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Age and growth of ghost sharks

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7. Executive Summary

Von Bertalanffy growth curves were fitted using MULTIFAN to trawl survey length-frequency data sets from around southern New Zealand. Most data sets had few small fish, and weak modal structure, making it difficult for MULTIFAN to fit growth curves. Nevertheless, growth curves fitted to 7 dark ghost shark data sets and 4 pale ghost shark data sets, showed considerable within-species agreement. These growth curves suggested that both species grow moderately fast, with dark ghost sharks reaching 50 cm in 5–9 years, and pale ghost sharks reaching 50 cm in 4–5 years. Female dark ghost sharks appeared to grow faster than males, but this requires confirmation. Up to 12 age classes were distinguished for dark ghost shark, and 9 for pale ghost shark. However, MULTIFAN tends to underestimate the number of age classes in a population so the longevity of both dark and pale ghost sharks may be substantially greater than this.

The vertebral column, eye lens weights and diameters, and thin sections of the dorsal fin spine were examined to determine their utility in ageing ghost sharks. The vertebral column of both ghost sharks is essentially uncalcified, and is unsuitable for ageing. Lens core diameters for dark ghost sharks showed a modal pattern that was consistent for both sexes. The lengths of the ghost sharks comprising each lens age group agreed closely with the MULTIFAN growth curves, suggesting that the lens groups were equivalent to age classes. The oldest age class of dark ghost sharks identified from eye lens diameters was 13 years. A lack of small pale ghost sharks in our samples made it impossible to determine whether similar eye lens age groups occur in that species. Eye lens diameter measurements, but not weights, may be useful for developing or

corroborating growth curves. For individual fish, eye lens ageing may provide estimates of age that are within ±2 years of the true value.

Thin spine sections contain bands that may be age-related. However the bands were unclear and difficult to count, resulting in subjective and uncertain age estimates. Initial band counts appeared to underestimate the ages of ghost sharks, relative to the ages expected from MULTIFAN analyses. Careful inspection of the inner part of the spine revealed further bands, which when counted produced age estimates that seemed more realistic. However the variability in length-at-age was high, suggesting that even if the structures being counted were annual, our ability to age individual fish from their spines is limited. Further fine increment structure of unknown periodicity was present, particularly in dark ghost sharks. Until the significance of these finer bands is determined, and a better technique developed for resolving band structure, we are not confident about our spine-based estimates of age.

Use of eye lens diameters as a means of developing growth curves seems promising. We recommend that a further similar-sized sample of dark ghost shark lenses be collected at the same time of year as the present sample (December–January) to increase the sample size and thereby confirm the existence and diameter of the modes. Partial validation of the annual nature of the lens age groups could be achieved by collecting a further large sample of lens in June–July. It is not known whether eye lens modes are present in pale ghost sharks; larger samples would help determine this by clarifying modal structure and diameter.

8. Objectives

Overall Objective:

1. To determine the growth and mortality rates of the ghost shark species *Hydrolagus novaezelandiae* (dark ghost shark) and *Hydrolagus* sp. A (pale ghost shark).

Specific Objective:

1. To determine the feasibility of ageing dark and pale ghost shark species.

The specific objective was achieved.

9. Methods

MULTIFAN analysis of length-frequency data

Length-frequency data for dark and pale ghost sharks were extracted by Horn (1997) for trawl surveys of Chatham Rise, west coast South Island, east coast South Island, Stewart–Snares Shelf, and Southland–Campbell Plateau up to 1996. Horn's data were updated in the present study by producing length-frequency distributions for recent surveys (up to early 1999) in each of the regions. Length-frequency distributions were scaled up to provide population distributions using the *Trawlsurvey* program (Vignaux 1994) on the Empress database *trawl* (see Appendix 1). Sample sizes of dark ghost shark were large in all regions, but pale ghost shark were caught in significant numbers only in the deeper surveys of the Chatham Rise and Southland–Campbell Plateau. Most regions were surveyed at the same time each year, but the timing of the east coast South Island and Southland–Campbell Plateau surveys varied (Appendix 1).

We used MULTIFAN software (Fournier et al. 1990) to identify length modes, assign ages to them, and fit von Bertalanffy growth curves. The von Bertalanffy growth model is:

$$L_t = L_\infty\left(1 - e^{-K[t-t_0]}\right) \quad (1)$$

where L_t is the expected length at age t years, L_∞ is the asymptotic maximum length, K is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length. The seasonal form of the von Bertalanffy model is:

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

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

MULTIFAN models were fitted separately to both species, and to both sexes (because males and females grow to different maximum lengths; Horn 1997). MULTIFAN simultaneously analyses multiple length-frequency distributions using a maximum likelihood method to estimate the proportions of fish in each age class, and the von Bertalanffy growth parameters. 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).

MULTIFAN estimates the von Bertalanffy parameters L_∞ and K by conducting a systematic search across a matrix of plausible K values and age classes. t_0 is estimated from the equation:

$$t_0 = t_1 - a_1 \quad (3)$$

where t_1 is the estimated age (in years since the theoretical birthday), and a_1 is the age estimated by MULTIFAN (in years since zero length), of the youngest age class at the time it first appears in the length-frequency samples. There was no information from which to define a theoretical birthday (= theoretical date of hatching from the egg case), so it was arbitrarily defined as 1 January.

For the identified age classes, MULTIFAN also 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). For the east coast South Island and Southland–Campbell Plateau survey series, two additional growth models were fitted: (c) constant length standard deviation with seasonal growth; and (d) variable length standard deviation with seasonal growth.

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

Development and application of ageing techniques

Ghost shark samples

Dark ghost sharks were collected from the east coast of South Island during a *Kaharoa* trawl survey (KAH9917, December 1999 – January 2000). Pale ghost sharks were collected from the Chatham Rise during a *Tangaroa* trawl survey (TAN0001, December 1999 – January 2000). Since the aim of the project was to determine the feasibility of ageing, the region from which samples were obtained was not crucial. Specimens were spread evenly between the two sexes, and across the full length range. Some specimens were frozen whole, but for most, the heads were removed and frozen. Both species were measured fresh to the centimetre below caudal length (distance between the tip of the snout and the posterior end of the caudal fin, excluding the filament).

Vertebrae

Vertebrae are routinely used to age sharks, including New Zealand school shark, rig and skates (Francis & Mulligan 1998; Francis & Ó Maolagáin 2000). However, some deepwater elasmobranchs, and elephantfish, have poorly calcified vertebrae (Ridewood 1921; pers. obs.). Blocks of vertebral column were removed from both dark and pale ghost sharks and cleaned in household bleach (sodium hypochlorite) to remove muscle and connective tissue. The vertebral columns of both species were poorly calcified, and consisted mainly of hyaline cartilage; they could be cut easily with a scalpel. Lateral X-rays of the whole vertebral column revealed numerous vertical "disks", but it was difficult to isolate these by dissection because they were not clearly distinguishable from the inter-vertebral connective tissue. The vertebral centra showed no concentric bands when X-rayed transversely, and the core of the centra was gelatinous (a probe could easily be passed along the length of the vertebral column). The lack of calcification and banding, and the absence or loss of the young vertebral tissue near the centrum core, mean that the vertebrae are unsuitable for ageing.

Eye lenses

Eye lenses are suspended in fluid, and their growth may be uncoupled from growth of the rest of the body (in the same way that otoliths continue growing after somatic growth ceases). This means that eye lenses may continue growing after body growth has slowed or stopped. They may therefore provide a useful ageing technique for juvenile and possibly adult ghost sharks. Eye lens weights have been used to identify juvenile age classes of several teleosts (Carlton & Jackson 1968; Burkett & Jackson 1971; Crivelli 1980) and spiny dogfish (Hanchet 1986; Siezen 1989), but they were only useful for discriminating the first few age classes. Johnson and Horton (1972) found that dry eye lens weight increased with body length in male *Hydrolagus colliei* but not in females. They speculated that most of the increase in lens weight in females occurred in juveniles (which were poorly represented in their samples), or that the density of the lens decreased with increasing size in females. We are not aware of eye lens dimensions being used for fish ageing.

Both eye lenses were removed from samples of dark and pale ghost sharks, sealed in zip-lock plastic bags, and frozen. The lenses consisted of a solid crystalline core surrounded by a sticky gelatinous fluid, and encapsulated in a tough membrane. Whole lenses and lens cores were measured to the nearest 0.01 mm (diameter) with a digital micrometer, and weighed wet (to 1 mg precision). Lens cores were then oven-dried at 80 °C to constant weight before re-weighing.

Fin spines

Growth bands deposited on fin spines have been used successfully to age the closely related elephantfishes (Sullivan 1977; Freer & Griffiths 1993; M. P. Francis and C. Ó Maolagáin, NIWA, unpubl. data) and spiny dogfishes (*Squalus acanthias, S. blainvillei,* and *Centrophorus acus*) (Holden & Meadows 1962; Ketchen 1975; Soldat 1982; Hanchet 1986; Tanaka 1990; Cannizzaro et al. 1995).

