers of vertebrae from older sharks.

A range of alternative growth models was fitted to the final vertebral length-at-age dataset using maximum likelihood methods. Additive and multiplicative von Bertalanffy and Schnute growth models that assumed and did not assume separate growth by sex were fitted and compared using the likelihood ratio test. Selection of an appropriate case of Schnute's model was made using Akaike's Information Criterion (AIC). The fit of a Schnute model (case 1) assuming separate parameters by sex and multiplicative normal errors was preferred among the suite of models fitted ( $L_{1,male} = 65.21$ ,  $L_{2,male} = 217.48$ ,  $\kappa_{male} = 0.1650$ ,  $\gamma_{male} = 0.16$ ,  $L_{1,female} = 63.50$ ,  $L_{2,female} = 200.60$ ,  $\kappa_{female} = 0.2297$ ,  $\gamma_{female} = 0.07$ ; asymptotes calculated from the parameter estimates are  $L_{\infty,male} = 297.18$  and  $L_{\infty,female} = 235.05$ ). Reference ages of 2 and 10 years were assumed for all Schnute models fitted.

From the fit of the preferred model, female blue sharks appear to approach a lower mean asymptotic maximum length and grow at a faster rate than males. This contradicts studies on the age and growth of blue shark from other oceans, where female sharks typically approach a larger mean asymptotic maximum size than males. This is thought to result from the presence of relatively few larger (over 250 cm FL), older female blue sharks in length-at-age dataset in this study. The data suggest that larger females are missing from the commercial catch despite anecdotal evidence to the contrary. Hence, the vertebral growth estimates produced are probably biased. Growth rates (the values of growth model rate parameters) are broadly comparable with overseas studies, however. A MULTIFAN analysis of length-frequency data was uninformative.

The oldest male and female blue sharks in the final vertebral length-at-age dataset were 22.76 and 19.73 years, respectively. From these results, it appears that male blue sharks in the New Zealand EEZ reach at least their 22nd year and females approach their 20th year. Although crude, these estimates are preferred to estimates of longevity calculated from von Bertalanffy model parameter estimates. Natural mortality estimates derived from the former using Hoenig's regression are 0.19 for male sharks and 0.21 for females. Age at maturity appears to be about 8 years for male sharks and about 7–9 years for females in the New Zealand EEZ. Blue sharks in the New Zealand EEZ appear to mature later than blue sharks from other oceans, although growth rates and longevity are roughly comparable. Blue sharks caught in the New Zealand EEZ are almost certainly part of a larger South Pacific stock, however.

Collecting, preparing, and reading vertebrae from larger (over 250 cm FL), older female blue sharks and updating the analyses presented in this study is a priority for research on this species in the New Zealand EEZ. The possible difference in interpretation in vertebrae of older sharks between-readers should also be investigated further; an inter-laboratory exchange is suggested.

## 1. INTRODUCTION

Blue sharks (*Prionace glauca*) are large, highly migratory, pelagic carcharhinids found throughout the world's oceans in all tropical and temperate waters. They are slender in build, rarely exceeding 3 m in total length and 200 kg in weight. They feed opportunistically on a range of living and dead prey, including bony fishes, smaller sharks, squids, and carrion. Blue sharks were little studied prior to the 1970s, although since then efforts have been made to better understand their basic biology and ecology, given their relatively low intrinsic rate of increase, relatively high global catch, and ecological importance as apex predators. However, little is known about the biological productivity of blue shark in the south Pacific Ocean.

In the New Zealand Exclusive Economic Zone (EEZ), blue sharks are the single most common bycatch species caught in the tuna surface longline fishery. Estimated total annual catches of blue sharks in this fishery during the 2000–01 and 2001–02 fishing years were 1478 t and 1969 t, respectively (Ayers et al. 2004). Francis et al. (2004) concluded that blue shark bycatch in the tuna surface longline fishery was unlikely to be affecting the blue shark stock in the New Zealand EEZ, but they were concerned about the rapid increase in domestic fishing effort in recent years, and poor coverage of the fisheries by the Ministry of Fisheries Observer Programme (MFish OP). A more recent analysis has shown that fishing effort has continued to rise, and that observer coverage remains low (2–3% of effort) (Ayers et al. 2004).

Given the lack of knowledge on the productivity of the regional stock and the increase in tuna fishing effort, the aim of our study was to investigate the basic biological productivity of blue sharks in the New Zealand EEZ and to quantify key demographic parameters. Funding was provided by the New Zealand Ministry of Fisheries under research project TUN2002-01 Objective 1. The project's specific objective was to determine the growth rate, age-at-maturity, longevity, and natural mortality rate of blue, mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) sharks.

In this report we present estimated ages for blue sharks in the New Zealand EEZ derived from translucent zone counts in vertebrae collected from the commercial and recreational catch. We present a series of growth models fitted to the length-at-age data and compare them quantitatively. We qualitatively compare the vertebral-derived growth model results with those derived from MULTIFAN (Fournier et al. 1990) analysis of length-frequency data. We also present estimates of length- and age-at-maturity and natural mortality. We compare our results with data on the age, growth, longevity, natural mortality, and maturity of blue sharks from other oceans.

## 2. METHODS

### 2.1 Dataset

Length, sex, and maturity data collected by the MFish OP from blue sharks caught in the tuna surface longline fishery between the 1992–93 and 2001–02 fishing years were extracted from the Ministry of Fisheries research database *tuna* (Wei 2004). Blue shark length, sex, maturity data, and vertebrae were also collected opportunistically from recreational catches by M. Francis (National Institute of Water and Atmospheric Research Ltd) and C. Duffy (Department of Conservation) at major recreational fishing competitions in the North and South Islands since February 1986. These data were pooled to produce a single composite dataset. Blue shark vertebrae were collected from the commercial catch by the MFish OP since the 2001–02 fishing year. The data are summarised in Table 1. Data and sample collection positions are plotted in Figure 1.

## 2.2 Age estimation

### 2.2.1 Age estimates derived from whole vertebrae and vertebral sections

Vertebrae were collected from specimens in the commercial and recreational catch using the same method: a block of 4–6 vertebrae situated beneath the first dorsal fin was removed from each shark, trimmed of neural and haemal arches, muscle, and connective tissue and then frozen. Shark length (fork length, FL) was recorded to the nearest centimetre below actual length, as well as sex, and maturity data. All vertebrae were frozen at -20 °C for long-term storage. A subset of 440 vertebrae, one per individual shark, was selected for reading after stratifying by length and sex. Approximately equal numbers of vertebrae covering the full length range of the catch of each sex were selected.

Vertebrae from sharks less than 150 cm FL were read whole and unstained. Henderson et al. (2001) found this to be simple, fast, and as effective and accurate for small blue sharks as other more time-consuming methods (e.g., sectioning). Vertebrae from sharks 150 cm FL or larger were sectioned frontally by making two cuts with a single diamond-edged saw blade. This produced a section about 1 mm in width. Because many vertebrae were too large for sectioning in NIWA's Accutom-2 precision wafering saw, a larger, less precise saw (a modified valve-grinder) was used. Many of the sections produced by this saw were of variable width and poor overall quality. All sections were stored wet in 70% 2-propanol (isopropyl alcohol).

Sections were removed from propanol and read wet using a Wild M400 binocular microscope under reflected white light at  $\times 6.3$  magnification, following the methods of Natanson et al. (2002) and Skomal & Natanson (2003). All completed opaque zones were counted and scored using a five-point "readability" score (Table 2) and a three-point "marginal-state" score (Table 3). All counts excluded the "birth-band", an opaque zone which is laid down at or soon after birth. The birth band in blue sharks from other oceans is unusually easily recognisable as the innermost band in the centrum and is often marked by a change in the angle of the corpus calcareum (Skomal & Natanson 2003).

### 2.2.2 Age estimates derived from X-radiographs of vertebral sections

X-radiographs were taken of all sections and read using the same methods as for the vertebral sections, except that transmitted light was used to illuminate developed X-radiograph film. This resulted in images with the same polarity as sections viewed under reflected light, that is translucent zones appeared dark and opaque zones appeared bright. All X-radiographs were read blind, without knowledge of shark length, sex, date of capture, or the opaque zone counts obtained from the corresponding wet sections.

### 2.2.3 Converting opaque zone counts to estimated ages

Opaque zone counts were converted to estimated ages by treating age as the sum of three time elements. The estimated age of the  $i$ th shark,  $\hat{a}_i$ , is

$$\hat{a}_i = t_{i,1} + t_{i,2} + t_{i,3}, \quad (1)$$

where  $t_{i,1}$  is the elapsed time from parturition (birth) to the end of the first opaque zone,  $t_{i,2}$  is the elapsed time from the end of the first opaque zone to the end of the outermost fully-formed opaque zone, and  $t_{i,3}$  is the elapsed time from the end of the outermost fully-formed opaque zone to the date of capture of the  $i$ th shark. Hence,

$$\begin{aligned}
t_{i,1} &= t_{i, \text{ end first opaque zone}} - t_{i, \text{ birth date}} \\
t_{i,2} &= (n_i + w) - 1 \\
t_{i,1} &= t_{i, \text{ capture}} - t_{i, \text{ end last opaque zone}}
\end{aligned}
\tag{2}$$

where  $n_i$  is the total number of opaque zones present for shark  $i$  excluding the birth band, and  $w$  is an edge interpretation correction after Francis et al. (1992) applied to  $n_i$ :  $w = 1$  if the recorded margin state = "wide" and shark  $i$  was collected after the date when opaque zones are assumed to be fully formed,  $w = -1$  if the recorded margin state = "narrow" and shark  $i$  was collected before the date when opaque zones are assumed to be fully formed, otherwise  $w = 0$ .

Information on the seasonality of parturition in blue sharks is poor. The most comprehensive studies, from the North Atlantic and North Pacific oceans, indicate that parturition occurs mainly in spring to early summer (April–July) (Pratt 1979, Nakano 1994). The limited information from the southern hemisphere is also consistent with spring–early summer parturition. In the South Atlantic off Brazil, parturition apparently occurs in November–December (Amorim et al. 1998) and two Australian studies based on very small sample sizes suggested October–November and December–March respectively (Stevens 1984, Stevens & McLoughlin 1991).

The data from the New Zealand region are equally sparse. Blue sharks 50–70 cm FL are caught year-round but only in small numbers. The few embryos examined consisted of mid-term pups 21–37 cm FL collected in July and a full-term pup of 54 cm FL collected in February (the latter coinciding with a number of records of free-living sharks of 50–53 cm). Although the New Zealand data are fragmentary, when viewed in the context of the Australian and northern hemisphere data they suggest spring-early summer parturition. We therefore chose 1 November as the theoretical birthday.

Skomal & Natanson (2003) suggested that opaque zones in North Atlantic blue sharks were fully completed by 1 May in the northern spring. From this, we assumed that opaque zones in South Pacific blue sharks were fully completed by 1 November (1 May + six months to account for the change in hemispheres = 1 November), hence  $t_{i,1}$  reduces to 1.

## 2.2.4 Quantifying reading precision

Reading precision was quantified by carrying out within- and between-reader comparison tests following Campana et al. (1995). A sample of 110 vertebrae was randomly selected from the set of 440 prepared vertebrae and re-read by the first reader and a second reader. Once the opaque zone counts in each set of re-readings had been converted to estimated ages, both sets of results were compared with the first reader's first set of results. The Index of Average Percentage Error, IAPE (Beamish & Fournier 1981), and mean coefficient of variation, mean c.v. (Chang 1982), were calculated for each test using the "R" statistical programming language (R Development Core Team 2003), a dialect of the "S" language (Becker et al. 1988). Where  $X_{ij}$  is the  $i$ th count of the  $j$ th vertebra,  $R$  is the number of times each vertebra is read, and  $N$  is the number of otoliths read or re-read,

$$\text{IAPE} = 100 \times \frac{1}{N} \sum_{j=1}^N \left[ \frac{1}{R} \sum_{i=1}^R \left| \frac{X_{ij} - X_j}{X_j} \right| \right],
\tag{3}$$

and

$$\text{mean c.v.} = 100 \times \frac{1}{N} \sum_{j=1}^N \left[ \frac{\sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R-1}}}{X_j} \right] \quad (4)$$

Where two readings are compared (i.e., two different readings of the same vertebra, either within- or between-readers), the IAPE differs from the mean c.v. only by the multiplicative constant  $\sqrt{2}$ ; however, we present both statistics for ease of comparison with the literature.

## 2.3 Growth

### 2.3.1 Fitting growth models to the vertebral length-at-age data

We fitted a series of growth models to the vertebral length-at-age data. Following Manning & Sutton (2004), we tested for differences in growth between the sexes by fitting a full von Bertalanffy growth model that assumed separate parameters by sex, and a reduced model that did not assume separate parameters by sex, using maximum likelihood methods. We then compared the model fits using the likelihood ratio test (Kimura 1980). Full and reduced models were fitted assuming additive and multiplicative normal errors. The null hypothesis for each test was that the full and reduced model obeyed a set of linear constraints such that their parameters were equivalent; the alternative hypothesis was that they obeyed no such constraints (Kimura 1980).

We then fitted Schnute's (1981) growth model to the data. Schnute's model has four possible solutions or submodels, which are commonly referred to as "cases". A fifth case, equivalent to Cerrato's (1990) alternative parameterisation of the von Bertalanffy model, also exists (Appendix A). We selected the most parsimonious model from each of the five contending Schnute models by first fitting the models using maximum likelihood estimation assuming first additive then multiplicative normal errors, a single model for all the data, and a single common variance parameter, then computing Akaike's (Akaike 1973) Information Criterion (AIC) for each fitted model. The most parsimonious model is the model with the lowest AIC (Appendix A).

Once the most parsimonious model was selected, we then fitted, using the same methods, a second model of the same type that assumed separate Schnute parameters by sex. We then compared the full and reduced models using the likelihood ratio test. Confidence intervals for each model's parameters were calculated from the hessian matrix for each model (see Appendix A).

### 2.3.2 Estimating growth using MULTIFAN

#### 2.3.2.1 Length-frequency distributions

Ministry of Fisheries observers have been collecting blue shark length-frequency data aboard tuna longline vessels since the 1991–92 fishing year. The longline fishery operates in two main regions: along east and west coasts of South Island (the southern fishery) and along the northeast coast of North Island (the northern fishery) (Francis et al. 2004). The northern fishery operates year-round, and fishing effort has been increasing steadily since 1997 due to an influx of domestic fishing vessels. The southern fishery is carried out mainly during April–June 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) (Ayers et al. 2004).



Most blue shark length-frequency data from the northern fishery were collected during May–August, but sample sizes were often small when broken down by sex and year (Appendix B). Sample sizes from the southern fishery were large for females, and variable for males (Appendix C). We decided not to combine data from both fisheries, because although tagging data indicate that blue 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 southern fishery were analysed.

Length-frequency data collected from the southern fishery during April–June were grouped by sex and calendar year into 3 cm length intervals for analysis (Appendix C). 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  $L_\infty$  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  $S_R$ ). Because all data were collected during the same three-month season, they contain no information on seasonal variability of growth, and no seasonal parameters were fitted. The constant standard deviation hypothesis was fitted to the data first, followed by the addition of the parameter for variable standard deviation.

For each combination of  $K$ , number of age classes, and growth hypothesis, the maximum log-likelihood ( $\lambda$ ) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the increase in  $\lambda$  is distributed as a  $\chi^2$  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 test for improvement resulting from the addition of the parameter for variable standard deviation was 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 birthday and the first appearance of the youngest year class in the samples. We used the same theoretical birthday for the MULTIFAN analysis that we used in the vertebral-based age and growth analyses described above, namely 1 November.

## 2.4 Longevity

The oldest shark in our (vertebral) length-at-age dataset provides an initial, albeit crude, estimate of longevity for New Zealand blue sharks. However, in a fished population such as ours, this is likely to be an underestimate of true longevity. Taylor (1958) defined longevity,  $A$ , as the time required to

attain 95% of  $L_{\infty}$  in a fitted von Bertalanffy model. Skomal & Natanson (2003), adapted Taylor's approach, defining longevity as the time required to attain 99% of  $L_{\infty}$ , yielding the equation

$$A_{0.99} = t_0 - \frac{1}{k} \ln(1 - 0.99). \quad (5)$$

Note that the equation given by Skomal & Natanson (2003) is incorrect; the correct equation is given above. Skomal & Natanson (2003) also used the approach of Fabens (1965), who calculated the time required to attain 99% of  $L_{\infty}$ , using the equation

$$A_{0.99} = 5 \frac{\ln 2}{k}, \quad (6)$$

and compared the results of both methods. We do the same.

## 2.5 Natural mortality

We used Hoenig's (1983) empirical relationship between the natural mortality coefficient,  $M$ , and longevity to estimate  $M$  for blue sharks in the New Zealand EEZ. Hoenig's relationship is derived from a linear regression of log-transformed natural mortality and longevity data for a diverse range of species, and is useful when  $M$  is difficult to estimate using other means. Where  $t_{\max}$  is longevity, Hoenig's regression is

$$\ln M = 1.46 - 1.01[\ln t_{\max}]. \quad (7)$$

We estimated  $t_{\max}$  from the oldest shark of each sex in our length-at-age dataset and computed  $M$  separately for each sex.