The first dorsal fin spine was removed from subsamples of dark and pale ghost sharks. Thin transverse sections were cut near the spine tip, using a modification of the method used for elephantfish (Sullivan 1977; Freer & Griffiths 1993). The best sectioning location was determined by taking serial transverse sections at different distances from the tip, to locate the zone where all spine growth is represented. Elephantfish and spiny dogfish spines grow by deposition of new cones of dentine on the inside of the older cones (Sullivan 1977; Soldat 1982). Sections taken too close to the spine tip do not contain the most recently deposited cones, and sections taken too close to the base do not contain the oldest cones. The spine was cleaned in bleach for 30–45 minutes, washed in water, air dried for about one week, and embedded in a block of epoxy resin. Thin sections were cut with a dual-blade diamond saw. One side of the section was polished with carborundum paper, then glued to a glass microscope slide using thermoplastic cement. The other side of the section was then ground and polished until growth rings became apparent when viewed under cross-polarised, transmitted light.

Growth bands in the spine sections were counted independently by two readers: reader 1 counted the sections once and reader 2 counted them twice. The first count by each reader was carried out without any knowledge of the size of the ghost sharks, or the results of the MULTIFAN and eye lens analyses; the second count by reader 2 was carried out after the MULTIFAN growth curves were available.

10. Results

MULTIFAN analysis of length-frequency data

MULTIFAN models were fitted to seven dark ghost shark length-frequency data sets, and four pale ghost shark data sets (Table 1). The remaining data sets (Appendix 1) were either too small, or had insufficient modal length structure to allow MULTIFAN to identify age classes.

For seven out of 11 data sets, the best-fit MULTIFAN model had variable standard deviation. However, in six of those models, the length standard deviation decreased (often substantially) with increasing age. This is implausible; length standard deviation should increase with age due to variation in growth rates. We therefore accepted the constant standard deviation models as the best fits, except for one data set. For female dark ghost shark on the Chatham Rise, the "best" constant standard deviation model contained 16 age classes (the maximum number fitted). Inspection of the model fit showed that MULTIFAN was attempting to fit all minor peaks in the length-frequency distributions with separate age classes, leading to an improbably slow growth rate. We therefore retained the variable standard deviation model for that data set.

Seasonal growth parameters significantly improved the model fit for female and male pale ghost sharks in Southland–Campbell Plateau, and for female dark ghost sharks in east coast South Island, but not for male dark ghost sharks in east coast South Island (Table 1).

Most pale ghost sharks were over 50 cm (females) or 60 cm (males) long (Appendix 1). Most dark ghost sharks were over 30 cm except for the east coast South Island where there were a moderate number of 20–30 cm fish in some years. MULTIFAN estimates a_1, the age of the youngest age class when it first appears in the length-frequency samples, by extrapolating the growth curve backwards until it intersects the age axis. The paucity of small ghost sharks means that substantial extrapolation was required. Furthermore, length modes for small fish were often indistinct. Therefore the estimates of a_1 were high (mean 4.3 years, range 3.2–6.7 years), and subject to considerable error. The length at which ghost sharks hatch from their egg cases is unknown, but is likely to be around 10 cm (by analogy with elephantfish (Francis 1997)). We therefore adjusted the estimates of t_0 obtained from equation (3) in one-year increments until the growth curve intersected the length axis as near as possible to 10 cm. Thus the growth curves derived from MULTIFAN may not be accurately positioned in relation to the age axis, and length-at-age estimates may be erroneous, but estimates of growth rate derived from them should be reliable.

The resulting growth curves for both dark and pale ghost sharks suggest that they grow moderately fast (Fig. 1). Dark ghost sharks reached 50 cm in 5–9 years, and pale ghost sharks in 4–5 years. In all three regions for which a comparison could be made, female dark ghost sharks grew faster than males; however the growth rate of the two sexes was similar in pale ghost sharks (Fig. 1). MULTIFAN distinguished up to 12 age classes for dark ghost shark, and nine age classes for pale ghost shark.

Development and application of ageing techniques

Eye lenses

The weights of the left and right lens cores were not significantly different for either species: paired *t*-test (Sokal & Rohlf 1981) dark ghost shark $p = 0.99$, N = 42; pale ghost shark $p = 0.14$, N = 22. Therefore, only data from the left lens are presented here.

The weight and diameter of whole lenses and lens cores increased with body length in both sexes of dark ghost shark (Fig. 2). Diameter increased approximately linearly with length, and weight increased linearly up to about 50 cm, and exponentially thereafter. Lens weight and diameter were similar for males and females at lengths up to about 50 cm; thereafter, weight and diameter were greater for males than for females. Modes were present in most of the frequency distributions of eye lens weight and diameter for the individual sexes, but patterns were difficult to discern (Figs 3 and 4), probably because of the small sample sizes. We therefore combined the data for the two sexes to increase the sample sizes (Fig. 5). If modes in lens weight or diameter are a function of *age*, then the differences between the two sexes in lens weight and diameter at a given length (Fig. 2) are unimportant. However, if the modes are a function of *length*, then combining the two sexes will tend to blur the modes among the larger ghost sharks. The clearest modal pattern in the combined sexes data was for lens core diameter (Fig. 5). Modes were present at 1 mm intervals between 3 mm and 13 mm. Inspection of the data for the individual sexes showed that the positions of these modes were similar for both males and females, though not all modes were apparent in these smaller samples (Figs 3 and 4).

Dark ghost sharks were assigned to modal groups (hereafter called lens age groups) based on their lens core diameters. This allocation was done by truncating the lens diameter modes at the troughs as shown in Fig. 5. The length ranges of the fish in each lens age group lie close to the MULTIFAN growth curves derived for east coast South Island dark ghost sharks (Fig. 6).

The weight and diameter of whole lenses and lens cores increased with body length in both sexes of pale ghost shark (Fig. 2), but there was a lot of variability. Most pale ghost sharks were greater than 60 cm, and lens weight and diameter tended to be greater for males than for females. Some modal structure was present in the lens core diameters of pale ghost sharks, but the near-absence of fish less than 60 cm makes it difficult to detect patterns (Fig. 7).

Fin spines

Fin spine sections from both species contained light and dark bands, but they were diffuse and lacked contrast, and band width was often irregular. Bands were clearest and easiest to count in sections taken 5–7 mm from the spine tip. Figures 8–11 illustrate spine sections from two individuals of each species that had relatively clear banding; most sections were not as clear these. Altering the plane of focus within the section sometimes made a major difference to the number of visible bands. In both species, but most notably for dark ghost sharks, major bands could be resolved into multiple (usually 4–10) finer bands, though this was not always apparent across the whole section (Figs 8–11; in particular, see Fig. 9 right). Readers were uncertain about what constituted a band, making it difficult to decide whether to include fine bands in the age estimate, or to group them into larger units. Age estimates were therefore subjective and uncertain.

Reader 1 aged most of the 30 dark ghost sharks as 3 or 4 years, with a maximum age of 7 years (Fig. 6). On his first count, reader 2 aged most dark ghost sharks as 3–6 years, with a maximum of 7 years. Comparison of the length-at-age estimates from these two counts with the MULTIFAN growth curves suggested that both readers were underestimating the ages (Fig. 6). Reader 2 then re-counted all sections, paying particular attention to the banding structure near the core of the spine (where the most recently formed cones are deposited; see arrowed bands in Fig. 9 right), but he did not count the multiple fine bands that comprised the major bands. Age estimates from this second count tended to be higher (mainly 3–7 years, maximum 9 years), and they fell on both sides of the MULTIFAN growth curves, but the ages of many fish still seemed to be under-estimated. The lengths-at-age were also highly variable.

Similar patterns were observed for 30 pale ghost sharks (Fig. 12). Reader 1 aged most of them as 4–6 years (maximum 7 years) and reader 2 (count 1) aged most as 4–10 (maximum 12 years). There was little relationship between length and the age estimate, and both readers appeared to underestimate age relative to the MULTIFAN growth curves (Fig. 12). Reader 2 then re-counted all sections as for dark ghost sharks, and aged most as 7–11 (maximum 14 years). The age estimates of reader 2 (count 2) were more consistent with the MULTIFAN curves than were the other two readings.