## 2.6 Age at maturity

Francis & Duffy (in press) presented length-at-maturity estimates for blue sharks in the New Zealand region. They directly estimated length-at-maturity from paired maturity and length data collected by the MFish OP using probit analysis (Pearson & Hartley 1962), fitting the probit model using maximum likelihood estimation. Unfortunately, the maturity data in our vertebral length-at-age datasets were too sparse to permit repeating Francis & Duffy's analysis with maturity-at-age data. We crudely estimate age-at-maturity by substituting Francis & Duffy's median lengths-at-maturity for male and female blue sharks into our two-sex von Bertalanffy models and then solving the resulting equations for male and female age.

## 3. RESULTS

### 3.1 Review of aspects of blue shark age, growth, longevity, natural mortality, and maturity outside the New Zealand EEZ

#### 3.1.1 Age, growth, longevity, and natural mortality

Stevens (1975) developed a silver nitrate staining method for estimating the ages of North Atlantic blue sharks. In his method, silver salts are substituted for calcium salts in the calcified cartilage matrix of whole vertebrae. Growth zones were counted on the conical, calcified, articulating surfaces (corpus

calcareum). Growth models fitted to length-at-age data derived from the vertebral counts agreed well with growth models fitted to tag-recapture data (Stevens 1975, 1976, 1990), thus providing verification of the vertebral age estimation technique.

Cailliet et al. (1983) estimated growth rates of northeast Pacific blue sharks from their vertebrae, using Stevens's silver nitrate technique and X-radiography. Both methods produced clear growth zones, but Cailliet et al. preferred silver nitrate for historical and comparative reasons. Estimated growth rates were similar to those in the Atlantic up to about 3–4 years, but the Pacific sharks were shorter than Atlantic sharks at 5–6 years. The difference may have been an artefact caused by a lack of large specimens in the Pacific samples, reflected in values of  $\hat{L}_{\infty}$  less than 3 m TL for both sexes (Cailliet et al. 1983). Nevertheless, Japanese studies of North Pacific blue sharks, also using silver nitrate, produced similar results (Nakano 1994).

Tanaka et al. (1990) compared age estimation techniques and fitted growth models to length-at-age data from blue sharks caught off California and Japan. They were unable to detect differences between the two areas, or between the two sexes, and attributed this to reader precision and variability, natural variability in length-at-age, and model-fitting techniques. In addition, sample sizes in this and other studies have usually been inadequate for detecting differences. Scientists in the two regions generally agreed on the ages of small sharks (under 155 cm TL), but differed in their interpretation of fine growth zones in medium-sized sharks (155–215 cm TL). Sectioning the vertebral centra made these fine growth rings more visible, but increased problems with interpretation.

Henderson et al. (2001) estimated the ages of blue sharks from the northeast Atlantic. They compared whole unstained vertebrae with whole vertebrae stained by silver nitrate and alizarin S, and found no differences in the age estimates obtained by the three methods. They preferred examination of whole unstained vertebrae under reflected lighting as being the most convenient method.

Skomal & Natanson (2003) recently completed a large study of blue shark growth in the northwest Pacific using vertebral age estimates and tag-recapture data. Their age estimation method involved counting growth zones in 600  $\mu\text{m}$  thick sections cut from vertebrae and viewed unstained under reflected light. They partially validated their age estimation method using marginal increment analysis and recaptures of two oxytetracycline injected sharks. Both sexes grew at a similar rate up to seven years, after which the male growth rate decreased and the two growth curves diverged.

The oldest blue sharks in most of the studies described above were 6–12 years (Cailliet et al. 1983, Tanaka 1990, Nakano 1994, Henderson et al. 2001). However, these studies did not have access to large blue sharks, so longevity is probably considerably greater. Skomal & Natanson's (2003) samples covered the full length range and produced growth models that differ markedly from those in other studies. Maximum ages were 16 and 15 years for males and females respectively. A shark that was 151 cm TL at tagging and with a predicted age of 3–4 years was recaptured after 10.7 years at liberty (Stevens 1990). Longevity is likely to be about 20 years (Stevens 2000).

The natural mortality statistic,  $M$ , for northwest Atlantic blue sharks was estimated as 0.28 by Fogarty et al. (1989), who used Hoenig's (1983) method and an estimated longevity of 16 years. If longevity is 20 years, then  $M$  would be about 0.23 using Hoenig's method.

### 3.1.2 Maturity

The reproductive biology of blue sharks has been well studied (Gubanov & Grigor'yev 1975, Pratt 1979, Stevens 1984, Hazin et al. 1994, Nakano 1994, Castro & Mejuto 1995, Stevens 2000, Henderson et al. 2001). Determination of maturity status is complicated by the existence of pre-mature mating and sperm storage in subadult females, and the lack of rapid elongation of claspers at maturity

in males. In addition, maturation occurs over a wide size-range, even within studies that used consistent criteria for determining maturity.

In the North Atlantic and off eastern Australia, clasper length increases uniformly with total length in male blue sharks (Pratt 1979, Stevens 1984), though in the North Pacific, Nakano (1994) observed a slight inflection in the relationship that coincided with completion of clasper calcification. Clasper length by itself may not be a good indicator of maturity. Pratt (1979) concluded that the presence or absence of spermatozeugmata, unencapsulated bundles of sperm, was the most reliable method for determining maturity. The percentage of males containing spermatozeugmata increases rapidly at maturity (Pratt 1979, Nakano 1994). Spermatozeugmata are macroscopically visible in the vas deferens and ampulla epididymis, being 0.5–2.0 mm in diameter (Pratt 1979). However, some large blue sharks that were clearly mature lacked spermatozeugmata, suggesting that their production may be seasonally variable (Hazin et al. 1994, Nakano 1994). A combination of clasper length and development, whether calcified or not, and the presence or absence of spermatozeugmata, may be the best indicators of blue shark maturity.

Mature female blue sharks are often pregnant, and their maturity status is unambiguous. However, maturing, subadult females may be difficult to classify. The diameter of ovarian ova increases rapidly at maturity (Pratt 1979, Stevens 1984), and ova greater than 10 mm in diameter are approaching the size at ovulation. Thus, the presence or absence of ova or embryos in the uteri, and the size of ovarian ova, can be used to indicate female maturity.

Elsewhere, female blue sharks mature at 182–275 cm TL and males at 173–280 cm TL. In both sexes, 50% maturity appears to be reached around 210–230 cm TL. Some studies suggest that males mature at a greater length than females (Stevens 1984, Hazin et al. 1994), whereas others have found no difference between the sexes. Resolving this uncertainty requires adequate sample sizes, and access to representative samples of both mature and immature sharks of both sexes. Pacific blue sharks may mature at lengths slightly shorter than Atlantic sharks. Age at maturity is about 4–6 years for male and 5–7 years for female blue sharks elsewhere in the Pacific Ocean (Cailliet et al. 1983, Nakano 1994, Stevens 2000).

## **3.2 Age and growth estimation**

### **3.2.1 Vertebral age estimation**

Vertebrae have been collected from 899 blue sharks caught in the New Zealand EEZ. Vertebrae from 440 individual sharks were prepared and read in this study. (Table 1). Vertebrae were selected to cover as large a size range as possible of both sexes. Nevertheless, about twice as many female than male vertebrae were prepared and read.

All vertebral sections, regardless of preparation method, exhibited alternating opaque and translucent zones. However, the contrast between zones varied markedly between preparation methods. Photomicrographs of representative whole vertebrae are given in Figure 2, an X-radiograph of a prepared wet section in Figure 3, and a photomicrograph of the same wet section in Figure 4 for comparison. Figure 3 also illustrates how opaque zone counts were converted to age estimates. Readability scores are presented in Table 4. Margin state scores are presented in Table 5. X-radiographs offered improved contrast between opaque and translucent zones and produced images that were easier to interpret than the corresponding wet sections viewed under a light microscope. The change in angle of the corpus calcareum noted in studies of blue sharks from other oceans and used to identify the position of the birth band (Skomal & Natanson 2003) was apparent in both the X-radiographs and wet sections (Figure 3 and Figure 4).

Given the improvements in clarity and interpretation achieved in X-radiographs relative to wet sections viewed with white light, we compiled a final vertebral length-at-age dataset composed of whole-vertebral ages for sharks less than 150 cm FL and X-radiograph ages for sharks 150 cm FL or greater. If an X-radiograph age was not available for sharks 150 cm FL or greater, then a wet-section (2 sharks) or whole vertebral age (1 shark) was used in descending order of preference. Conversely, if a whole-vertebral age was unavailable for a shark less than 150 cm FL, then an X-radiograph or wet-section derived age (8 sharks) was used in descending order of preference. After deleting sharks with readabilities greater than 4, or with missing sex or length data, the final vertebral length-at-age dataset was composed of data from 428 sharks, 140 males and 288 females (Table 6). The length and age frequency distributions of male and female sharks in the dataset are summarised in Figure 5 and Figure 6, respectively.

### 3.2.2 Vertebral reading precision

The LAPE and mean c.v. were 5.99% and 8.47% respectively for the within-reader test and 9.02% and 12.76% respectively for the between-reader test (Table 7). Diagnostic bias plots following Campana et al. (1995) are presented in Figure 7. For the within-reader comparison, the symmetry of the difference histogram in Figure 7(A), the relatively even distribution of plotted points about the zero line in Figure 7(B), and the position of the error bars about the 1:1 line in Figure 7(C) all suggest that there is no systematic bias. However, there is some evidence of a difference in interpretation between readers. The error bars drop below the 1:1 line for ages of 13 years or older produced by the first reader in the between-reader plot in Figure 7(C), suggesting that the second reader was under-counting opaque zones relative to the first reader. This may be due to a difference in interpretation of opaque zones near the distal margins of vertebrae from older sharks. We preferred the estimated ages produced by reader 1 and only estimated ages produced by reader 1 were used to compile the final vertebral length-at-age dataset. A comparison of the results produced by reader 1 with published, partially validated photomicrographs of blue shark vertebrae produced by Skomal & Natanson (2003), suggested that the results produced by reader 1 were closer to Skomal & Natanson's method than those produced by reader 2. No attempt was made to resolve differences in interpretation between readers or to produce agreed ages before compiling the final dataset.

An age-bias plot of the X-radiograph and wet-section ages produced by the first reader is presented in Figure 8. The error bars drop below the 1:1 line for ages over 5 years derived using X-radiography, suggesting that there was a systematic differences between ages derived from the same sections using the different methods, with wet-section ages tending to be less than the X-radiograph ages. This suggests that X-radiography revealed opaque zones towards the distal margin of the vertebral sections that were missed in wet sections due to their poor quality, which we interpret as support for our decision to compile a final length at-age dataset derived from whole-vertebrae and X-radiograph opaque zone counts only.

### 3.2.3 Vertebral growth estimates

Parameter estimates and corresponding 95% confidence intervals for the von Bertalanffy models to the final vertebral length-at-age dataset are given in Tables 8–9. The fitted curves for the models assuming separate growth are overlaid on the length-at-age data in Figure 9. Fitted MULTIFAN growth curves are also overlaid for comparison (see below). Diagnostic residual plots (Appendix F) suggest that the multiplicative models fit the data better than the additive models; funnelling present in the plots of deviance residuals against fitted values for the additive models is reduced in the corresponding plots for the multiplicative models. The male and female curves appear to have diverged, and, interestingly, females appear to approach a lower mean asymptotic maximum length than males regardless of the error structure assumed.

We next fitted Schnute's model to the data. Selection of an appropriate case of Schnute's model was guided by a preliminary analysis where reduced, additive and multiplicative versions of all five cases of Schnute's model were fitted to the data (summarised in Table 10). Comparing relative fits to the data using the AIC statistic suggests that case 5 was the most parsimonious model when additive normal errors were assumed, and that case 1 was the most parsimonious model when multiplicative normal errors were assumed. Parameter estimates and corresponding 95% confidence intervals are given in Tables 11–12 for the case 1 and 5 additive and multiplicative model fits, respectively. The fitted curves are overlaid on the data in Figure 10.

Following on from these results, we fitted full, additive, and multiplicative versions of the first and fifth cases of Schnute's model to the data. Parameter estimates and corresponding 95 % confidence intervals are given in Tables 13–14 for the additive and multiplicative models, respectively. Diagnostic residual plots again suggested that the multiplicative models fitted the data better than the corresponding additive models. The fitted Schnute curves are compared with the fitted von Bertalanffy curves in Figure 11.

Despite different parameterisations, the fits of the fifth case of Schnute's model and of von Bertalanffy's model to the data are virtually identical (the fifth case of Schnute's model is equivalent to the alternative parameterisation of the von Bertalanffy model presented by Cerrato (1990)). Case 1 of Schnute's model produces lower asymptotes and different rate parameter estimates than either of these models with the same error structure. Nevertheless, female blue sharks appear to approach a lower mean asymptotic maximum length than males, regardless of the model fitted and error structure assumed.

The full and reduced, additive and multiplicative, von Bertalanffy and Schnute case 1 and 5 models are quantitatively compared using the likelihood ratio test in Table 15. The p-values for comparisons of the additive models are low, providing strong evidence against the null hypotheses that the full and reduced models are equivalent. The p-values for comparisons of the multiplicative models are low, providing less evidence against the null hypothesis than with the additive model fits, although the values obtained are all less than 0.01, suggesting that growth differs significantly between the sexes. As noted, the fits of the multiplicative models to the data are preferred to the fits of the corresponding additive models, and we give more credence to the multiplicative model comparisons here.

Of the different multiplicative models fitted assuming separate growth by sex, the Schnute case 1 model has the lowest AIC score, suggesting that it has the best relative fit to the data. The differences between the fitted curves when overlaid on the data are very small, however. Parameter estimates for the multiplicative, two-sex, case 1 model are  $L_{1,male} = 65.21$ ,  $L_{2,male} = 217.48$ ,  $\kappa_{male} = 0.1650$ ,  $\gamma_{male} = 0.16$ ,  $L_{1,female} = 63.50$ ,  $L_{2,female} = 200.60$ ,  $\kappa_{female} = 0.2297$ , and  $\gamma_{female} = 0.07$ ; asymptotes calculated from the parameter estimates are  $L_{\infty,male} = 297.18$  and  $L_{\infty,female} = 235.05$ .

### 3.2.4 MULTIFAN growth estimates

The length-frequency distributions from the southern fishery varied markedly between the sexes and among years (Appendix C). In most years, there were one or more modes between 60 cm and 100 cm, though these were often not well defined. The female distributions were usually dominated by a strong mode of subadults at 140–180 cm, and in the male distributions a slightly smaller mode (120–170 cm) was sometimes present. The best fit MULTIFAN models consisted of constant length standard deviation with 7 and 8 age classes for males and females respectively (Table 16). The fits of the models to the data are shown in Appendix D and Appendix E. The von Bertalanffy growth curves are shown in Figure 9, where they are compared with those calculated from the vertebral length-at-age dataset.

### 3.3 Longevity, natural mortality, and age-at-maturity estimates

The maximum ages estimated from vertebral opaque zone counts were 22.76 years for males and 19.73 years for females. Longevity estimates for males and females calculated using the methods of Taylor (1958) and Fabens (1965) and the full von Bertalanffy models fitted are given in Table 17. Given the very few very large female blue sharks collected and included in the dataset, and the uncertainty around the male and female asymptotes ( $\hat{L}_{\infty, \text{male}}$  and  $\hat{L}_{\infty, \text{female}}$ ) in the fitted models as reflected in the width of the corresponding 95% confidence intervals, we regard the latter estimates with suspicion and do not consider them further. Thus, on the best available data, male blue sharks in the New Zealand EEZ probably reach at least 22 years of age, and females probably approach at least 20 years of age.

Natural mortality estimates for male and female blue sharks in the New Zealand EEZ calculated using the maximum ages in the final vertebral length-at-age dataset as estimates of longevity and Hoenig's (1983) method are presented in Table 18. Assuming a longevity of 22 years produces an estimate of 0.19 using Hoenig's method; a longevity of 20 years produces an estimate of 0.21. Taking the average, we suggest a value of around 0.20 is plausible.

Francis & Duffy (in press) estimated length-at-maturity for male and female blue sharks in the New Zealand EEZ to be 190–195 cm FL and 170–195 cm FL, respectively. Substituting the lower and upper values in these ranges into our two-sex von Bertalanffy models yields ages-at-maturity of about 8 years for males and between about 7–9 years for females (Table 19). The greater uncertainty in female age-at-maturity reflects the greater uncertainty in female length-at-maturity estimated by Francis & Duffy (in press) and in the von Bertalanffy models fitted in this study.

## 4. DISCUSSION

### 4.1 Interpretation of blue shark vertebrae

Blue shark vertebrae are typically difficult to read with poor contrast between opaque and translucent zones (e.g., Skomal & Natanson 2003). This was found in this study, and was exacerbated by the difficulty we experienced in cutting even sections. However, X-radiographs of the vertebral sections greatly enhanced zone contrast and allowed us to count opaque zones that may have been missed using light microscopy. For older sharks, estimated ages derived from the vertebral sections were systematically lower than estimated ages derived from X-radiographs of the same sections. We regard the latter estimates as being more plausible.

Vertebral reading precision was fair within-reader, and, although lower between-readers, compares favourably with between-reader precision from overseas studies (e.g., between-reader mean c.v. = 15%, Skomal & Natanson 2003). There was no evidence of systematic bias within-reader, but there was evidence of a difference in interpretation between-readers in vertebrae from older sharks where we believe the second reader was undercounting opaque zones near the distal margin of the vertebral centrum. This issue should be investigated further in future. Our final vertebral length-at-age dataset consisted only of estimated ages produced by the first reader; no effort was made to resolve differences between-readers or to produce so-called "agreed ages". We believe that the results produced by reader 1, on which we have based the remainder of our analysis, are closer to Skomal & Natanson's (2003) published, partially validated method than those produced by reader 2. Skomal & Natanson validated the first four or so opaque zones in sectioned blue shark vertebrae using oxytetracycline; opaque zones in older sharks remain unvalidated.

## 4.2 Vertebral growth models

A range of alternative growth models was fitted to our vertebral length-at-age data. Our decision to fit Schnute's model was motivated by the uncertainty around the male and female length asymptote estimates in our full von Bertalanffy models,  $\hat{L}_{\infty, \text{male}}$  and  $\hat{L}_{\infty, \text{female}}$ , as reflected in the corresponding 95% confidence interval widths. Given that the  $L_{\infty}$  and  $k$  parameters in the von Bertalanffy model are very strongly negatively correlated, which can lead to poor fit, we were looking for an alternative growth model with more stable parameters that might fit our data better. Given that Schnute's model has five possible solutions depending on whether or not combinations of the two model parameters,  $\kappa$  and  $\gamma$ , are equal to zero or not (see Appendix A), we fitted all five cases to our data. Comparing AIC statistics suggested that case 5, a reparameterisation of the von Bertalanffy model with less correlated parameters, was the most parsimonious model when additive normal errors were assumed and that case 1 was most parsimonious when multiplicative normal errors were assumed; we thus fitted full (additive and multiplicative) versions of cases 1 and 5 to the data.

Of the additive and multiplicative full models fitted, whether von Bertalanffy, Schnute case 1, or Schnute case 5, we prefer the multiplicative Schnute case 1 model for the following reasons: (1.) diagnostic residual plots suggest the multiplicative models fit the data better than the additive models; (2.) the results of the likelihood ratio tests suggest that sex matters; and (3.), of the three full multiplicative models fitted, the Schnute case 1 model has the lowest AIC score, despite the presence of an extra parameter in the model (the AIC has a penalty term that increases as the number of model parameters increases). Nevertheless, the three full models produced nearly identical growth curves for each sex over the range of observed data. A visual inspection of the fitted curves suggests that there is little to choose between them.

From the fit of our preferred model, female blue sharks in the New Zealand EEZ appear to approach a lower mean asymptotic maximum length and growth at a faster rate than males. This contradicts overseas studies (e.g., Skomal & Natanson 2003) where female sharks typically approach a larger mean maximum size than males. Although the trend in the length asymptotes is not consistent with overseas studies, the overall values of the rate parameters are roughly comparable with these studies (e.g., see table 2, Skomal & Natanson 2003). We believe that this results from the presence of relatively few larger (over 250 cm FL), older female blue sharks in our dataset. The length composition of the commercial catch sampled by the MFish OP suggests that very few large females are caught in the commercial catch; however, anecdotal information indicates that very large (over 300 cm FL) female blue sharks are caught in the commercial catch in waters around northern New Zealand.

Furthermore, in the North Pacific, Nakano (1994) found that large, pregnant, female blue sharks tended to be caught in subtropical and temperate latitudes between 30–40° N. In the New Zealand EEZ, MFish OP data, although sparse, record catches of pregnant female blue sharks in similar southern latitudes, 27–34° S. Tuna longline effort in the northern New Zealand EEZ is dominated by the domestic fleet, but relatively little MFish OP sampling effort has been applied to the domestic fleet (1.5% of 9.5 million domestic hooks set in the 2001-02 fishing year were observed, Ayers et al. 2004). MFish OP sampling effort is concentrated on chartered foreign vessels which dominate tuna longline effort in more southern waters (Ayers et al. 2004). Blue shark samples collected by the MFish OP may thus be biased, missing larger, reproductively mature females that are caught by the commercial fleet in more northern waters. Making efforts to collect, prepare, and read vertebrae from larger (over 250 cm FL) female blue sharks in the New Zealand EEZ and refitting the growth models presented might well change our conclusions. Blue sharks caught in the New Zealand EEZ are almost certainly part of a larger, South Pacific stock (West et al. 2004).



### **4.3 Comparing vertebral and MULTIFAN growth estimates**

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). The MULTIFAN estimates are very different from those produced using the vertebral growth models beyond ages of about 5 years, regardless of the model actually fitted. We suggest the MULTIFAN parameter estimates are implausible, and that they should not be considered further.

### **4.4 Longevity, natural mortality, and age-at-maturity**

If we accept that our age estimates are valid, then it appears that male and female blue sharks in the New Zealand EEZ live longer than blue sharks in other oceans. The oldest North Atlantic blue shark ages produced by Skomal & Natanson (2003) were 16 and 15 for males and females respectively, compared with 22 and 19 years respectively in this study. Using Faben's (1965) method, Skomal & Natanson presented a longevity estimate of 20.7 years; however, Cortés (2000) found that theoretical *longevity estimates almost always exceed empirical estimates, even in lightly fished populations*. The maximum ages in our study are consistent with the 20-year longevity estimate produced by Stevens (2000) for North Pacific blue sharks.

Natural mortality estimates using methods other than Hoenig's regression have not been published for blue sharks from other oceans. Thus we are unable to compare natural mortality estimates meaningfully between oceans. Attempting to estimate natural mortality of blue sharks in the New Zealand EEZ using a different method would be very useful. Once the relationship between length and age of New Zealand blue sharks is better understood, estimating age-frequency distributions for historical catches where data permit and carrying out a catch-curve analysis could be attempted. However, all such methods of estimating  $M$  rely on obtaining a representative sample of the study population, which may be difficult for a species that appears to segregate by size, sex, and spans a wide range of latitudes (Nakano 1994).

Our estimates of age-at-maturity for male and female blue sharks in the New Zealand EEZ are reasonably well defined, despite our imperfect knowledge of the relationship between length and age for New Zealand blue sharks and the crudeness of our analysis. Males appear to mature at about 8 years of age and females between about 7 and 9 years of age. In comparison, age at maturity is about 4–6 years for male and 5–7 years for female blue sharks elsewhere in the Pacific Ocean (Cailliet et al. 1983, Nakano 1994, Stevens 2000).

### **4.5 Suggestions for further study on the age and growth of blue sharks in the New Zealand EEZ**

Much can be done to further refine our knowledge of the age and growth of blue sharks in the New Zealand EEZ. The greatest gains can probably be made by altering sampling to account for the apparent size and sex segregation within the EEZ. Sampling of the commercial catch by the MFish OP should be continued, but additional sampling effort should be allocated to the northern tuna longline fishery, specifically the domestic fleet, to cover larger, reproductively mature and possibly pregnant females that may not be caught in the southern fishery (where, historically, most observer sampling effort has been allocated). Within the sampling programme, although sampling should continue to be representative of the catch, efforts should also be made to collect vertebrae from larger (over 250 cm

FL), older, female blue sharks. These data should then be used to update the analyses presented in this paper.

## 5. ACKNOWLEDGMENTS

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**Table 1: Summary of data and vertebral samples collected from blue sharks caught in commercial tuna longline and recreational fisheries up to the end of the 2001–02 fishing year. Data from the commercial catch were collected by the Ministry of Fisheries Observer Programme. Data from the recreational catch were collected by M. Francis (National Institute of Water and Atmospheric Research Ltd) and C. Duffy (Department of Conservation).**

	Fishery		
	Tuna longline	Recreational	Total
When data collection commenced	1992–93	1986–87	1986–87
When vertebral sample collection commenced	2001–02	1986–87	1986–87
Length measurements	15 461	115	15 576
Maturity data collected?	Yes	Yes	Yes
Vertebrae collected	784	115	899
Vertebrae prepared and read in this study			
Male	127	16	143
Female	284	11	295
Unknown	2	0	2
Total	413	27	440

**Table 2: Five-point “readability” score used in vertebral section and X-radiograph readings.**

Score	Description
1	Vertebra very easy to read; excellent contrast between opaque and translucent zones; no difference between subsequent counts of this vertebra
2	Vertebra easy to read; good contrast between opaque and translucent zones, but not as marked as in 1; $\pm 1$ difference between subsequent counts of this vertebra
3	Vertebra readable; less contrast between opaque and translucent zones than in 2, but alternating zones still apparent; $\pm 2$ differences between subsequent counts of this vertebra
4	Vertebra readable with difficulty; poor contrast between opaque and translucent zones; $\pm 3$ or more differences between subsequent counts of this vertebra
5	Vertebra unreadable

**Table 3: Three-point "marginal state" score used in vertebral section and X-radiograph readings.**

Score	Description
Narrow	Last opaque zone deemed to be fully formed; a very thin, hairline layer of translucent material is present outside the last completed opaque zone
Medium	Last opaque zone deemed to be fully formed; a thicker layer of translucent material, not very thin or hairline in width, is present outside the last completed opaque zone; some new opaque material may be present outside the translucent material, but this generally does not span the entire distal margin of the vertebra
Wide	Last opaque zone deemed not to be fully formed; a thick layer of translucent material is laid down outside the last fully formed opaque zone, with opaque material present outside the translucent layer, spanning the entire distal margin of the vertebra

**Table 4: Readability scores for all prepared vertebrae. X-radiographs were taken of nearly all vertebral sections and are included here for comparison with readings taken directly from the "wet" section. The readability scores are defined in Table 2.**

Shark length	Preparation method	Readability score					Total
		1	2	3	4	5	
< 150 cm FL	Whole vertebrae	5	120	50	11	—	186
	Sectioned vertebrae	—	6	8	2	—	16
	X-radiographs of sectioned vertebrae	—	5	12	—	—	17
≥ 150 cm FL	Whole vertebrae	—	1	—	—	—	1
	Sectioned vertebrae	—	43	144	46	4	237
	X-radiographs of sectioned vertebrae	—	10	127	96	3	236
Total	All	5	185	341	155	7	693

**Table 5: All vertebrae read by shark length, preparation method, and margin-state score. Note that X-radiographs were taken of nearly all vertebrae sections and are included here for comparison with readings taken directly from the prepared, wet, sections. The margin-state scores are defined in Table 3.**

Shark length	Preparation method	Margin state				Total
		Narrow	Medium	Wide	Null	
< 150 cm FL	Whole vertebrae	125	37	24	—	186
	Sectioned vertebrae	11	1	4	—	16
	X-radiographs of sectioned vertebrae	15	2	—	—	17
≥ 150 cm FL	Whole vertebrae	1	—	—	—	1
	Sectioned vertebrae	164	49	20	4	237
	X-radiographs of sectioned vertebrae	227	6	—	3	236
Total	All	543	95	48	7	693

**Table 6: Composition of the final vertebral length-at-age dataset.**

Shark length	Preparation method	MFish OP		Recreational		Total
		Male	Female	Male	Female	
< 150 cm FL	Whole vertebrae	68	110	4	3	185
	Sectioned vertebrae	–	–	–	–	–
	X-radiographs	4	3	–	–	7
≥ 150 cm FL	Whole vertebrae	–	1	–	–	1
	Sectioned vertebrae	1	1	–	–	2
	X-radiographs	54	165	9	5	233
Total	All	127	280	13	8	428

**Table 7: Precision of results for within- and between-reader tests for whole vertebrae and X-radiographs. Age estimates derived from sectioned vertebrae were not considered. The final vertebral length-at-age dataset was derived from the age estimates produced by the first reader only.**

Statistic	Within-reader test	Between-reader test
IAPE (%)	5.99	9.02
Mean c.v. (%)	8.47	12.76



**Table 8: Results of fitting full and reduced additive von Bertalanffy growth models to the final vertebral length-at-age dataset. The full model assumes separate von Bertalanffy growth by sex; the reduced model does not. Both models assume a single common variance parameter. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of how SEs, 95% CI LBs, and 95% CI UBs were calculated.**

Parameters	Males				Females			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
$L_{\infty,i}$	342.90	16.09	311.37	374.44	267.49	12.14	243.70	291.28
$k_i$	0.0878	0.0086	0.0709	0.1047	0.1259	0.0133	0.0997	0.1520
$t_{0,i}$	-1.2570	0.2090	-1.6666	-0.8475	-1.0467	0.2224	-1.4826	-0.6108
$\sigma^2$	235.08	16.07	203.59	266.58				
<b>Other</b>								
$N$	428	$(n_{\text{male}} = 140, n_{\text{female}} = 288)$						
Max. LL	-1775.73							
AIC	3565.47							
<b>(B) Reduced model:</b>								
Parameters	All							
	MLE	SE	95% CI LB	95% CI UB				
$L_{\infty,i}$	326.07	13.08	300.43	351.70				
$k_i$	0.0885	0.0071	0.0745	0.1025				
$t_{0,i}$	-1.4515	0.1724	-1.7895	-1.1136				
$\sigma^2$	255.38	17.46	221.16	289.59				
<b>Other</b>								
$n$	428							
Max. LL	-1793.45							
AIC	3594.90							

**Table 9: Results of fitting full and reduced multiplicative von Bertalanffy growth models to the final vertebral length-at-age dataset. The full model assumes separate von Bertalanffy growth by sex; the reduced model does not. Both models assume a single common variance parameter. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of how SEs, 95% CI LBs, and 95% CI UBs were calculated.**

**(A) Full model:**

	Males				Females			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>								
$L_{\infty,i}$	390.92	31.89	328.42	453.41	282.76	15.83	251.75	313.78
$k_i$	0.0668	0.0086	0.0500	0.0837	0.1106	0.0118	0.0875	0.1338
$t_{0,i}$	-1.7185	0.1593	-2.0308	-1.4063	-1.2427	0.1529	-1.5424	-0.9429
$\sigma^2$	0.0105	0.0007	0.0091	0.0119				
<i>Other</i>								
$n$	428	$(n_{\text{male}} = 140, n_{\text{female}} = 288)$						
Max. LL	367.09							
AIC	-720.18							

**(B) Reduced model:**

	All			
	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>				
$L_{\infty,i}$	340.21	17.67	305.58	374.85
$k_i$	0.0808	0.0070	0.0671	0.0945
$t_{0,i}$	-1.5910	0.1145	-1.8155	-1.3666
$\sigma^2$	0.0109	0.0007	0.0094	0.0123
<i>Other</i>				
$n$	428			
Max. LL	360.12			
AIC	-712.25			

**Table 10: Summary of a preliminary analysis evaluating the relative fits of different cases of Schnute's model to the final vertebral length-at-age dataset. Summarised results (number of parameters, maximum log-likelihood, AIC) are given by model case and assumed error structure.**

Schnute model	Additive normal errors			Multiplicative normal errors		
	Number of parameters	Max. log-likelihood	AIC	Number of parameters	Max. log-likelihood	AIC
Case 1	5	-1793.45	3596.90	5	363.38	-716.77
Case 2	4	-1798.79	3605.57	4	361.40	-714.81
Case 3	4	-1802.72	3613.44	4	346.38	-684.75
Case 4	4	-1999.14	4004.29	4	137.57	-269.14
Case 5	3	-1793.45	3594.90	3	360.12	-712.24

**Table 11: Results of fitting additive Schnute models (cases 1 and 5) to the final vertebral length-at-age dataset. All models assume a single common variance parameter and did not assume separate growth by sex. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of Schnute's model and how SEs, 95% CI LBs, and 95% CI UBs were calculated. Reference ages of  $\tau_1 = 2$  and  $\tau_2 = 10$  were used for all model fits.**

**(A) Case 1:**

	All			
	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>				
$L_{1,j}$	63.62	2.52	58.69	68.55
$L_{2,j}$	207.70	1.42	204.91	210.49
$\kappa_j$	0.0890	0.0235	0.0429	0.1351
$\gamma_{1,2}$	0.9935	0.2544	0.4949	1.4921
$\sigma^2$	255.37	17.46	221.16	289.59
<i>Other</i>				
$L_{\infty,j}$	325.57			
$L_{I,j}$	2.05			
$n_j$	428			
Max. LL	-1793.45			
AIC	3596.90			

**(B) Case 5:**

	All			
	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>				
$L_{1,j}$	63.58	2.08	59.50	67.66
$L_{2,j}$	207.68	1.21	205.30	210.06
$\kappa_j$	0.0884	0.0072	0.0744	0.1025
$\gamma_{1,2}$	—	—	—	—
$\sigma^2$	255.38	17.46	221.16	289.59
<i>Other</i>				
$L_{\infty,j}$	326.12			
$L_{I,j}$	0			
$n_j$	428			
Max. LL	-1793.45			
AIC	3594.90			

**Table 12: Results of fitting multiplicative Schnute models (cases 1 and 5) to the final vertebral length-at-age dataset. All models assume a single common variance parameter and do not assume separate growth by sex. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of Schnute's model and how SEs, 95% CI LBs, and 95% CI UBs were calculated. Reference ages of  $\tau_1 = 2$  and  $\tau_2 = 10$  were used for all model fits.**