11. Conclusions

Most length-frequency data sets had few small fish, and weak modal structure, making it difficult for MULTIFAN to fit von Bertalanffy growth curves accurately. Nevertheless, growth curves fitted to 7 dark ghost shark data sets and 4 pale ghost shark data sets, showed considerable within-species agreement. Estimates of t_0 were adjusted in increments of one year to ensure that the growth curves passed near a length of 10 cm at age zero (the assumed length at hatching). Therefore the estimates of length-at-age obtained from the growth curves may be biased. However growth rates were not affected by this problem. MULTIFAN growth curves suggested that both species of ghost shark grow moderately fast, with dark ghost sharks reaching 50 cm in 5–9 years, and pale ghost sharks reaching 50 cm in 4–5 years. The growth rate of pale ghost sharks is therefore similar to that of the related elephantfish (*Callorhinchus milii*), whereas that of dark ghost sharks is slower (Francis 1997). Female dark ghost sharks appeared to grow faster than males, but this requires confirmation because of the difficulties in fitting MULTIFAN curves. Up to 12 age classes were distinguished for dark ghost shark, and 9 for pale ghost shark. However, MULTIFAN tends to underestimate the number of age classes in a population because the older age groups merge together. This suggests that the longevity of both dark and pale ghost sharks may be substantially greater than 12 and 9 years respectively.

The vertebral column of dark and pale ghost sharks is essentially uncalcified, and is unsuitable for ageing.

Lens core diameters for dark ghost sharks (males and females combined) showed a modal pattern that was consistent for both sexes. The lengths of the ghost sharks comprising each lens age group agreed closely with the MULTIFAN growth curves, suggesting that the lens groups corresponded with age classes. The first lens age group, which was centred around 3 mm diameter and comprised ghost sharks of 18–24 cm long, appears to comprise 1 year old fish. The oldest age class identified from eye lens diameters was 13 years. A lack of small pale ghost sharks in our samples made it impossible to determine whether similar eye lens age groups occur in that species.

The "tails" of the dark ghost shark eye lens age groups overlapped adjacent age groups, so although fish with lens diameters near the modal values of each age group could be confidently assigned to age classes, fish in the tails of the distributions could not. By truncating the lens age groups at the troughs between adjacent groups, we probably also truncated the length ranges of ghost sharks comprising each age class at both upper and lower ends (see Fig. 6). Eye lens diameter measurements are probably useful for developing or corroborating growth curves. For individual fish, eye lens ageing may provide estimates of age that are within ±2 years of the true value (since the tails of the distributions are unlikely to overlap more than two adjacent age groups).

Thin spine sections contain bands that may be age-related. However the bands were unclear and difficult to count, resulting in subjective and uncertain age estimates. Initial band counts appeared to underestimate the ages of ghost sharks, relative to the ages expected from MULTIFAN analyses. Careful inspection of the inner part of the spine revealed further bands, which when counted produced age estimates that seemed more realistic. However these estimates still produced high variability in length-at-age, suggesting that even if the structures being counted were annual, our ability to age individual fish from their spines is limited. Further fine increment structure of unknown periodicity was present, particularly in dark ghost sharks. Until the significance of these finer bands is determined, and a better technique developed for resolving band structure, we are not confident about our spine-based estimates of age.

Use of eye lens diameters as a means of developing growth curves seems promising. Combining the lens diameter data for the two sexes did not blur the modes, suggesting that they are age-related rather than length-related. Our dark ghost shark sample size (210) was marginal, given the large number of modes (13) apparently present. We recommend that a further similar-sized sample of dark ghost shark lenses be collected at the same time of year as the present sample (December–January), and combined with it, to confirm the existence and location of the modes. Partial validation of the annual nature of the lens age groups could be achieved by collecting a further large sample of lens in June–July: if the modes progress forwards by about 1 mm annually, samples collected six months out of phase should have modes centred midway between those in the December–January samples (Fig. 5).

It is not known whether eye lens age groups are present in pale ghost sharks. Larger samples would help determine this by clarifying modal structure and location. However, samples of juvenile pale ghost sharks less than 60 cm in length will be required to determine the number of missing age groups, and therefore the absolute ages of the fish in the lens age groups.

12. Publications

Nil

13. Data Storage

Because this project was a feasibility study, the sample sizes were small, and the age estimates were highly uncertain, the data have not been stored on the *age* database. Data files are available from NIWA on request (contact M. P. Francis).

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Table 1: Von Bertalanffy growth parameters estimated from MULTIFAN models fitted to length-frequency data. Amplitude and phase parameters are given for models incorporating seasonal growth. SD, growth standard deviation (C, constant; V, variable). Ages, number of age classes distinguished by MULTIFAN.

				Von Bertalanffy growth parameters				
Region	Sex	SD	Ages	L_∞	K	t_0	Amplitude	Phase
Dark ghost shark								
East coast South Island	Female	V	10	135.3	0.052	–0.94	0.95	0.75
	Male	C	9	89.0	0.091	–0.61		
West coast South Island	Female	C	9	123.0	0.065	–1.15		
	Male	C	11	123.4	0.044	–1.43		
Stewart–Snares Shelf	Female	C	7	122.1	0.087	–1.01		
	Male	C	7	108.0	0.073	–1.34		
Chatham Rise	Female	V	12	97.0	0.090	–1.17		
Pale ghost shark								
Southland–Campbell Plateau	Female	C	9	142.9	0.070	–0.50	0.36	0.04
	Male	C	6	115.8	0.110	–0.53	0.95	0.60
Chatham Rise	Female	C	8	161.5	0.058	–0.94		
	Male	C	8	99.7	0.134	–0.05		

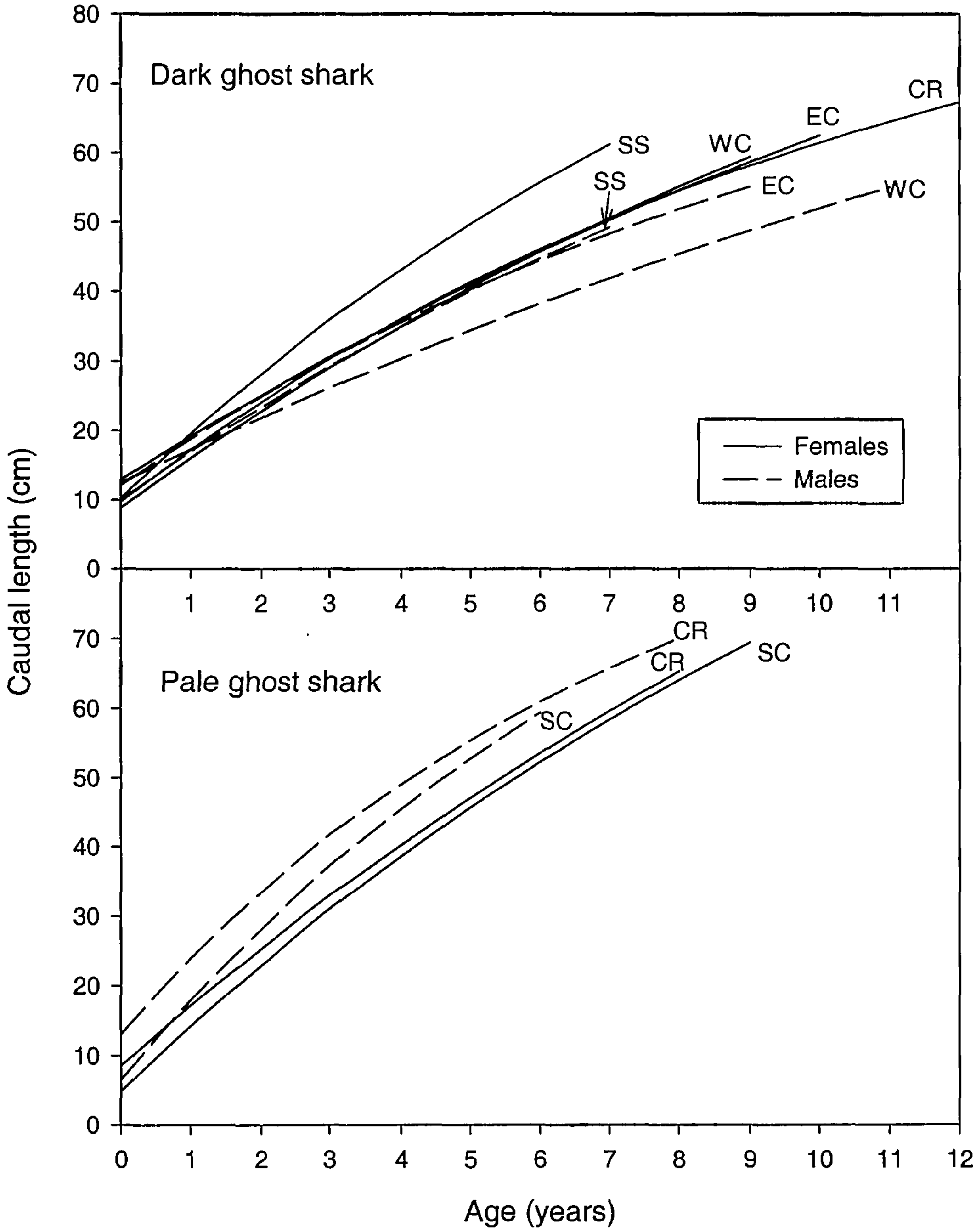


Figure 1: MULTIFAN growth curves for male and female dark and pale ghost sharks. Seasonal growth oscillations were determined for some growth curves (see Table 1) but are not shown here. EC, east coast South Island; WC, west coast South Island; CR, Chatham Rise; SS, Stewart-Snares Shelf; SC, Southland - Campbell Plateau.