(A) Case 1:	All			
	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>				
$L_{1,j}$	64.67	1.07	62.57	66.77
$L_{2,j}$	208.15	1.75	204.72	211.58
$\kappa_1$	0.1436	0.0274	0.0900	0.1973
$\gamma_{1,2}$	0.4708	0.2209	0.0379	0.9036
$\sigma^2$	0.0107	0.0007	0.0093	0.0121
<i>Other</i>				
$L_{\infty,j}$	285.38			
$L_{1,j}$	73.86			
$n_1$	428			
Max. LL	363.38			
AIC	-716.77			
(B) Case 5:	All			
	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>				
$L_{1,j}$	64.27	1.02	62.27	66.26
$L_{2,j}$	206.86	1.63	203.67	210.05
$\kappa_1$	0.0807	0.0072	0.0666	0.0949
$\gamma_{1,2}$	—	—	—	—
$\sigma^2$	0.0109	0.0007	0.0094	0.0123
<i>Other</i>				
$L_{\infty,j}$	340.38			
$L_{1,j}$	0			
$n_1$	428			
Max. LL	360.12			
AIC	-712.25			

**Table 13: Results of fitting additive Schnute models (cases 1 and 5) to the final vertebral length-at-age dataset assuming separate growth by sex. All models assume a single common variance parameter. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of Schnute's model and how SEs, 95% CI LBs, and 95% CI UBs were calculated. Reference ages of  $\tau_1 = 2$  and  $\tau_2 = 10$  were used for all model fits.**

(A) Case 1:	Male				Female			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>								
$L_{1,j}$	67.33	3.46	60.55	74.11	60.37	3.74	53.05	67.69
$L_{2,j}$	220.18	2.83	214.63	225.73	200.81	1.67	197.53	204.09
$\kappa_1$	0.1995	0.0526	0.0964	0.3026	0.1193	0.0386	0.0435	0.1950
$\gamma_{1,2}$	-0.2135	0.5554	-1.3020	0.8750	1.0659	0.3648	0.3508	1.7810
$\sigma^2$	230.78	15.77	199.86	261.70				
<i>Other</i>								
$L_{\infty,j}$	290.27				270.76			
$L_{1,j}$	117.27				-20.72			
$n_j$	140				288			
Max. LL	-1771.79							
AIC	3561.58							
(B) Case 5:	Male				Female			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>								
$L_{1,j}$	61.67	2.80	56.17	67.16	60.75	3.09	54.70	66.79
$L_{2,j}$	215.32	1.98	211.44	219.21	200.88	1.65	197.65	204.12
$\kappa_1$	0.0878	0.0087	0.0708	0.1048	0.1258	0.0134	0.0996	0.1521
$\gamma_{1,2}$	-	-	-	-	-	-	-	-
$\sigma^2$	235.089	16.07	203.59	266.58				
<i>Other</i>								
$L_{\infty,j}$	342.92				267.50			
$L_{1,j}$	0				0			
$n_j$	140				288			
Max. LL	-1775.73							
AIC	3565.47							

Table 14: Results of fitting multiplicative Schnute models (cases 1 and 5) to the final vertebral length-at-age dataset assuming separate growth by sex. All models assume a single common variance parameter. MLE, Maximum Likelihood Estimate; SE, Standard Error; 95% CI LB, 95% Confidence Interval Lower Bound; 95% CI UB, 95% Confidence Interval Upper Bound. See Appendix A for a description of Schnute's model and how SEs, 95% CI LBs, and 95% CI UBs were calculated. Reference ages of  $\tau_1 = 2$  and  $\tau_2 = 10$  were used for all model fits.

(A) Case 1:	Male				Female			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>								
$L_{1,j}$	65.21	1.40	62.47	67.95	63.50	1.70	60.16	66.84
$L_{2,j}$	217.48	3.25	211.11	223.86	200.60	2.33	196.03	205.17
$\kappa_j$	0.1650	0.0398	0.0870	0.2429	0.2297	0.0536	0.1247	0.3347
$\gamma_{1,2}$	0.1632	0.3254	-0.4745	0.8010	0.0775	0.4003	-0.7071	0.8620
$\sigma^2$	0.0102	0.0007	0.0088	0.0115				
<i>Other</i>								
$L_{\infty,j}$	297.18				235.05			
$L_{1,j}$	99.74				83.01			
$n_j$	140				288			
Max. LL	374.53							
AIC	-731.05							
(B) Case 5:								
(B) Case 5:	Male				Female			
	MLE	SE	95% CI LB	95% CI UB	MLE	SE	95% CI LB	95% CI UB
<i>Parameters</i>								
$L_{1,j}$	64.96	1.33	62.37	67.56	62.14	1.56	59.08	65.20
$L_{2,j}$	212.33	2.56	207.31	217.34	201.26	2.20	196.95	205.58
$\kappa_j$	0.0668	0.0089	0.0494	0.0843	0.1106	0.0120	0.0871	0.1341
$\gamma_{1,2}$	-	-	-	-	-	-	-	-
$\sigma^2$	0.0105	0.0007	0.0091	0.0119				
<i>Other</i>								
$L_{\infty,j}$	390.99				267.50			
$L_{1,j}$	0				0			
$n_j$	140				288			
Max. LL	367.09							
AIC	-720.18							

**Table 15: Results of likelihood ratio tests comparing full and reduced additive and multiplicative von Bertalanffy and Schnute growth models (cases 1 and 5). The full model for each test is the model assuming separate growth by sex. The reduced model is the corresponding model that does not assume separate growth by sex. Max. LL<sub>F</sub>, maximum log likelihood for the full model; Max. LL<sub>R</sub>, maximum log likelihood for the reduced model;  $\chi^2$ , likelihood ratio test statistic;  $f$ , degrees of freedom.**

**(A) Von Bertalanffy models:**

<i>Additive</i>					<i>Multiplicative</i>				
Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$	Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$
-1775.7	-1793.5	35.4	3	$9.84 \times 10^{-08}$	367.1	360.1	13.9	3	0.0030

**(B) Schnute models (case 1):**

<i>Additive</i>					<i>Multiplicative</i>				
Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$	Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$
-1771.8	-1793.5	43.3	4	$8.87 \times 10^{-09}$	374.5	363.4	22.3	4	0.0002

**(C) Schnute models (case 5):**

<i>Additive</i>					<i>Multiplicative</i>				
Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$	Max. LL <sub>F</sub>	Max. LL <sub>R</sub>	$\chi^2$	$f$	$P(X > x   H_0)$
-1775.7	-1793.5	35.4	3	$9.84 \times 10^{-08}$	367.1	360.1	13.9	3	0.0030

**Table 16: Von Bertalanffy growth model parameters derived by MULTIFAN analysis of April–June length frequency data from the southern tuna longline fishery (data presented in Appendix C, male model fit in Appendix D, and female model fit in Appendix E).**

Sex	Number of age classes	$L_\infty$ (cm)	$K$	$t_0$ (years)
Males	7	1295.7	0.017	-2.84
Females	8	355.7	0.077	-2.53

**Table 17: Longevity estimates for male and female blue sharks using the methods of Taylor (1958) and Fabens (1965) and corresponding parameter estimates from the full von Bertalanffy models fitted (Table 8 and Table 9). Values in parentheses are the Taylor and Fabens estimates calculated from the 95% confidence intervals about the von Bertalanffy model parameters. The maximum male and female estimated ages in the final vertebral length-at-age dataset are included for comparison.**

Sex	Maximum recorded estimated age (years)	Taylor's (1958) method		Fabens' (1965) method	
		Von Bertalanffy model		Von Bertalanffy model	
		Additive	Multiplicative	Additive	Multiplicative
Male	22.76	51 (43, 63)	67 (53, 90)	39 (33, 48)	51 (41, 69)
Female	19.73	35 (29, 44)	40 (33, 51)	27 (22, 34)	31 (25, 39)

**Table 18: Natural mortality estimates ( $\hat{M}$ ) for male and female blue sharks derived by applying Hoenig's (1983) method to the maximum recorded estimated ages in the final vertebral length-at-age dataset. Hoenig estimates for six different assumed longevity (ages 20–25 years) are provided for comparison.**

**(A) Applying Hoenig's method to the maximum recorded estimated ages in the final vertebral length-at-age dataset:**

Sex	Maximum age (years)	$\hat{M}$
Male	22.76	0.18
Female	19.73	0.21
All	22.76	0.18

**(B Hoenig estimates for six different assumed longevitys:**

Longevity (years)	$\hat{M}$
20	0.21
21	0.20
22	0.19
23	0.18
24	0.17
25	0.17

**Table 19: Age-at-maturity estimates for male and female blue sharks derived by substituting the lower and upper bounds of the median length-at-maturity estimates presented by Francis & Duffy (in press) into the additive and multiplicative two-sex von Bertalanffy models fitted in this study. LB, Lower Bound; UB; Upper Bound.**

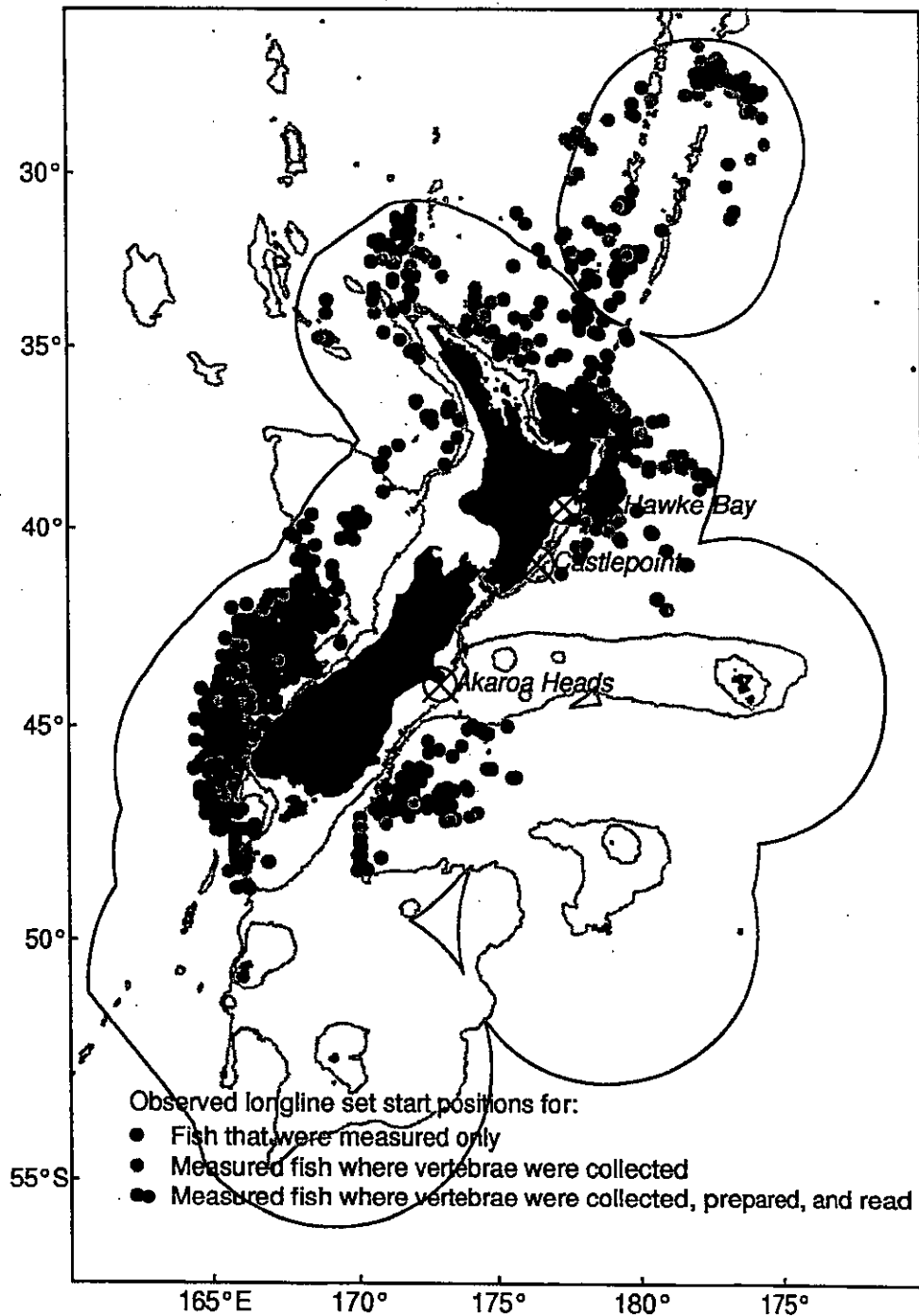
**(A) Length-at-maturity estimates presented by Francis & Duffy (in press):**

Sex	Length-at-maturity (cm FL)	
	LB	UB
Males	190	195
Females	170	190

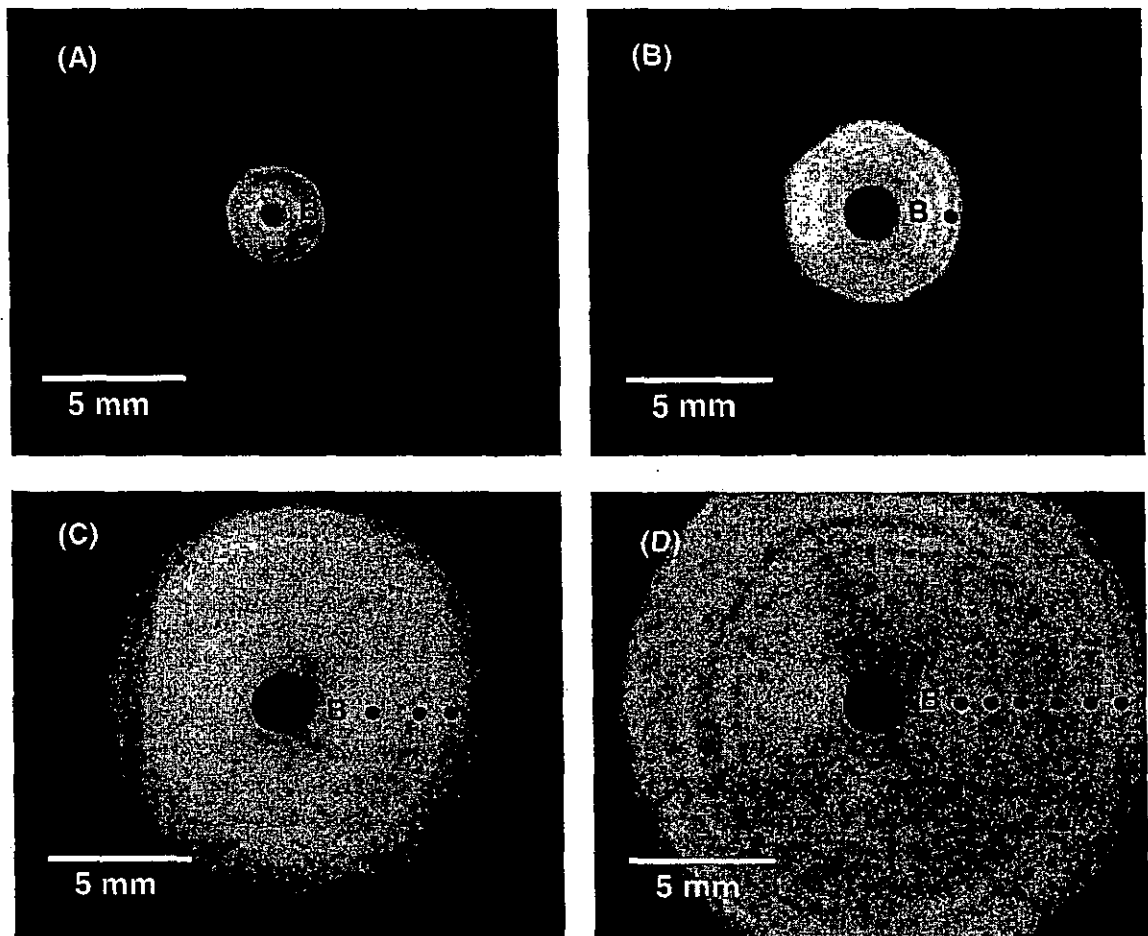
**(B) Corresponding age-at-maturity estimates:**

Von Bertalanffy model	Age-at-maturity estimate (years)			
	Males		Females	
	LB	UB	LB	UB
Additive	7.94	8.32	6.97	9.33
Multiplicative	8.24	8.62	7.07	9.33





**Figure 1: Commercial tuna longline set start positions and recreational fishing competition sites (Hawke Bay, Castlepoint, and Akaroa Heads) where blue sharks were caught and vertebrae collected for this study. The 250 and 1000 m isobaths are overlaid in grey. The boundary of the New Zealand EEZ is overlaid in black.**



**Figure 2: Photomicrographs of whole vertebrae from (A) a 45 cm FL male embryo collected from a 249 cm FL female caught on 5 February 1999 (0 completed opaque zones and an incomplete birth band; no estimated age); (B) a 65 cm FL male caught on 4 June 2002 (1 completed opaque zone other than the birth band; estimated age = 1.59 years); (C) a 128 cm FL female caught on a 11 May 2002 (3 completed opaque zones other than the birth band; estimated age = 3.52 years); and (D) a 181 cm FL female caught on 29 April 2002 (6 completed opaque zones; estimated age = 6.49 years). Completed opaque zones are marked with red dots. Birth bands are marked with red "B"s.**

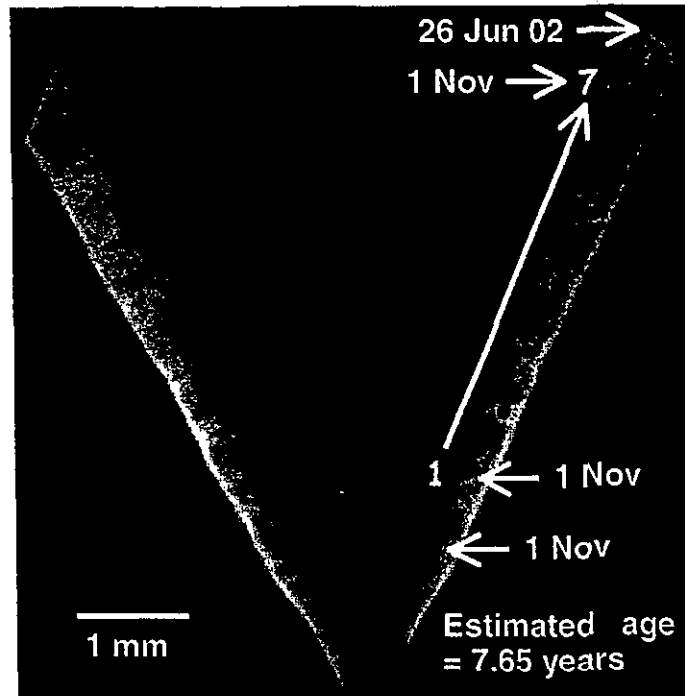


Figure 3: X-radiograph of a vertebral section illustrating how opaque zone counts were converted to estimated ages. The vertebra was collected from a 157 cm FL male caught on 26 June 2002. Seven completed opaque zones are marked with red dots. The birth band is marked with a red "B"; note the change in angle of the corpus calcareum. An eighth opaque zone may be forming on the distal margin of the centrum, indicated by the red question mark. The estimated age of this shark is  $\hat{a} = t_1 + t_2 + t_3 = 1 + 6 + 0.65 = 3.75$  years. Compare the contrast between opaque and translucent zones with those in Figure 4.

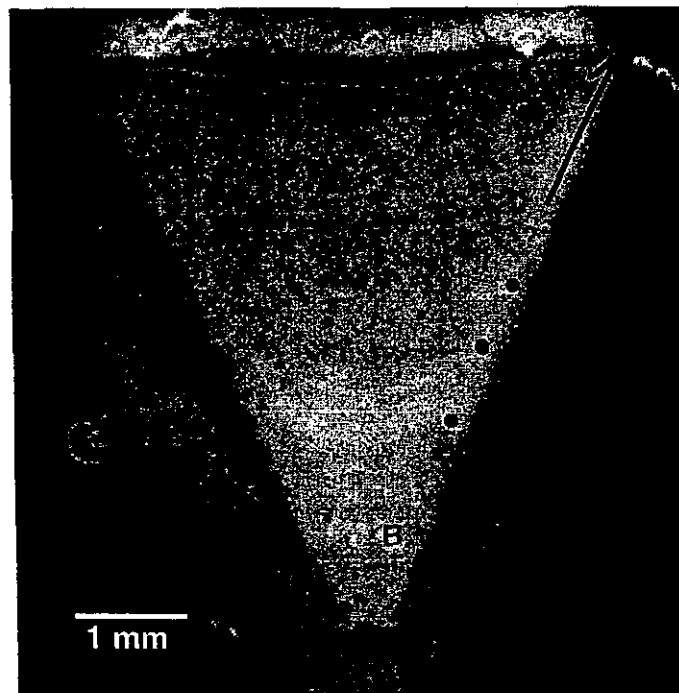
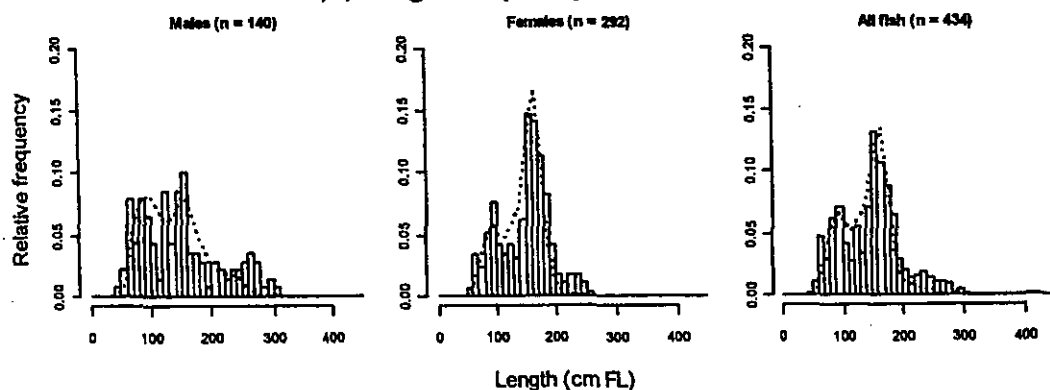
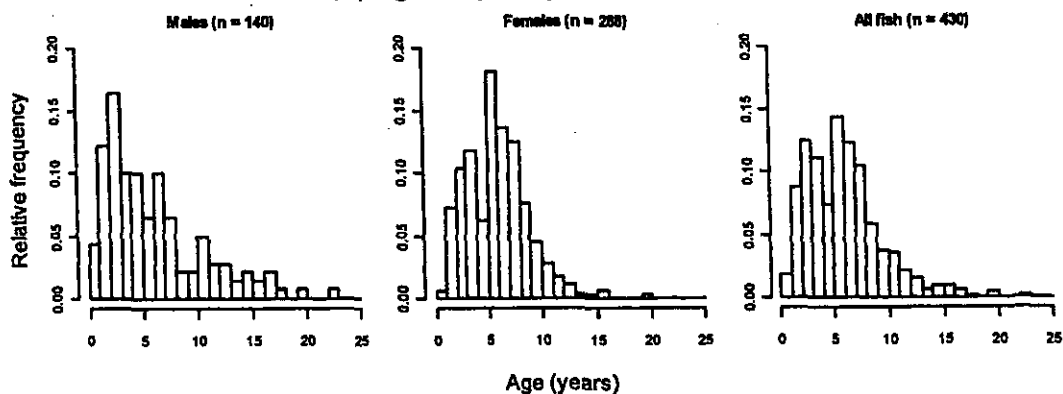


Figure 4: Photomicrograph of the same vertebral section shown in Figure 3. The number of completed opaque zones is uncertain, although six completed opaque zones were recorded by the first reader. Note that this was a typical section. Note also the improved contrast between opaque and translucent zones achieved with X-radiography in Figure 3.

### (A) Length-frequency distributions

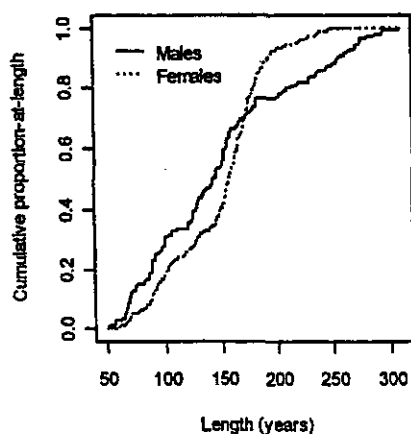


### (B) Age-frequency distributions

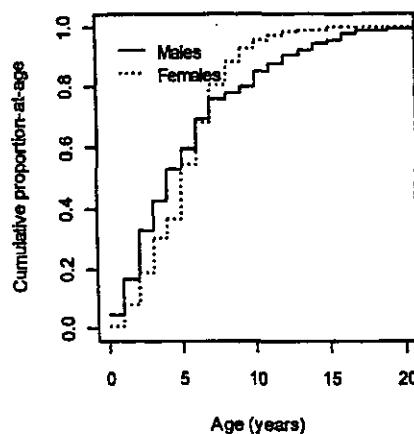


**Figure 5: Raw (A) length- and (B) (non-null) age-frequency distributions by sex for all non-embryonic sharks from which vertebrae were collected, prepared, and read in this study. Vertebrae from a total of 440 sharks, of which 6 were embryos, were prepared and read. The length distributions of all blue sharks measured by the MFish OP from the 1992–93 to the 2001–02 fishing year are overlaid on (A) for comparison (dotted lines).**

### (A) Cumulative proportions-at-length

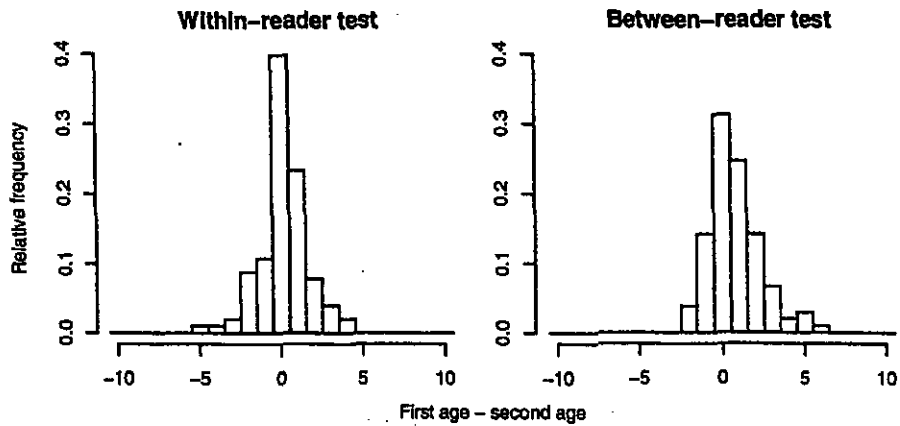


### (B) Cumulative proportions-at-age

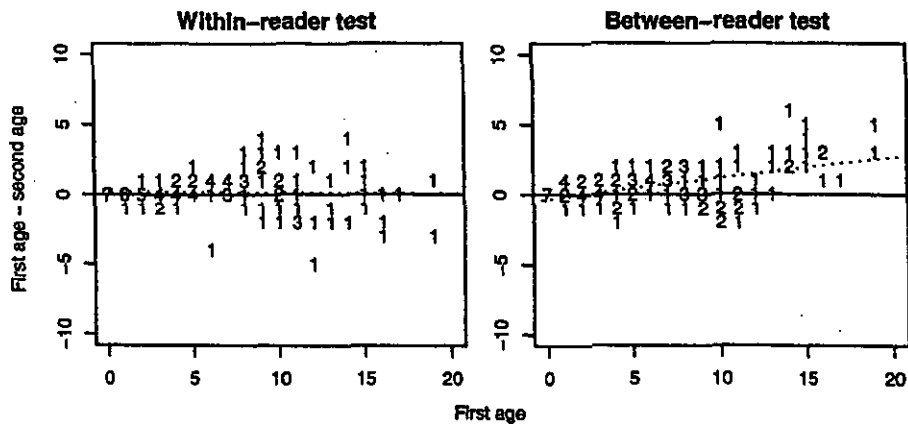


**Figure 6: Cumulative proportions at (A) length and at (B) age by sex for all non-embryonic sharks from which vertebrae were read. Note that the numbers-at-length and at-age were rescaled to be equal by sex prior to plotting the cumulative proportions. Non-null data only are plotted in (B). The composition of the final vertebral length-at-age dataset is given in Table 6.**

(A) Histograms of differences



(B) Differences between first and second ages relative to first age



(C) Age-bias plots

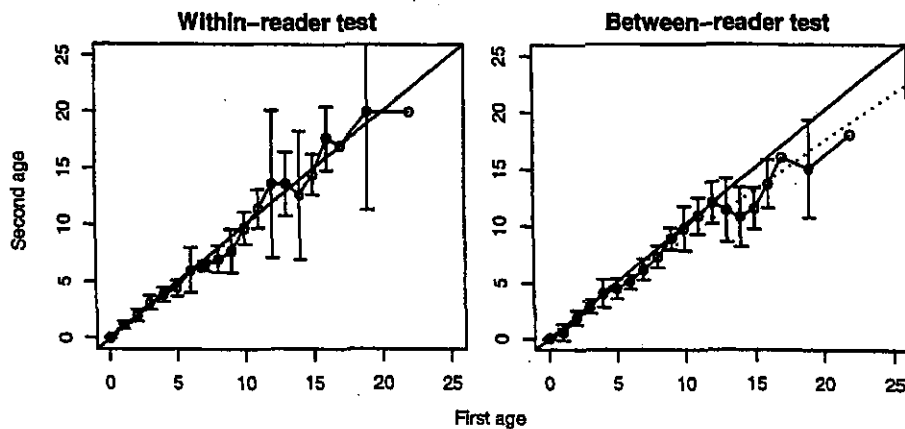
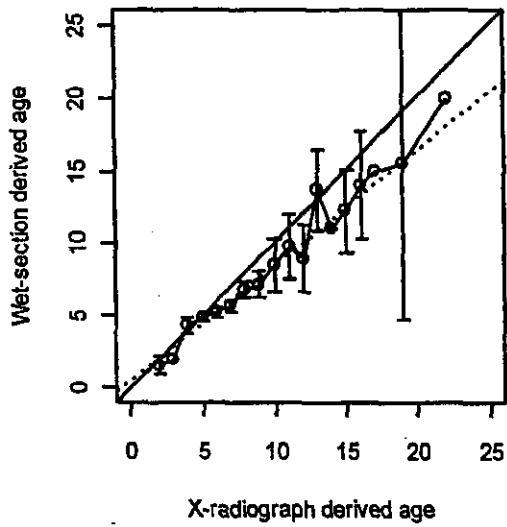


Figure 7: Results of within- and between-reader comparison tests: (A) histograms of differences between first and second readings; (B) differences between first and second readings relative to a given age produced during the first reading; and (C) age-bias plots. Note that the histograms in (A) are right-open (left-closed) and that each point in (B) may represent more than one data point (indicated by the numeral plotted). The error bars in (C) are 95% confidence intervals about the mean age produced during the second series of readings for a given age produced during the first series. The expected 1:1 lines in (B) and (C) are shown by the solid lines and the actual linear relationships by the dotted lines.



**Figure 8: Comparing estimated ages derived from wet section and X-radiograph opaque zone counts. The error bars are 95% confidence intervals about the mean age derived from a wet section opaque zone count for a given age derived from an X-radiograph of the same section. The expected 1:1 line is shown by the solid line and the actual linear relationship by the dotted line.**

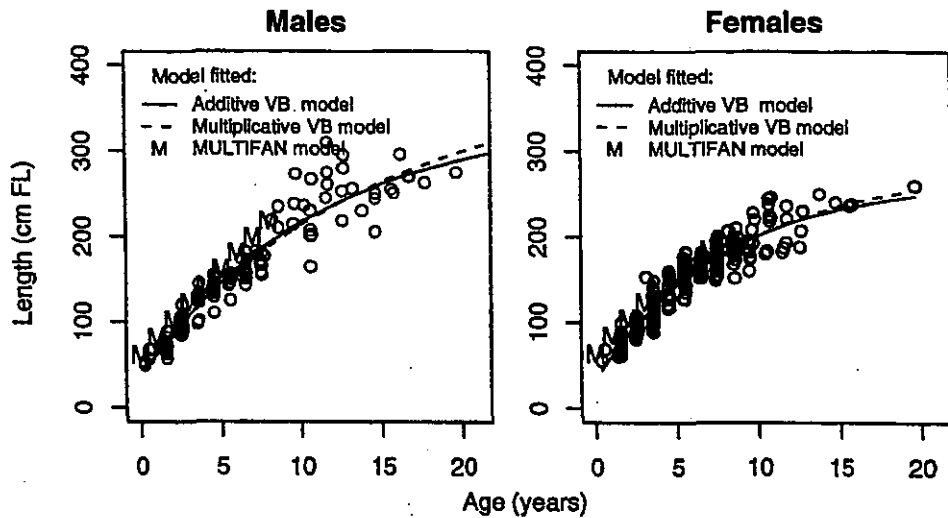


Figure 9: Results of fitting von Bertalanffy's model to the final vertebral length-at-age dataset where additive and multiplicative normal errors and differences in growth by sex were assumed. Parameter estimates are given in Tables 8–9. The fitted MULTIFAN models for each sex are overlaid for comparison (see Table 16 for MULTIFAN model parameter estimates).