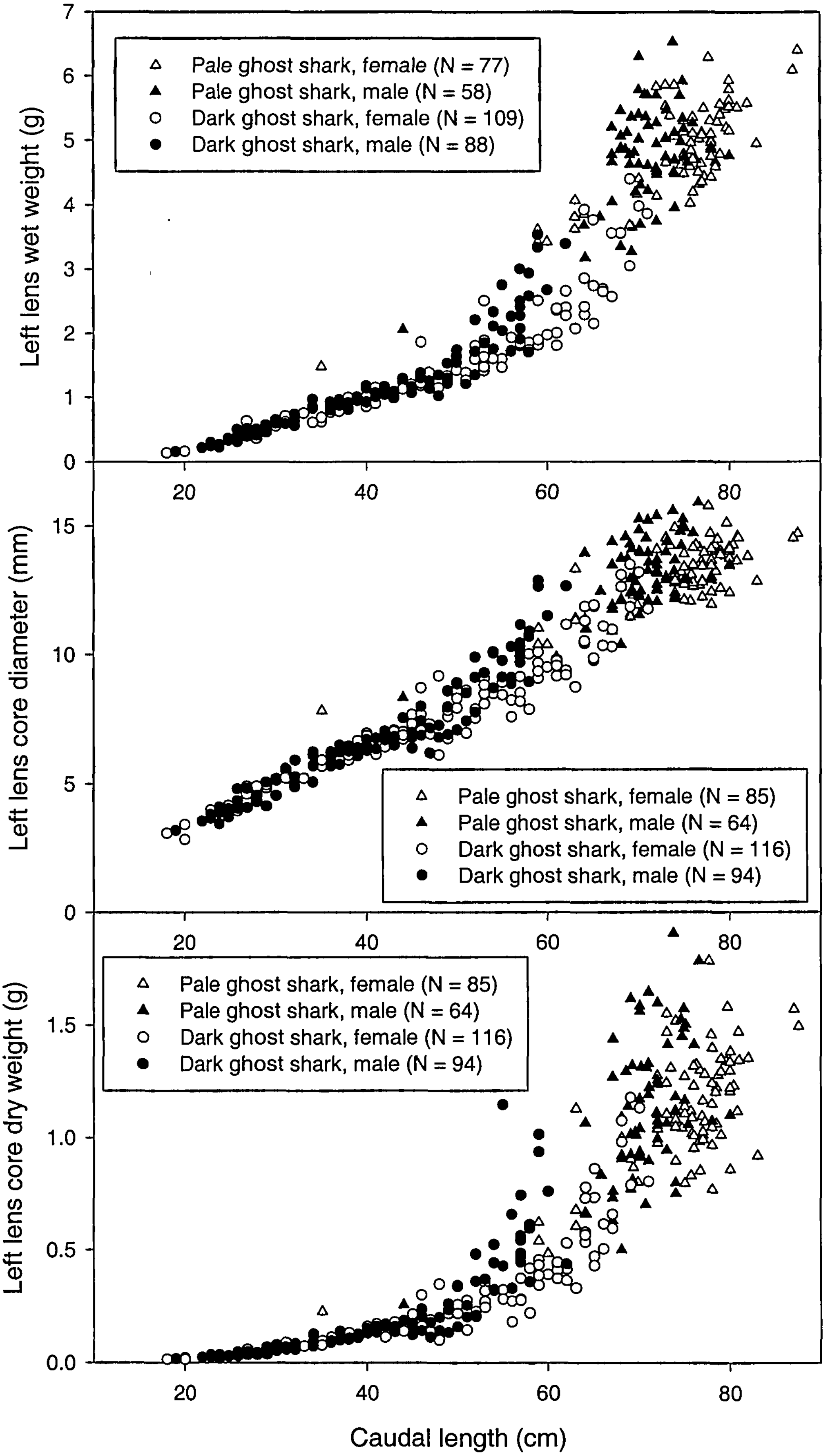


Figure 2: Variation in eye lens whole wet weight, core diameter and core dry weight with body length. .

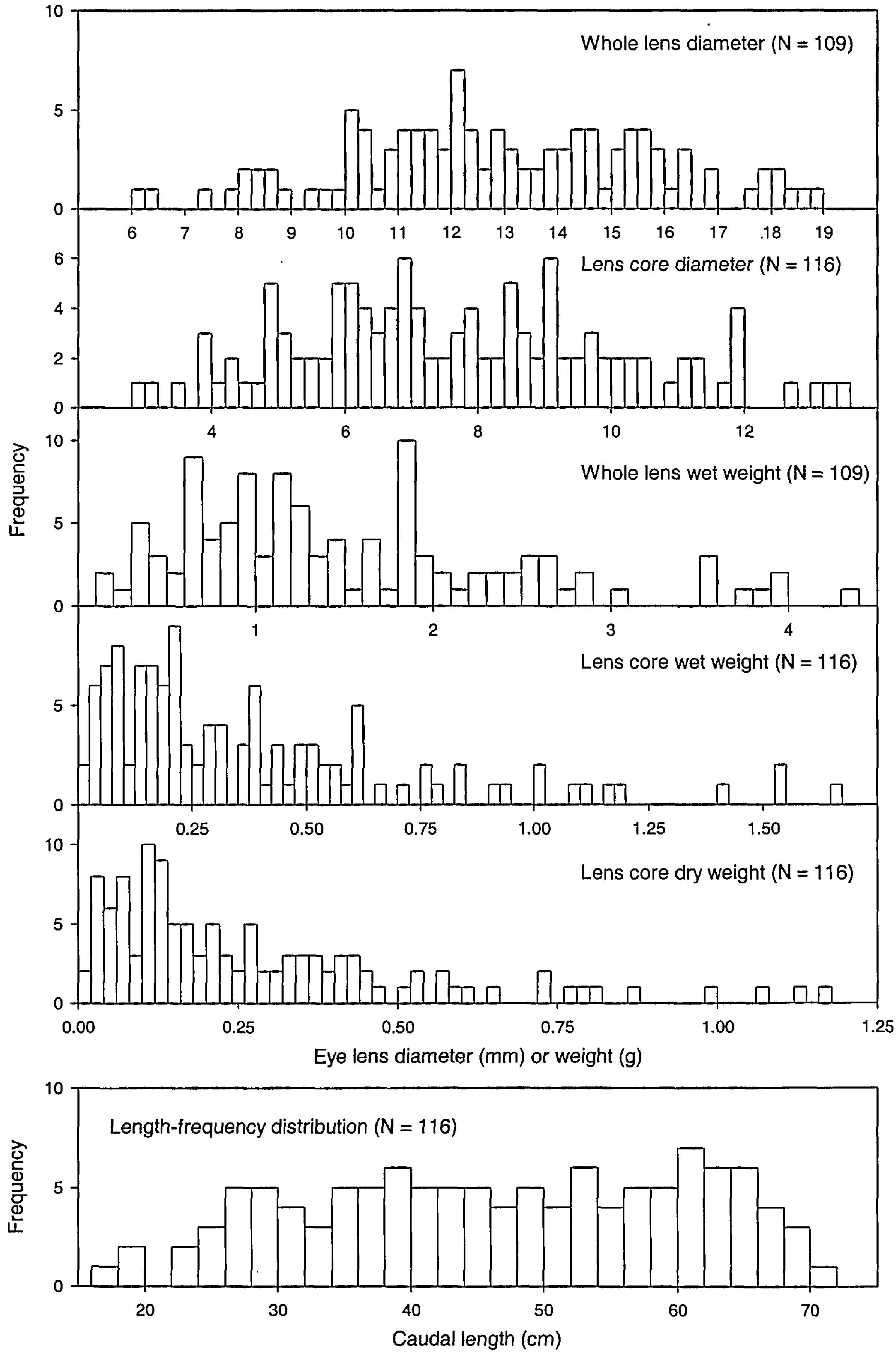
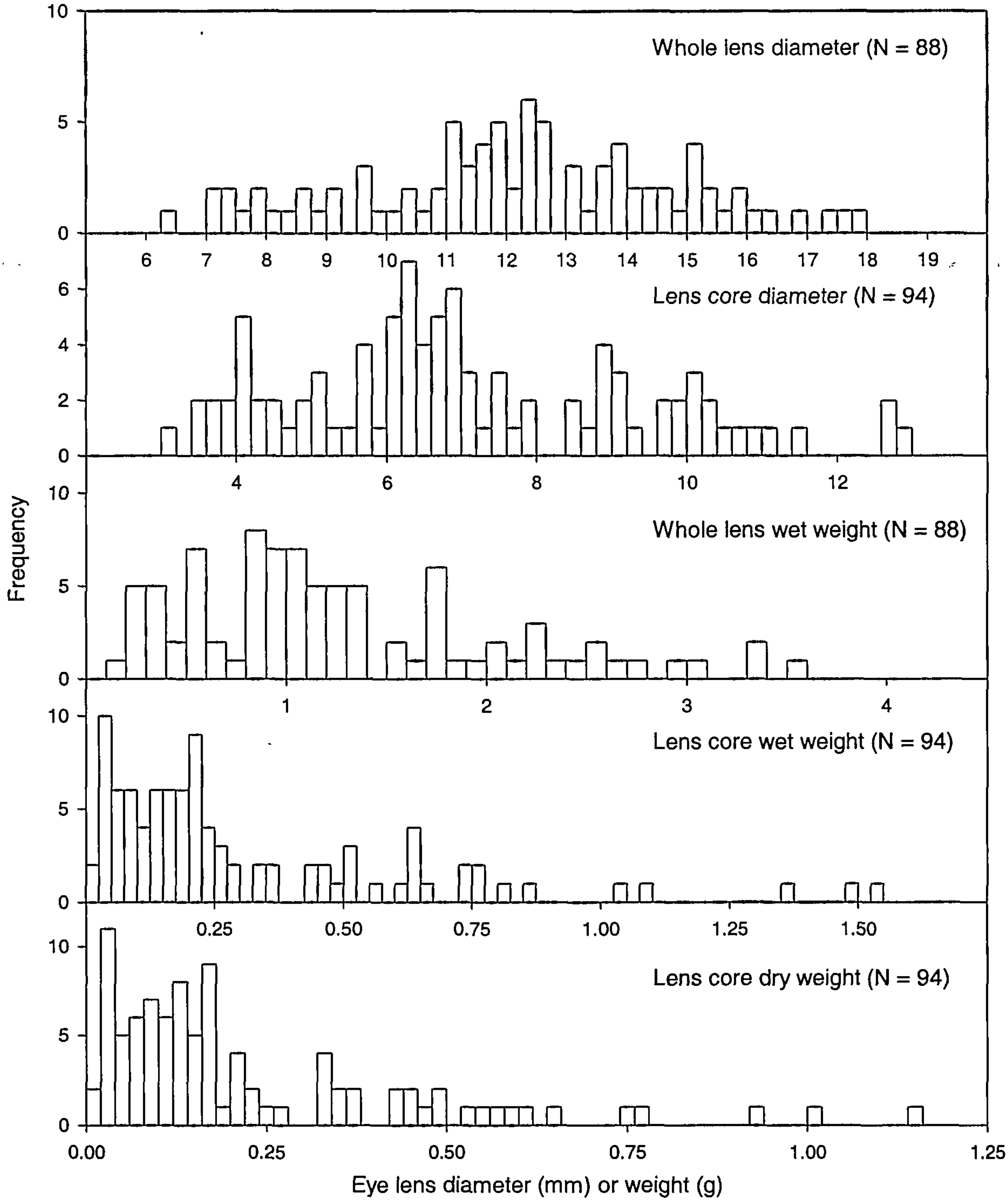


Figure 3: Frequency distributions of lens diameter and weight, and body length, for female dark ghost sharks.



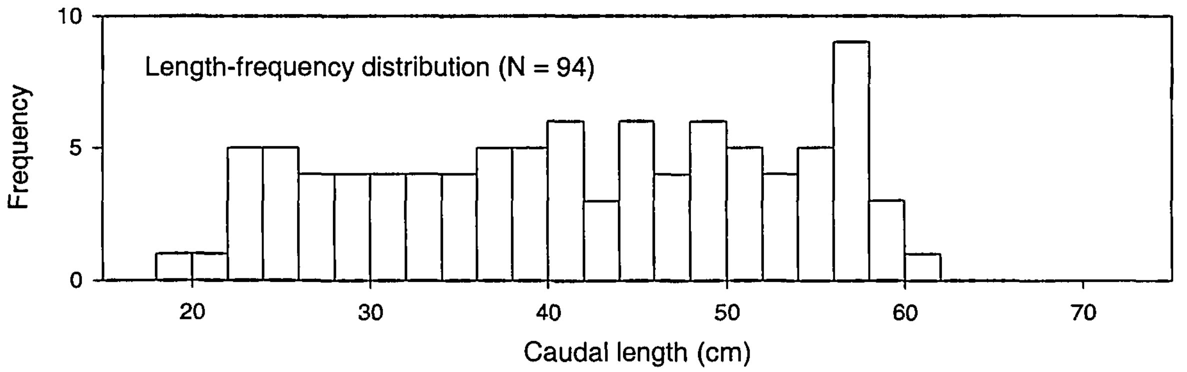


Figure 4: Frequency distributions of lens diameter and weight, and body length, for male dark ghost sharks.

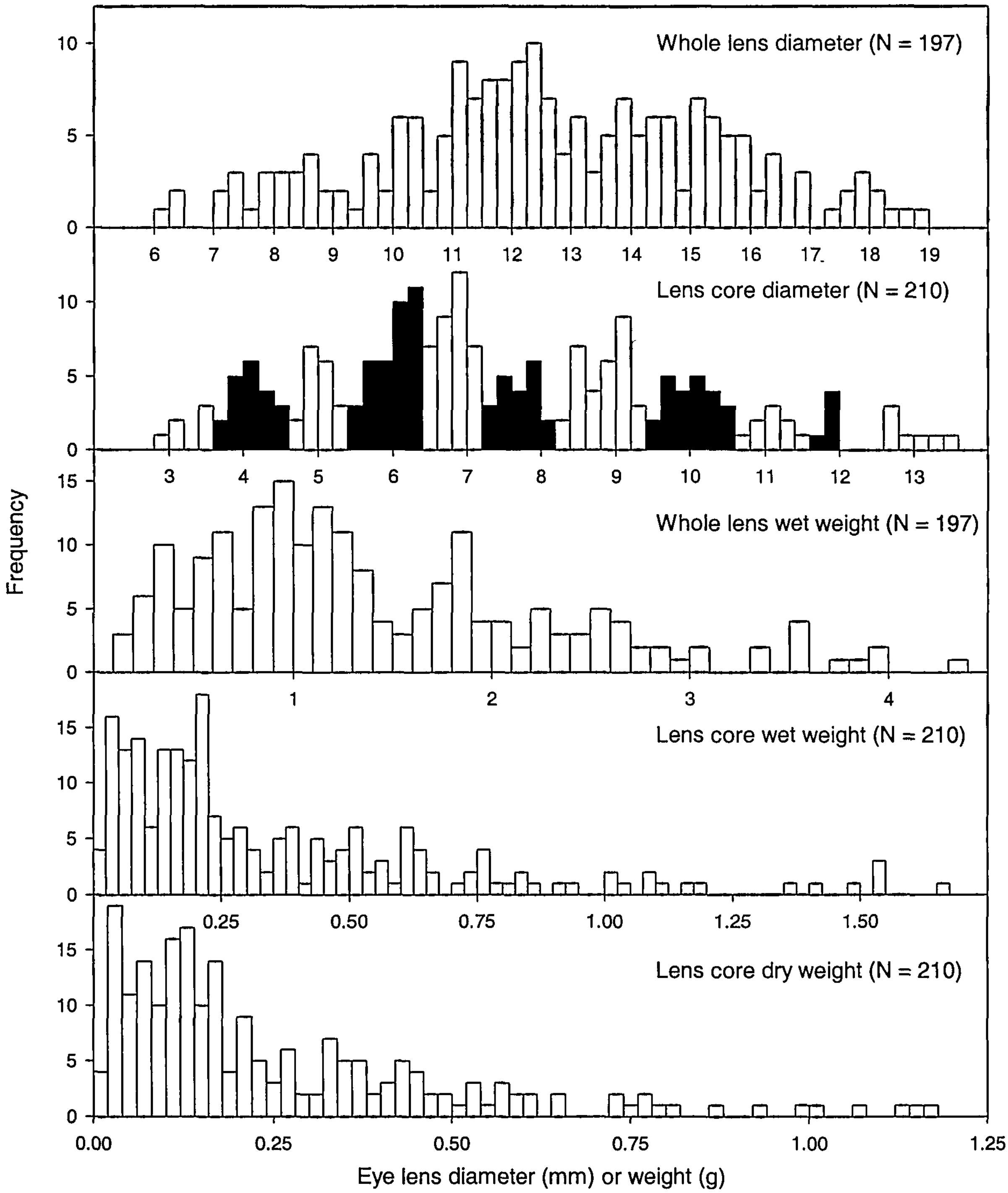


Figure 5: Frequency distributions of lens diameter and weight for male and female dark ghost sharks. Black and white fills in the second panel indicate lens diameter modal groups used to define lens age groups 1-11.