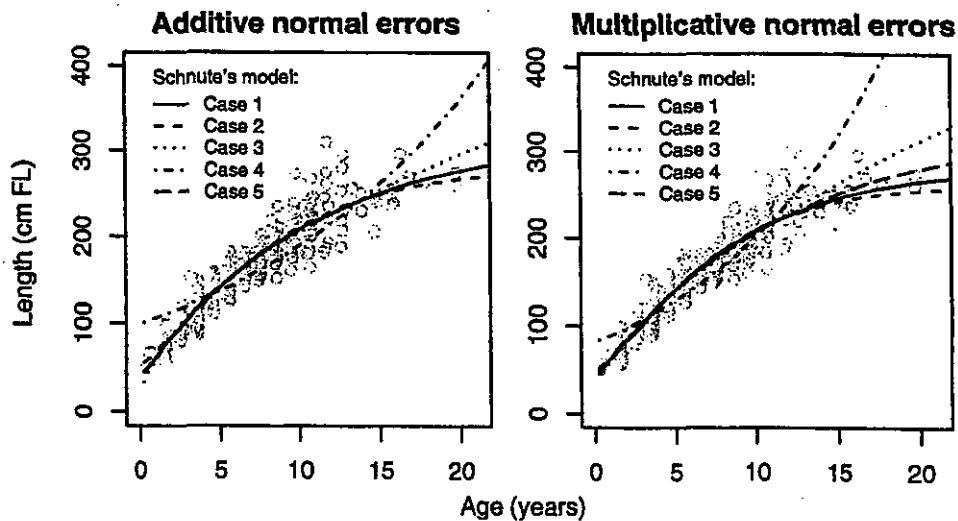
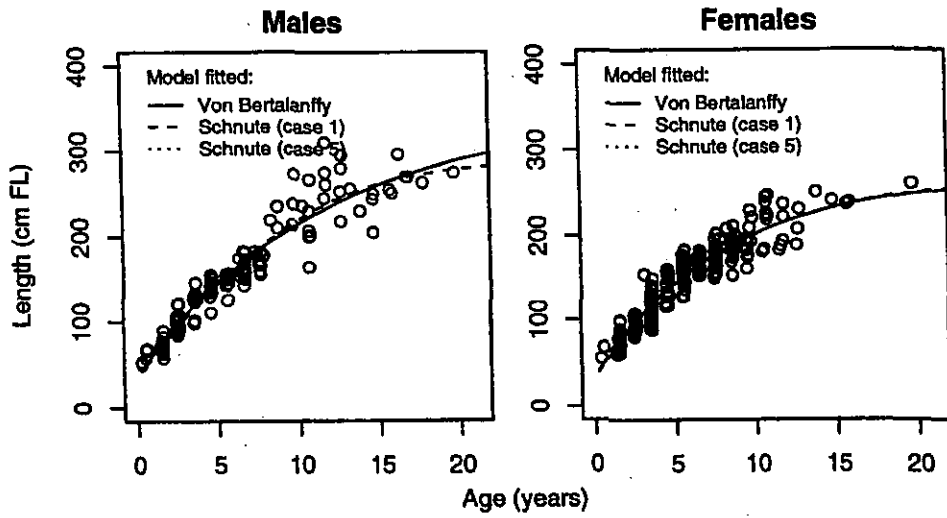


Figure 10: Results of fitting the five different cases of Schnute's (1981) model to the final vertebral length-at-age dataset where additive and multiplicative normal errors and no differences in growth by sex were assumed. Parameter estimates are given in Tables 11–12. Note that the fitted values from the case 1 and case 5 models are visually indistinguishable.

(A) Additive normal errors



(B) Multiplicative normal errors

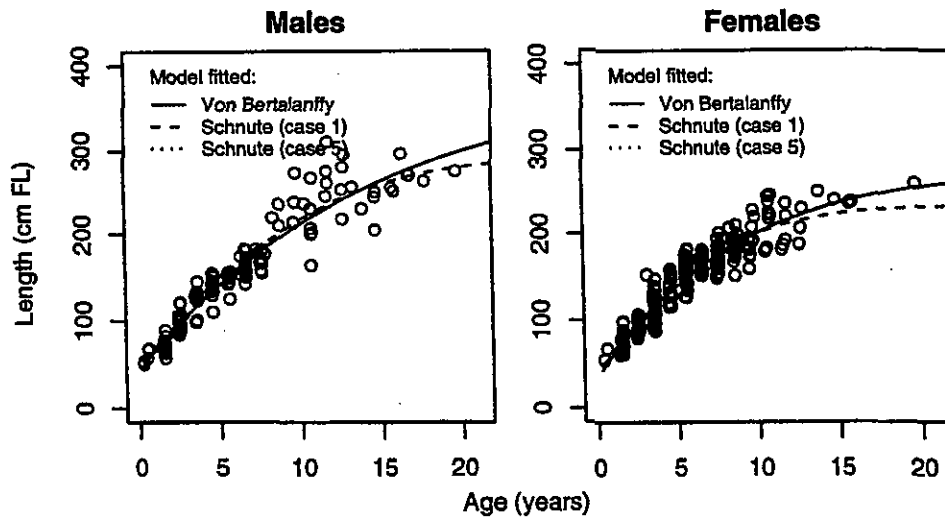


Figure 11: Comparing the results of fitting von Bertalanffy's and the first and fifth cases of Schnute's model to the final vertebral length-at-age dataset where differences in growth by sex were assumed. Fits of the models assuming additive normal errors are shown in (A). Fits of the models assuming multiplicative normal errors are shown in (B). Note that the fitted values from the case 1 and case 5 models are virtually identical. Parameter estimates are given in Tables 13–14. The fits of these full models to the data are compared with the fits of corresponding reduced models using the likelihood ratio test in Table 15.



## APPENDIX A SCHNUTE'S (1981) GROWTH MODEL

### A.1 Von Bertalanffy's (1938) growth model

Von Bertalanffy's (1938) model of the mean length,  $L_j$ , of the  $j$ th fish at age  $t_j$  is

$$L_j = L_\infty \left[ 1 - e^{-k(t_j - t_0)} \right] \quad (8)$$

where  $L_\infty$  is fish mean asymptotic maximum length, where  $k$  is a rate parameter indicating how quickly  $L_\infty$  is approached (the "Brody rate parameter"), and where  $t_0$  is the time, or age, at which mean length equals zero. Von Bertalanffy's model is probably the most common growth model used in the fisheries science literature, yet the parameters  $L_\infty$  and  $k$  are very strongly negatively correlated, and some attention has been given to finding alternative parameterisations of Von Bertalanffy's model with statistically more stable parameters (e.g., Schnute 1981, Ratkowsky 1986, Francis 1988, Cerrato 1990).

### A.2 Schnute's (1981) growth model

Schnute's (1981) model is a four-parameter growth model that is derived from solutions to the differential equations

$$Z = \frac{d}{dt} \ln L \equiv \left( \frac{1}{L} \right) \frac{dL}{dt} \quad (9)$$

and

$$\frac{dZ}{dt} = -Z(\kappa + \gamma Z), \quad (10)$$

where  $Z$  is relative rate of change in fish growth over time,  $t$  is time (or fish age), and  $L$  is fish length, and  $\kappa$  and  $\gamma$  are model parameters. Equation (10) can be solved if two initial conditions are met: e.g., that  $L(\tau_1) = L_1$  and  $L(\tau_2) = L_2$ . The values of  $\tau_1$  and  $\tau_2$  are usually specified and  $L_1$  and  $L_2$  estimated. The model parameters thus are usually  $\kappa$ ,  $\gamma$ ,  $L_1$ , and  $L_2$ .

Equation (10) has four possible solutions, depending on whether either  $\kappa$  or  $\gamma$  or both are equal to zero or not. These are:

Case 1, where  $\kappa \neq 0$  and  $\gamma \neq 0$ , is

$$L_j = \left\{ L_1 + (L_2 - L_1) \frac{1 - \exp[-\kappa(t_j - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}^{\frac{1}{\gamma}} \quad (11)$$

Case 2, where  $\kappa \neq 0$  and  $\gamma = 0$ , is

$$L_j = L_1 \exp \left\{ \ln \left( \frac{L_2}{L_1} \right) \frac{1 - \exp[-\kappa(t_j - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}. \quad (12)$$

Case 3, where  $\kappa = 0$  and  $\gamma \neq 0$ , is

$$L_j = \left[ L_1 + (L_2 - L_1) \frac{t_j - \tau_1}{\tau_2 - \tau_1} \right]^{\gamma}. \quad (13)$$

Case 4, where  $\kappa = 0$  and  $\gamma = 0$ , is

$$L_j = L_1 \exp \left[ \ln \left( \frac{L_2}{L_1} \right) \frac{t_j - \tau_1}{\tau_2 - \tau_1} \right]. \quad (14)$$

Quinn II & Deriso (1999) present a fifth case, a variant of case 1, where  $\kappa \neq 0, \gamma = 1$ . This is equivalent to Cerrato's (1990) alternative parameterisation of the von Bertalanffy model, which he considered to be superior to von Bertalanffy's original parameterisation:

Case 5, where  $\kappa \neq 0$  and  $\gamma \neq 0$ , is

$$L_j = \left\{ L_1 + (L_2 - L_1) \frac{1 - \exp[-\kappa(t_j - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}^{\gamma}. \quad (15)$$

### A.3 Asymptotes and inflection points for Schnute's (1981) model

Unlike Von Bertalanffy's, Schnute's model does not have an explicitly parameterised asymptote. Nevertheless, as noted by Quinn II & Deriso (1999), Schnute gave expressions for calculating asymptotes and inflection points from his model's parameters in his paper. Note that only cases 1, 2, and 5 have asymptotes or inflection points. For case 1, the asymptote is

$$L_{\infty} = \left[ \frac{L_2 - e^{-\kappa(\tau_2 - \tau_1)} L_1}{1 - e^{-\kappa(\tau_2 - \tau_1)}} \right]^{\gamma}, \quad (16)$$

and the length at the inflection point is

$$L_I = L_{\infty} (1 - \gamma)^{\gamma}. \quad (17)$$

For case 2, the asymptote is

$$L_{\infty} = \exp \left[ \frac{\ln L_2 - e^{-\kappa(r_2-r_1)} \ln L_1}{1 - e^{-\kappa(r_2-r_1)}} \right], \quad (18)$$

and the length at the inflection point is

$$L_l = L_{\infty} / e. \quad (19)$$

Quinn II & Deriso (1999) did not give expressions for the asymptote or inflection point for case 5. However, these can be found by simply taking the asymptote and inflection point expressions for case 1 and substituting  $\gamma = 1$ . The asymptote for case 5 is thus

$$\begin{aligned} L_{\infty} &= \left[ \frac{L_2^{(\gamma=1)} - e^{-\kappa(r_2-r_1)} L_1^{(\gamma=1)}}{1 - e^{-\kappa(r_2-r_1)}} \right]^{1/(\gamma=1)}, \\ &= \left[ \frac{L_2 - e^{-\kappa(r_2-r_1)} L_1}{1 - e^{-\kappa(r_2-r_1)}} \right], \end{aligned} \quad (20)$$

and the length at the inflection point reduces to

$$\begin{aligned} L_l &= L_{\infty}(1 - (\gamma = 1)) \\ &= L_{\infty}(0) \\ &= 0 \end{aligned} \quad (21)$$

#### A.4 On fitting Schnute's (1981) model to length-at-age data

Schnute's model presents one with one a range of possible options for modelling length-at-age data. The choice of which of the five cases described is the most appropriate for a given dataset is made by considering the statistical significance of the  $\kappa$  and  $\gamma$  parameters. Two algorithms for fitting Schnute's model were described by Quinn II & Deriso (1999).

First, one selects case 1 as the best model and fits it to the data using, say, non-linear least-squares. If  $\kappa$  or  $\gamma$  is not significantly different from 0 (e.g., the 95% confidence intervals for  $\kappa$  or  $\gamma$  do not contain 0), then case 2 or 3 is selected. Case 4 is only selected if both  $\kappa$  and  $\gamma$  are equal to 0.

Second, an  $F$ -test procedure may be used. Once the model has been fitted using non-linear least-squares, let  $RSS_x$  be the residual sum of squares for case  $x$  with  $f_x$  degrees of freedom. The estimate  $\hat{\sigma}_x^2$  is equal to  $RSS_x / f_x$ , the residual mean square. The residual sum of squares will always be lower for a model with additional parameters. To test the null hypothesis that case  $x$  is a better fit to the data than case  $y$ , one computes the statistic

$$F = \frac{RSS_y - RSS_x}{f_y - f_x}, \quad (22)$$

which is then compared to the critical value of the  $F$  distribution for a one-sided test of level  $\alpha$  with numerator and denominator degrees of freedom  $f_y - f_x$  and  $f_x$ , respectively. One then compares the competing models pairwise (e.g., cases 1 and 2, cases 1 and 3, cases 1 and 4, cases 1 and 5, etc.). One

decides between models with the same numbers of parameters (e.g., cases 2 and 3, 2 and 5, and 3 and 5) on the basis of which one has the lowest RSS as they have the same number of parameters. The best model overall is the model with the fewest parameters that is not significantly different from case 1 and that meets the underlying assumptions of the least-squares regression procedure, i.e., homoscedasticity (constant variance across the data) and goodness-of-fit (normality of errors).

We used a third, less cumbersome, procedure to select the most parsimonious model. We first fitted each of the competing models (cases 1–5) to the data using maximum likelihood estimation, assuming one growth model for all groups in the data, a single common variance parameter, and additive and multiplicative normal errors, using the methods described by Manning & Sutton (2004) (note that the mean-length-at-age functions given in Equations (11) to (15) replace the von Bertalanffy “mu” functions given by Manning & Sutton (2004)).

We then computed Akaike’s (1973) Information Criterion (AIC) for each fitted model. The AIC statistic is

$$AIC = -2 \ln L + 2p, \quad (23)$$

where  $\ln L$  is the maximum log-likelihood for each model (i.e., the log-likelihood function for each model evaluated at the maximum likelihood estimates of the model parameters), and  $p$  is the number of model parameters. The most parsimonious model is the model with the lowest AIC statistic. Note that the likelihood ratio test can only be used to compare nested or hierarchical models; the AIC can be used to compare models with essentially arbitrary structures fitted to the same dataset. We used the “R” statistical programming language (R Development Core Team 2003) to write a program to implement both the model fitting and comparison routines.

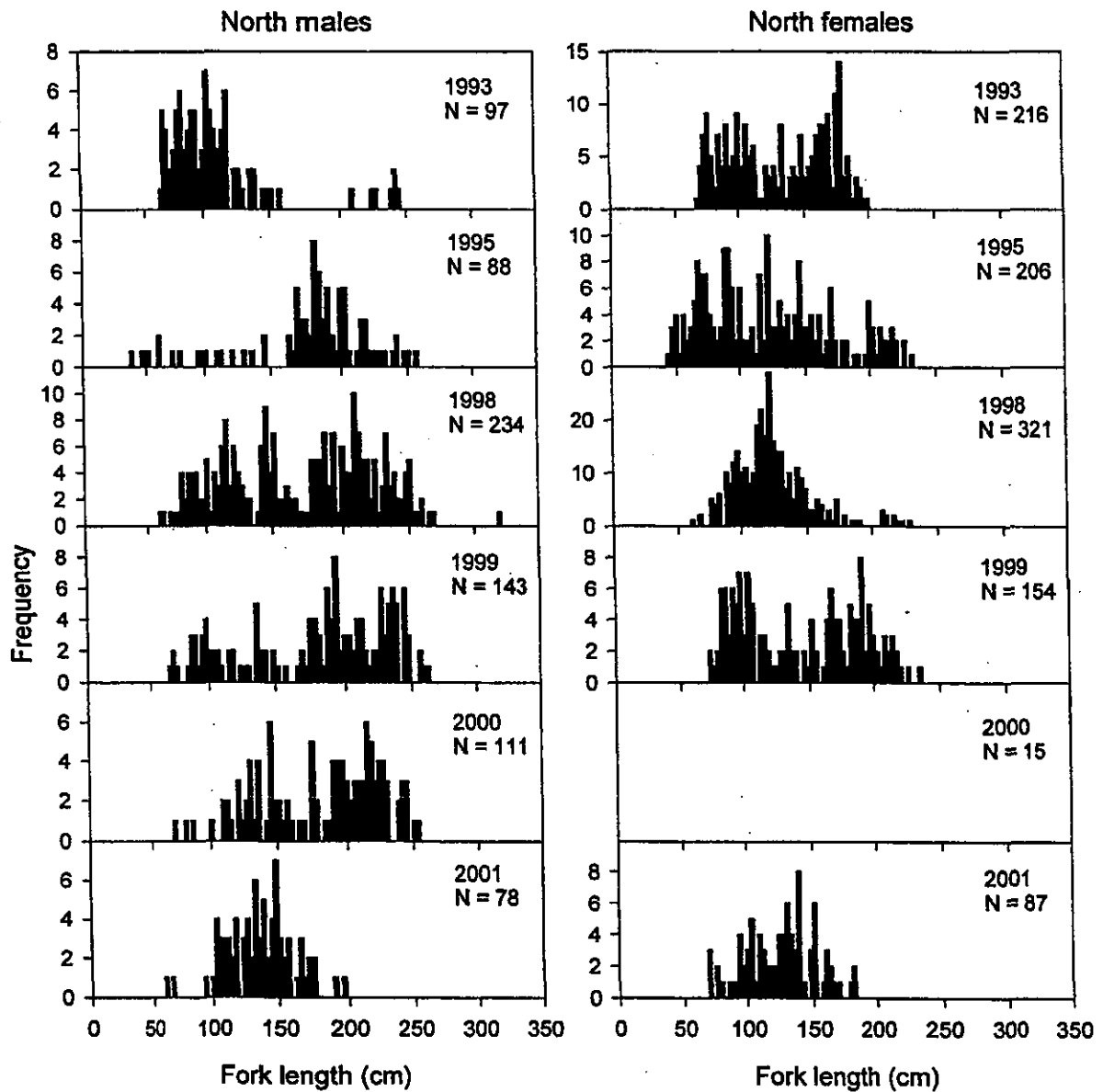
### A.5 Confidence intervals for Schnute model parameters