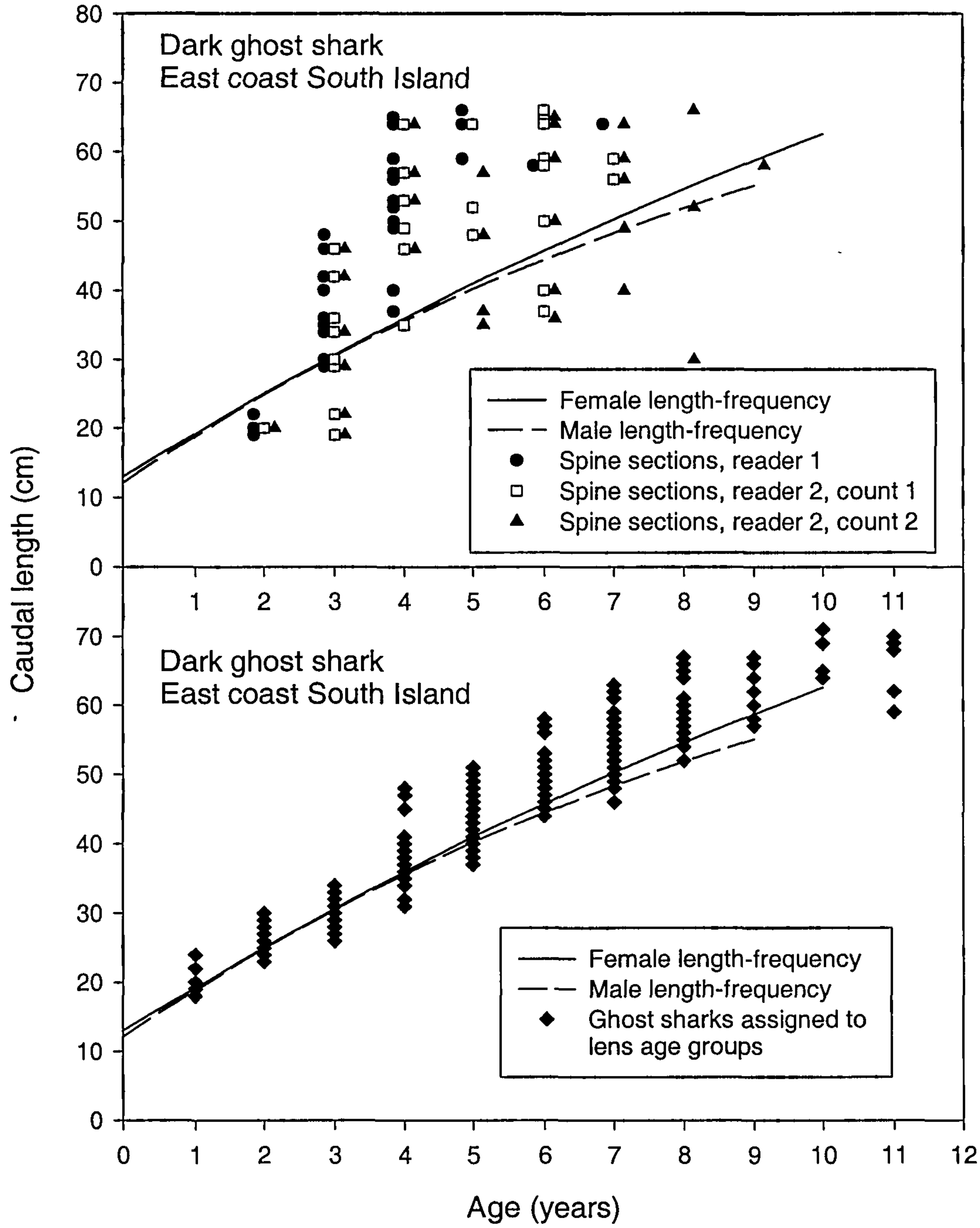


Figure 6: Comparison of growth curves obtained from MULTIFAN analysis of length-frequency data with age estimates obtained from (top) thin sections of dorsal fin spines, and (bottom) modal analysis of eye lens core diameters for east coast South Island dark ghost sharks. Spine section ages are slightly offset horizontally for clarity.

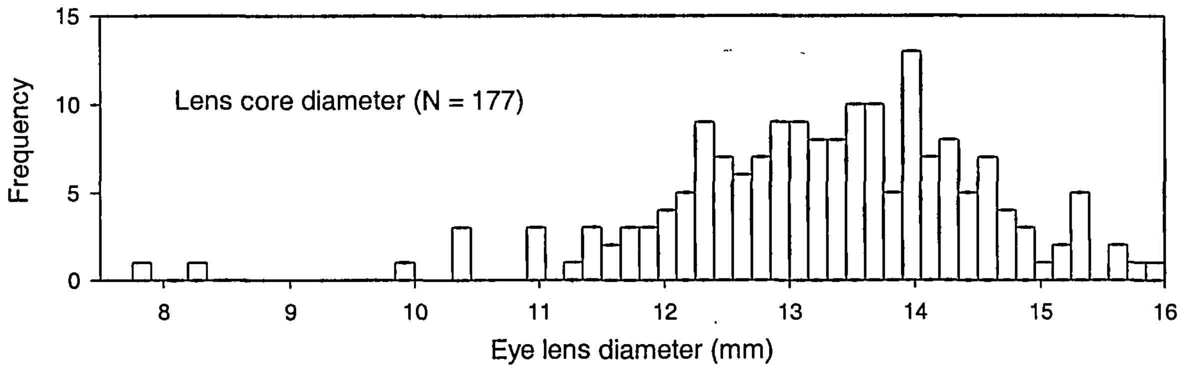


Figure 7: Frequency distributions of lens diameter for male and female pale ghost sharks.

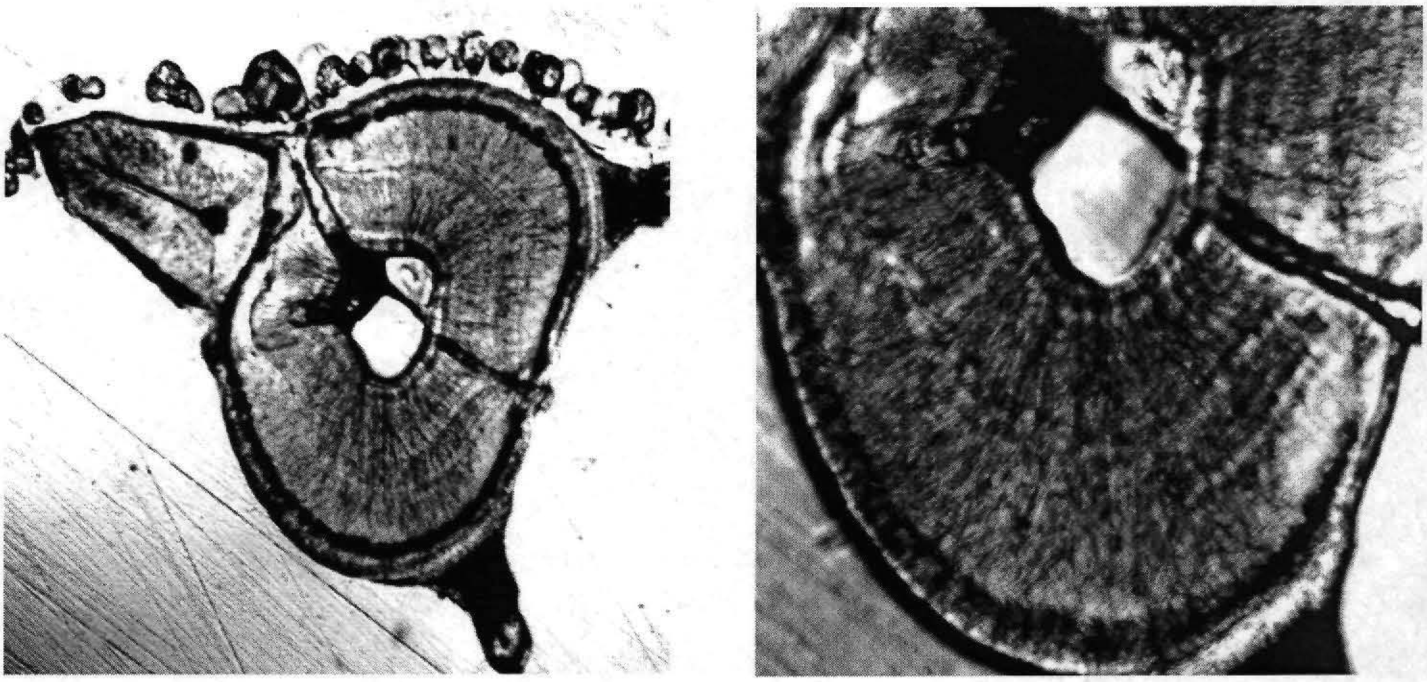


Figure 8: Dark ghost shark spine section (GSH14, 36 cm male).