The “R” program we wrote to implement the model fitting and comparison routines above returns a numerical approximation of the hessian matrix for the fitted model. The hessian matrix is a matrix of the second partial derivatives of the log-likelihood function evaluated at the maximum likelihood estimates of the model parameters. The hessian matrix,  $H(\theta)$ , is the inverse of the Fisher Information matrix,  $I(\theta)$ , and the Fisher Information matrix is an approximate covariance matrix of the model parameters,  $\theta$ . A  $100(1-\alpha)\%$  confidence interval for  $\theta_j$ , the  $j$ th model parameter, is thus approximately

$$\hat{\theta}_j \pm Z_{(1-\alpha/2)} I_{jj}(\theta), \quad (24)$$

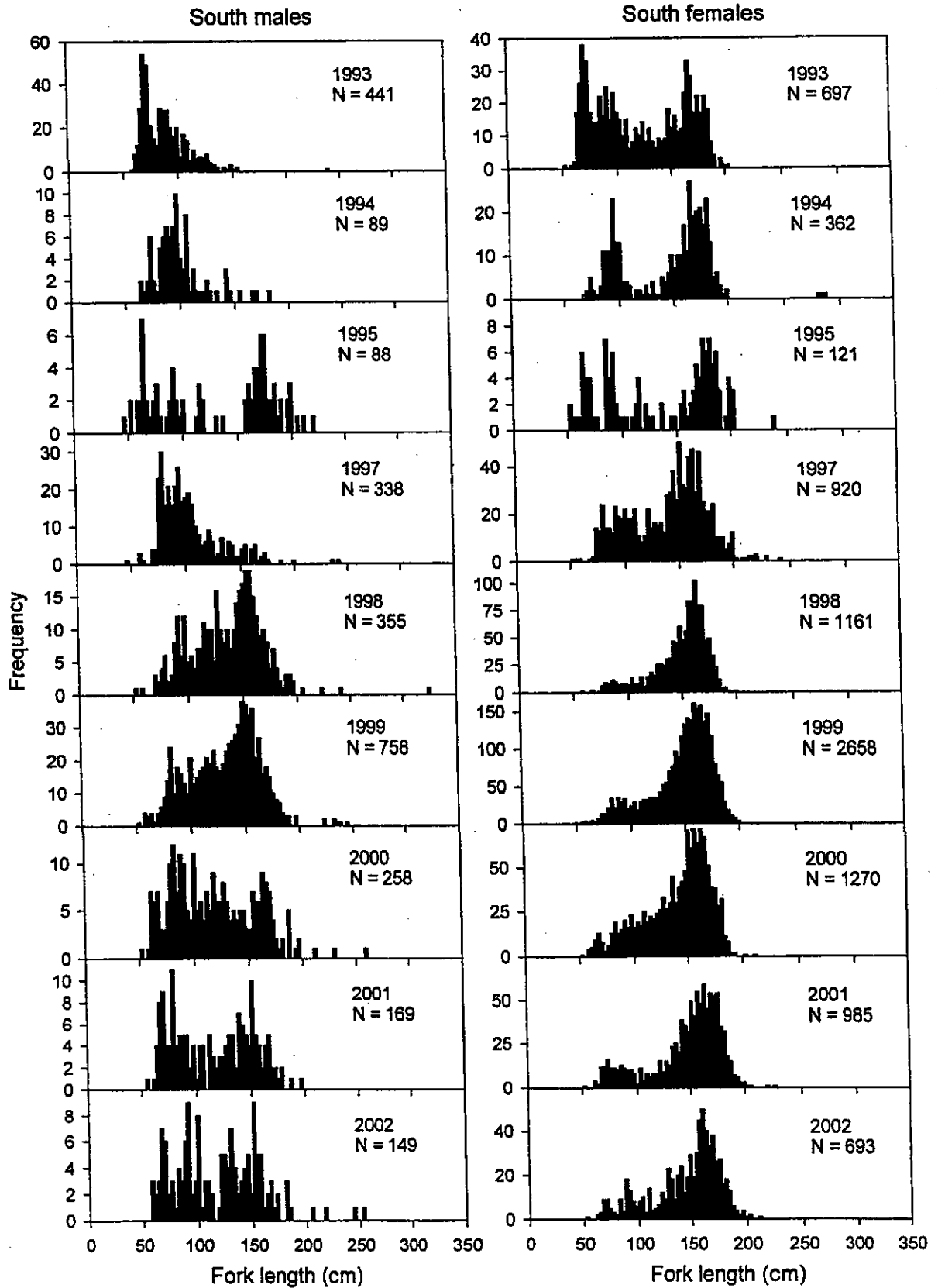
where  $\hat{\theta}_j$  is the maximum likelihood estimate of  $\theta_j$ , and  $Z_{(1-\alpha/2)}$  is the  $(1-\alpha/2)$ th quantile of the standard normal distribution, and  $I_{jj}$  is the  $j$ th diagonal element of  $I(\theta)$ . Comparing analytical confidence intervals such as these with confidence intervals calculated using the bootstrap (Efron & Tibshirani 1993) can be informative (see Manning & Sutton (2004), for examples), but we have not done so in this study.

**APPENDIX B LENGTH-FREQUENCY DATA COLLECTED FROM THE NORTHERN TUNA  
 LONGLINE FISHERY DURING THE CALENDAR YEARS 1993–2001**



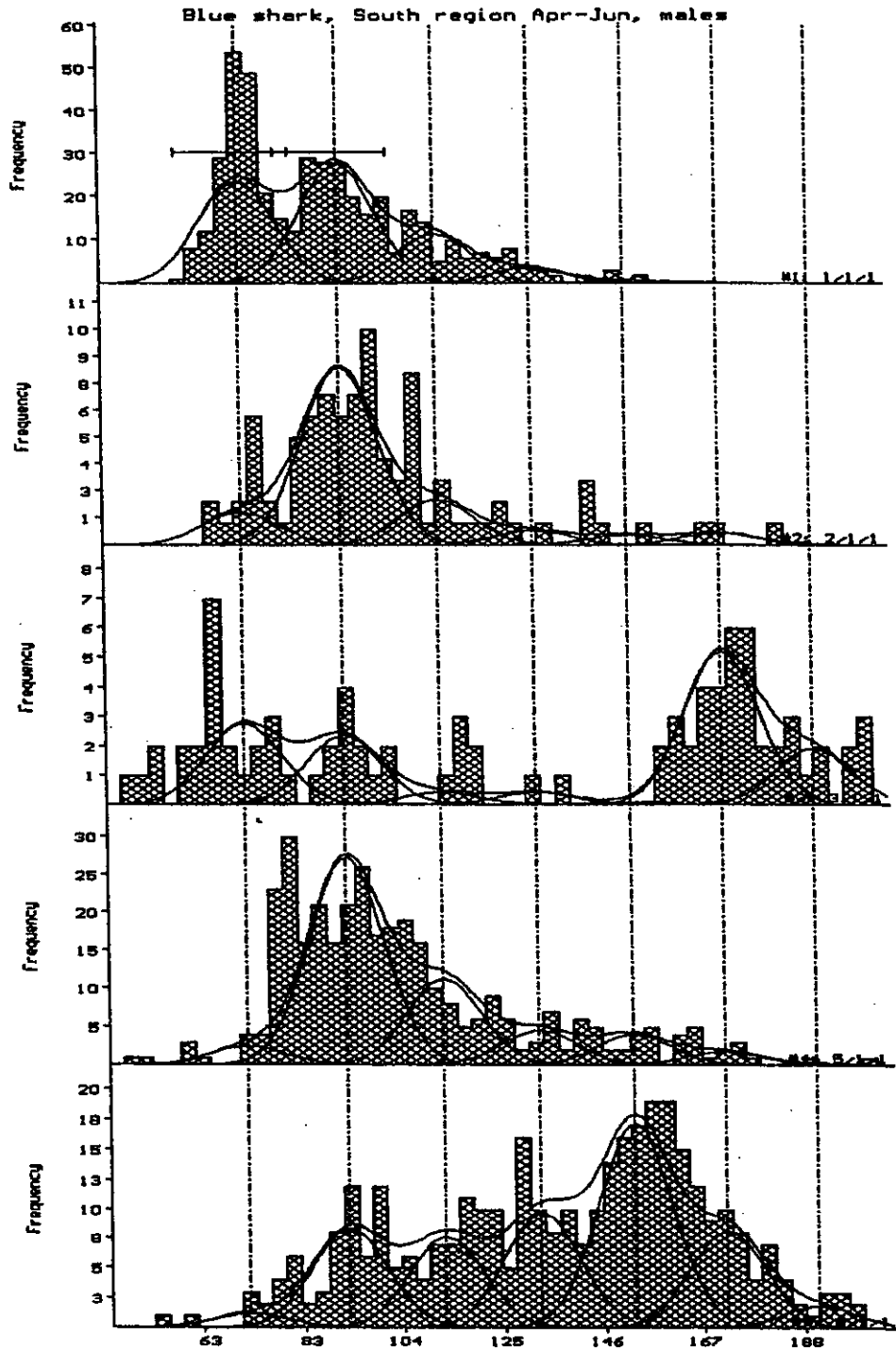
**Figure B1: Length-frequency distributions for male and female blue sharks collected from the northern tuna longline fishery in May–August of each year. No data were available for some years. Data for 2002 were not included because most were collected by an observer who rounded many lengths to the nearest 10 cm.**

**APPENDIX C LENGTH-FREQUENCY DATA COLLECTED FROM THE SOUTHERN TUNA LONGLINE FISHERY DURING THE CALENDAR YEARS 1993–2002**

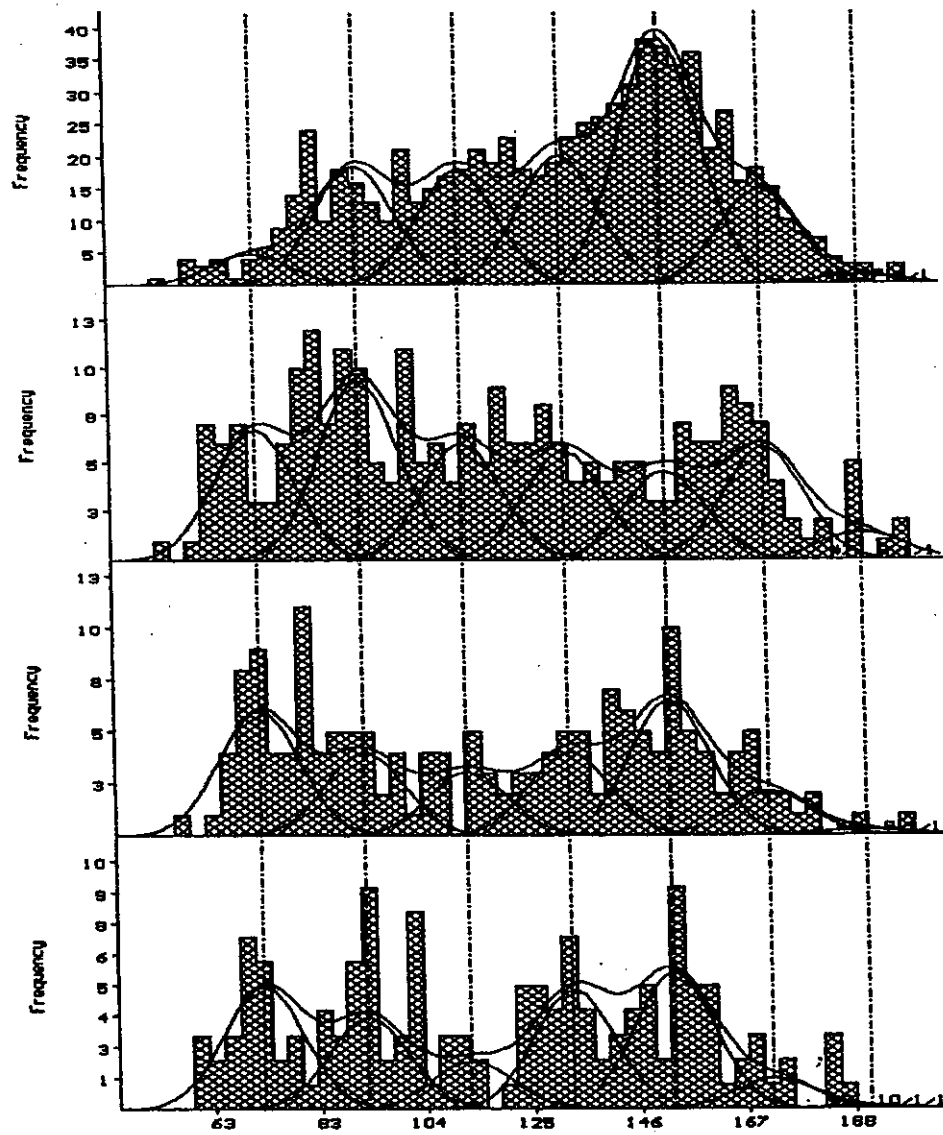


**Figure C1: Length-frequency distributions for male and female blue sharks collected from the southern tuna longline fishery in April–June of each year. No data were available for 1996.**

**APPENDIX D MULTIFAN RESULTS FOR MALE BLUE SHARKS SAMPLED IN THE SOUTHERN TUNA LONGLINE FISHERY DURING THE CALENDAR YEARS 1993–2002**



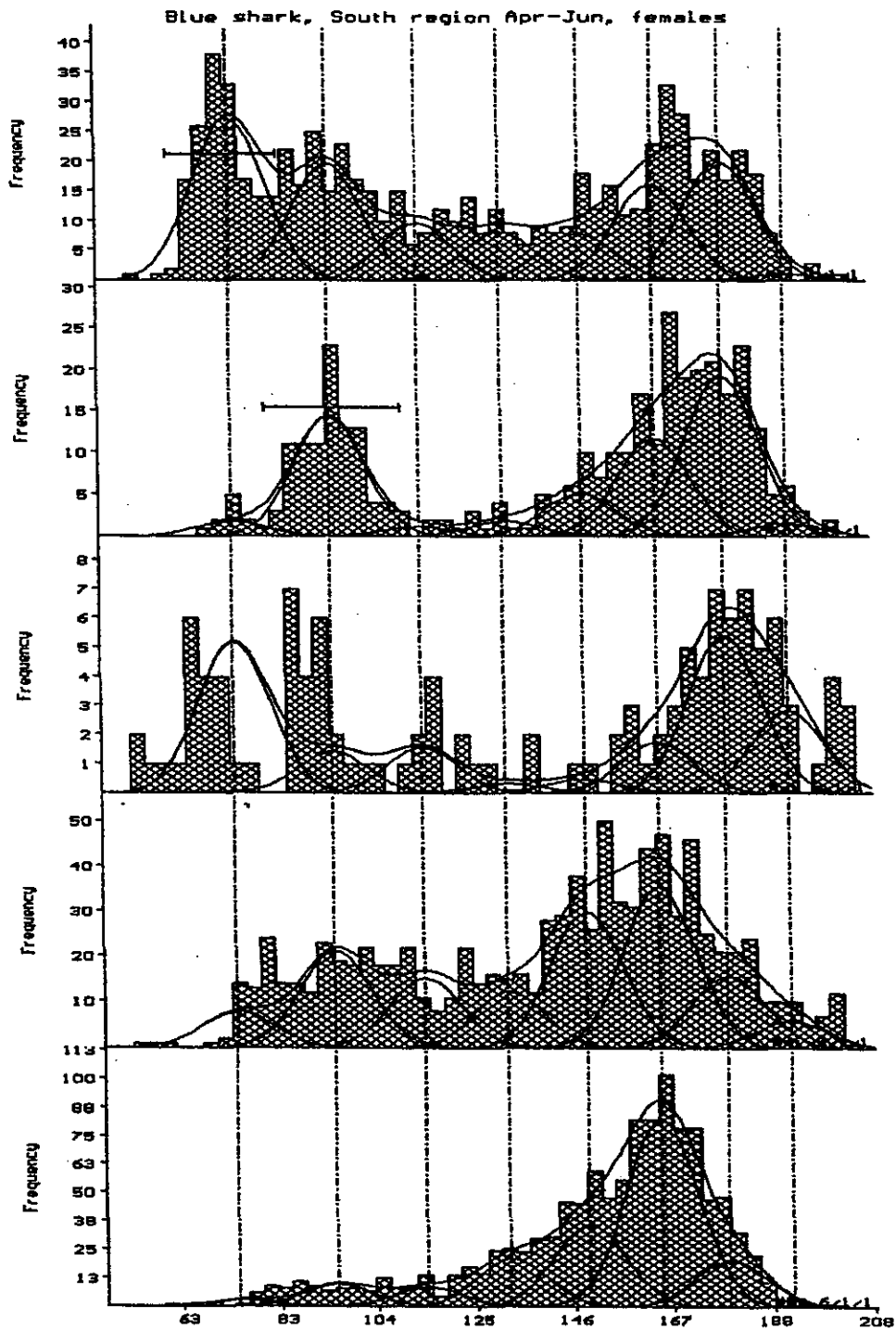
**Figure D1: 1993–1995 and 1997–1998 length-frequency distributions for male blue sharks collected from the southern tuna longline fishery showing the fit of the best MULTIFAN model containing seven age classes (continued).**



**Figure D1 (continued): 1999–2002 length-frequency distributions for male blue sharks collected from the southern tuna longline fishery showing the fit of the best MULTIFAN model containing seven age classes.**