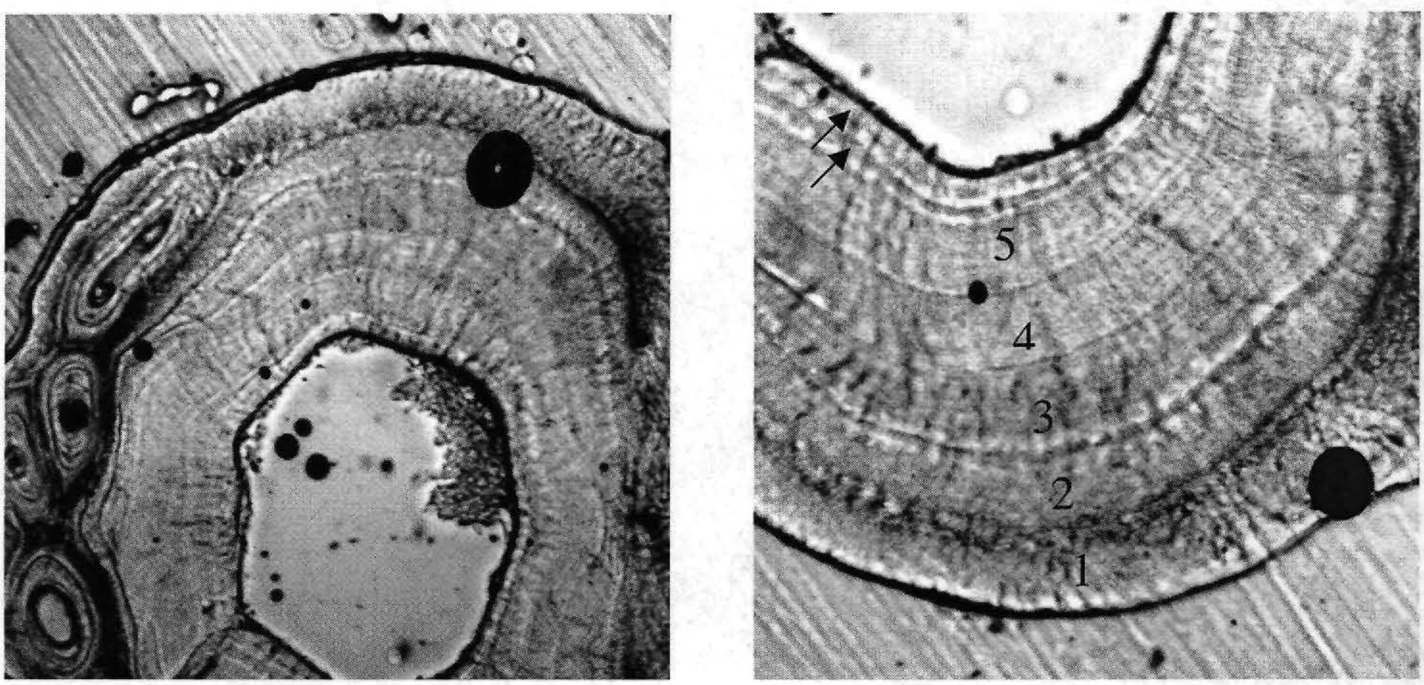


Figure 9: Dark ghost shark spine section (GSH20, 59 cm female). Numbers in the enlarged, right hand image indicate major growth bands, each of which is composed of multiple fine bands. Arrows indicate narrow, distinct bands near the spine core.

Figure 10: Pale ghost shark spine section (GSP16, 76 cm female).

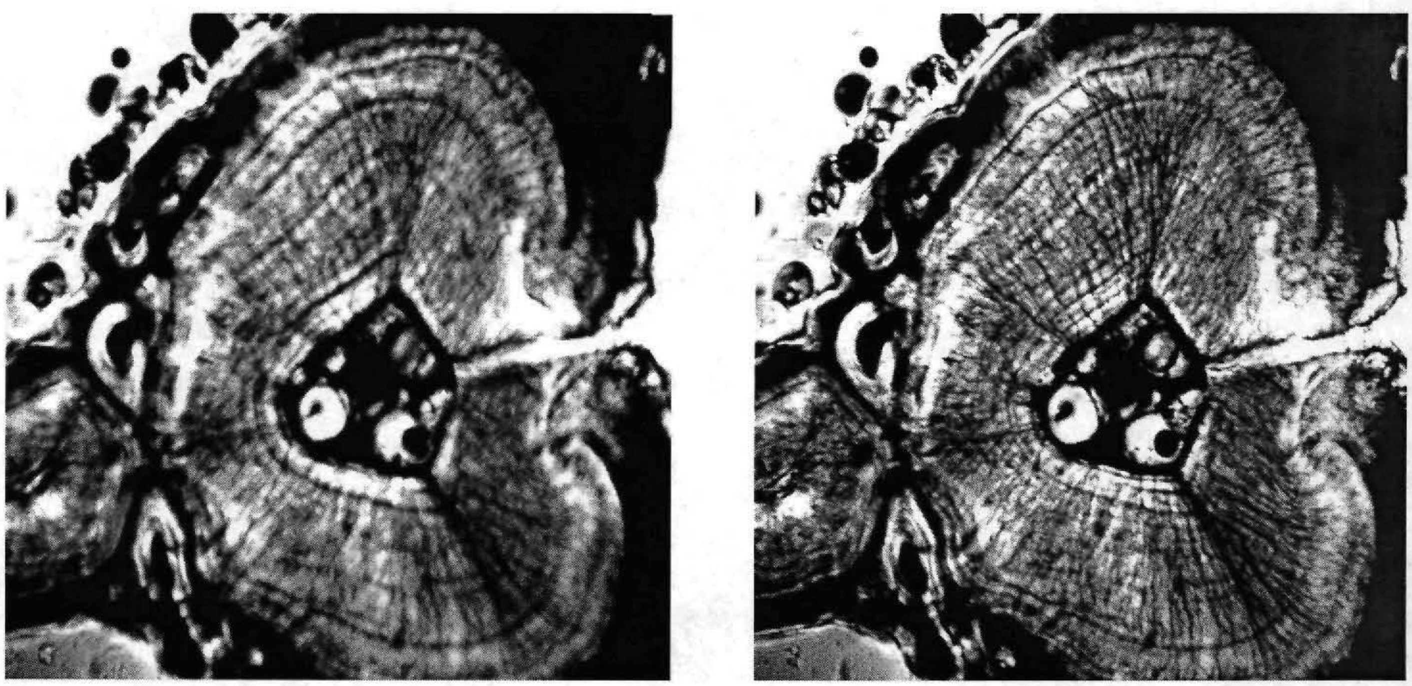


Figure 11: Pale ghost shark spine section (GSP20, 75 cm female).