**APPENDIX E MULTIFAN RESULTS FOR FEMALE BLUE SHARKS SAMPLED IN THE SOUTHERN TUNA LONGLINE FISHERY DURING THE CALENDAR YEARS 1993–2002**



**Figure E1: 1993–1995 and 1997–1998 length-frequency distributions for female blue sharks collected from the southern tuna longline fishery showing the fit of the best MULTIFAN model containing eight age classes (continued).**

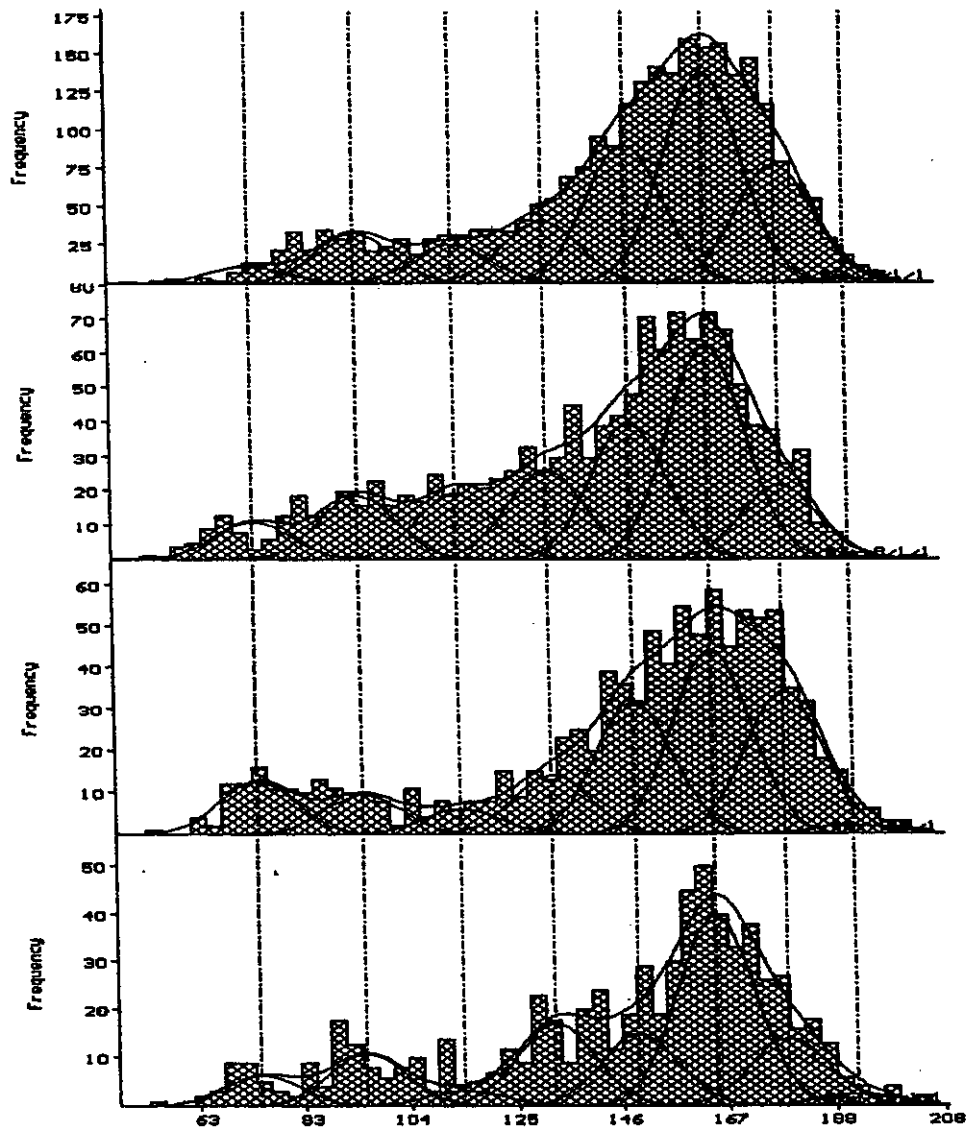
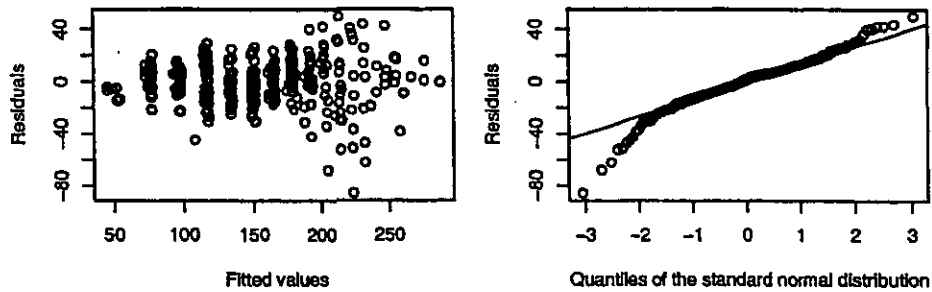


Figure E1 (continued): 1999–2002 length-frequency distributions for female blue sharks collected from the southern tuna longline fishery showing the fit of the best MULTIFAN model containing eight age classes.

## Appendix F Diagnostic residual plots for model fits

### F.1 Von Bertalanffy models

#### (A) Additive normal errors



#### (B) Multiplicative normal errors

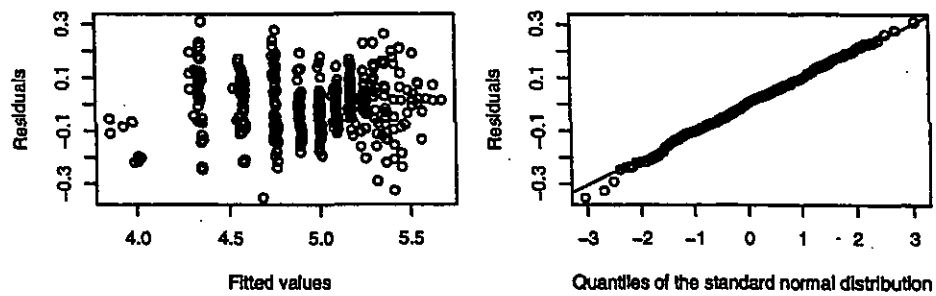
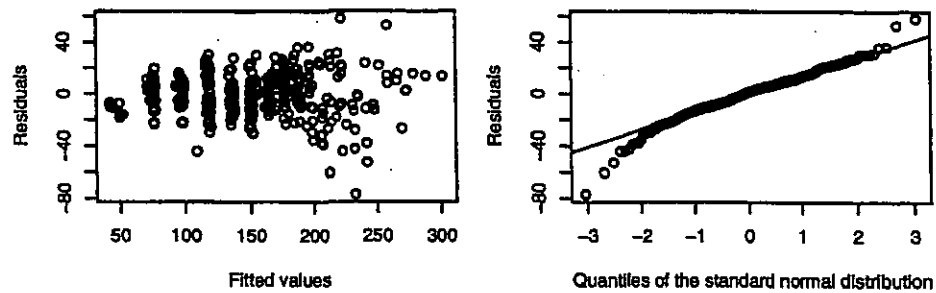


Figure F1: Diagnostic residual plots for the fit of the reduced von Bertalanffy growth models to the final vertebral length-at-age dataset. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B). The reduced models do not assume differences in growth by sex.

#### (A) Additive normal errors



#### (B) Multiplicative normal errors

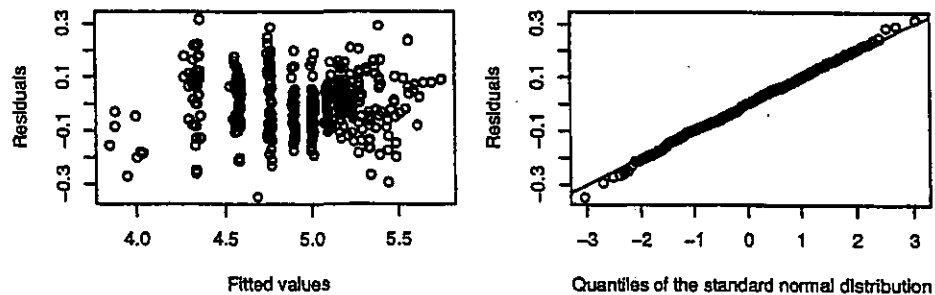
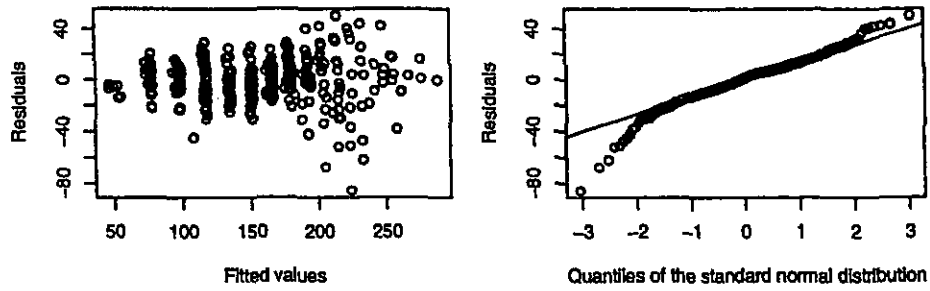


Figure F2: Diagnostic residual plots for the fit of the full von Bertalanffy growth models to the final vertebral length-at-age dataset. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B). The full models assume differences in growth by sex.

## F.2 Schnute models

(A) Additive normal errors



(B) Multiplicative normal errors

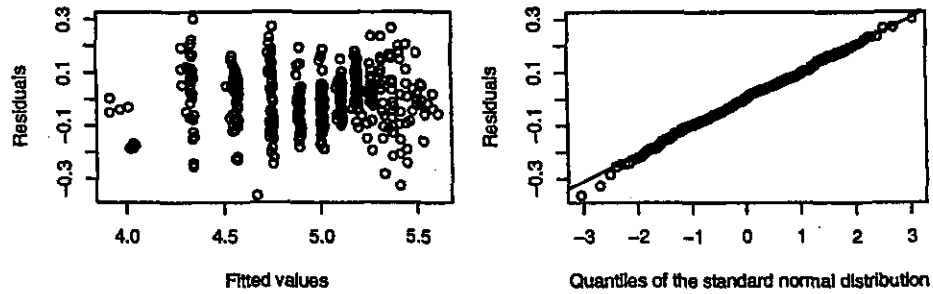
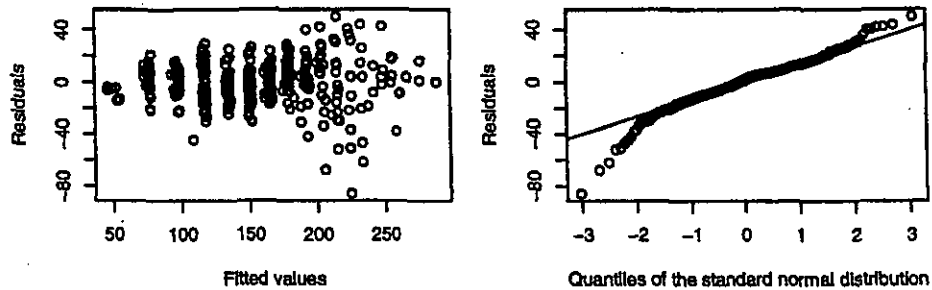


Figure F3: Diagnostic residual plots for the fits of the first case of Schnute's model to the final vertebral length-at-age dataset. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B). Neither model assumed separate growth by sex.

(A) Additive normal errors



(B) Multiplicative normal errors

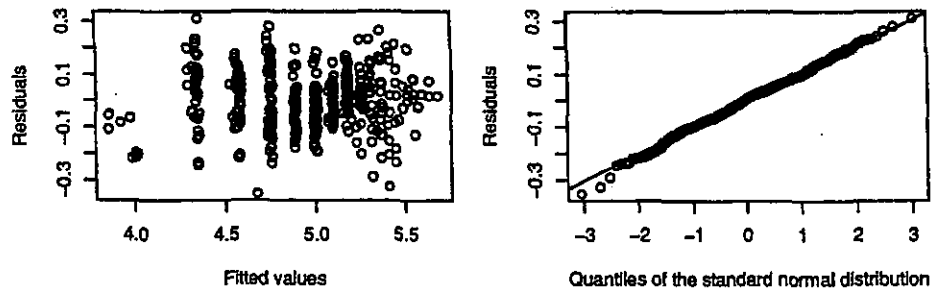
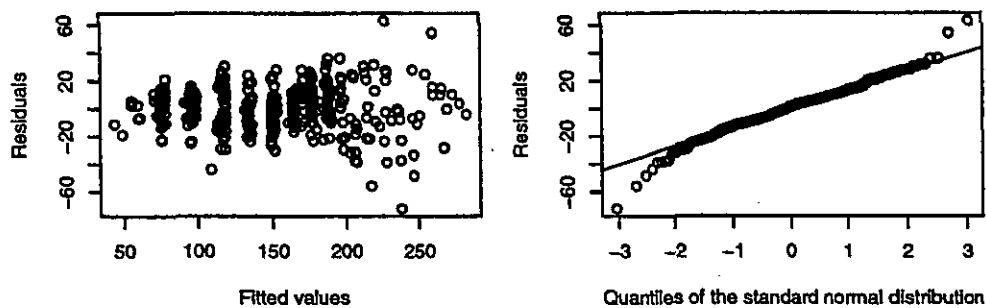


Figure F4: Diagnostic residual plots for the fits of the fifth case of Schnute's model (equivalent to the revised parameterisation of the von Bertalanffy model presented by Cerrato (1990)) to the final vertebral length-at-age dataset. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B). Neither model assumed separate growth by sex.

(A) Additive normal errors



(B) Multiplicative normal errors

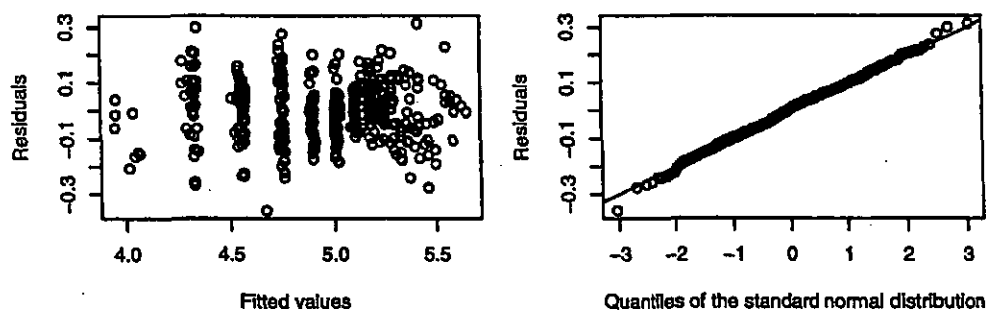
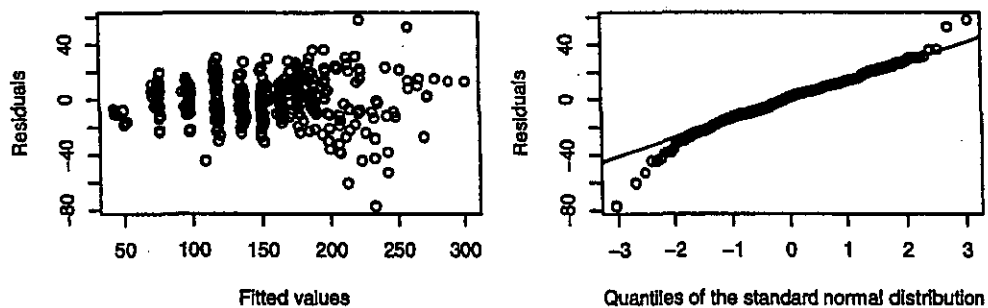


Figure F5: Diagnostic residual plots for the fits of the first case of Schnute's model to the final vertebral length-at-age dataset assuming separate growth by sex. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B).

(A) Additive normal errors



(B) Multiplicative normal errors

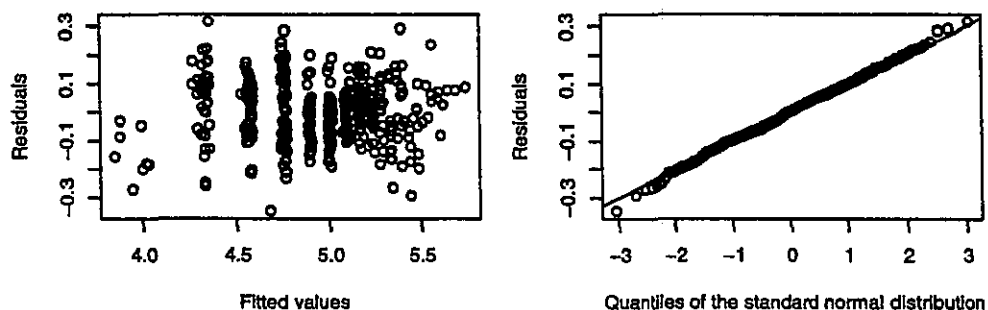


Figure F6: Diagnostic residual plots for the fits of the fifth case of Schnute's model to the final vertebral length-at-age dataset assuming separate growth by sex. The fit of the model assuming additive normal errors is shown in (A). The fit of the model assuming multiplicative normal errors is shown in (B).