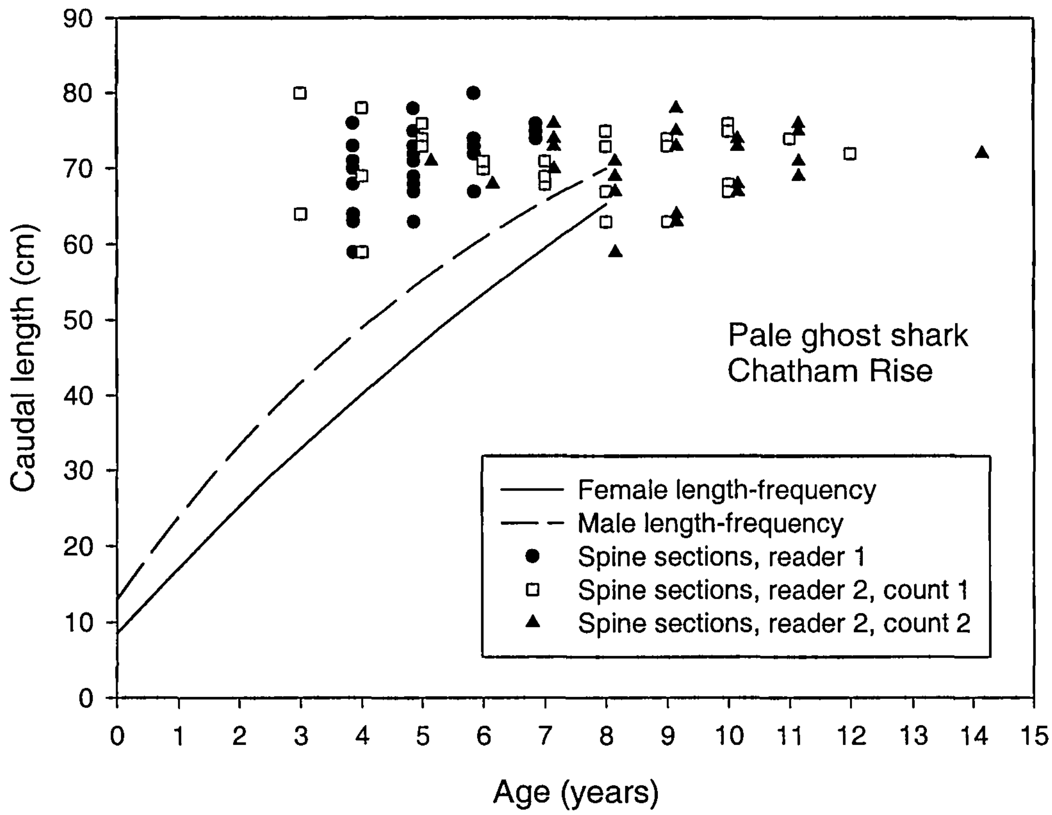
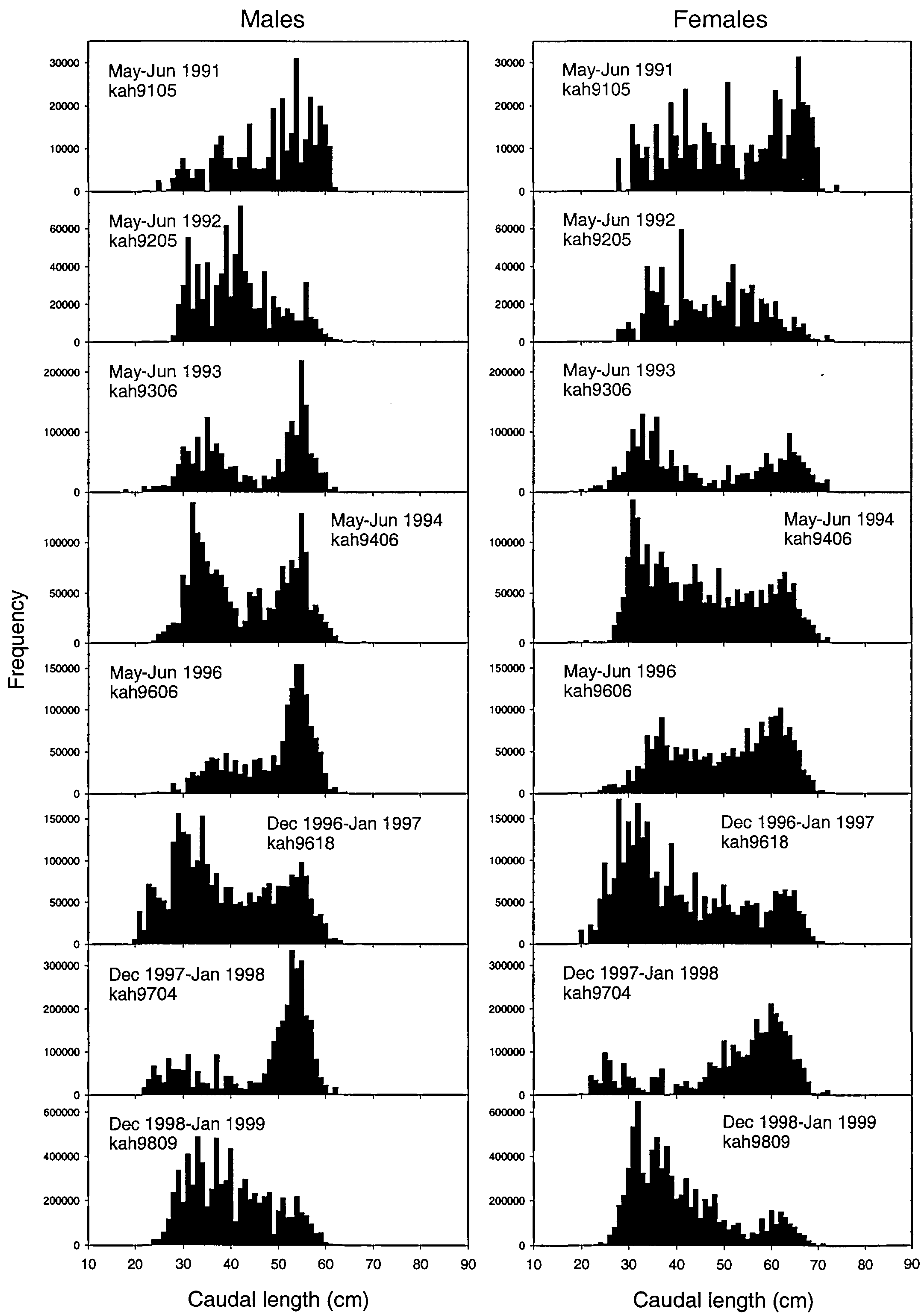
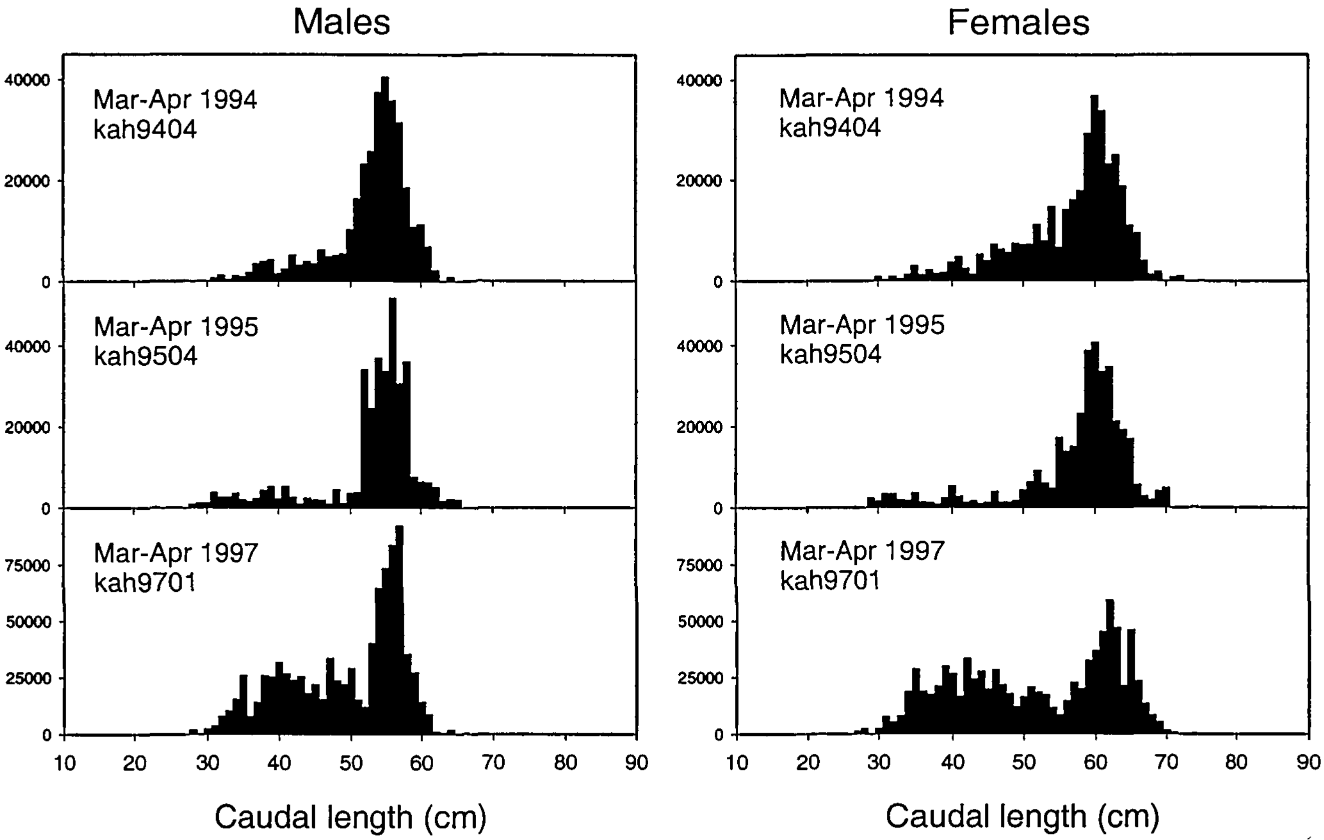


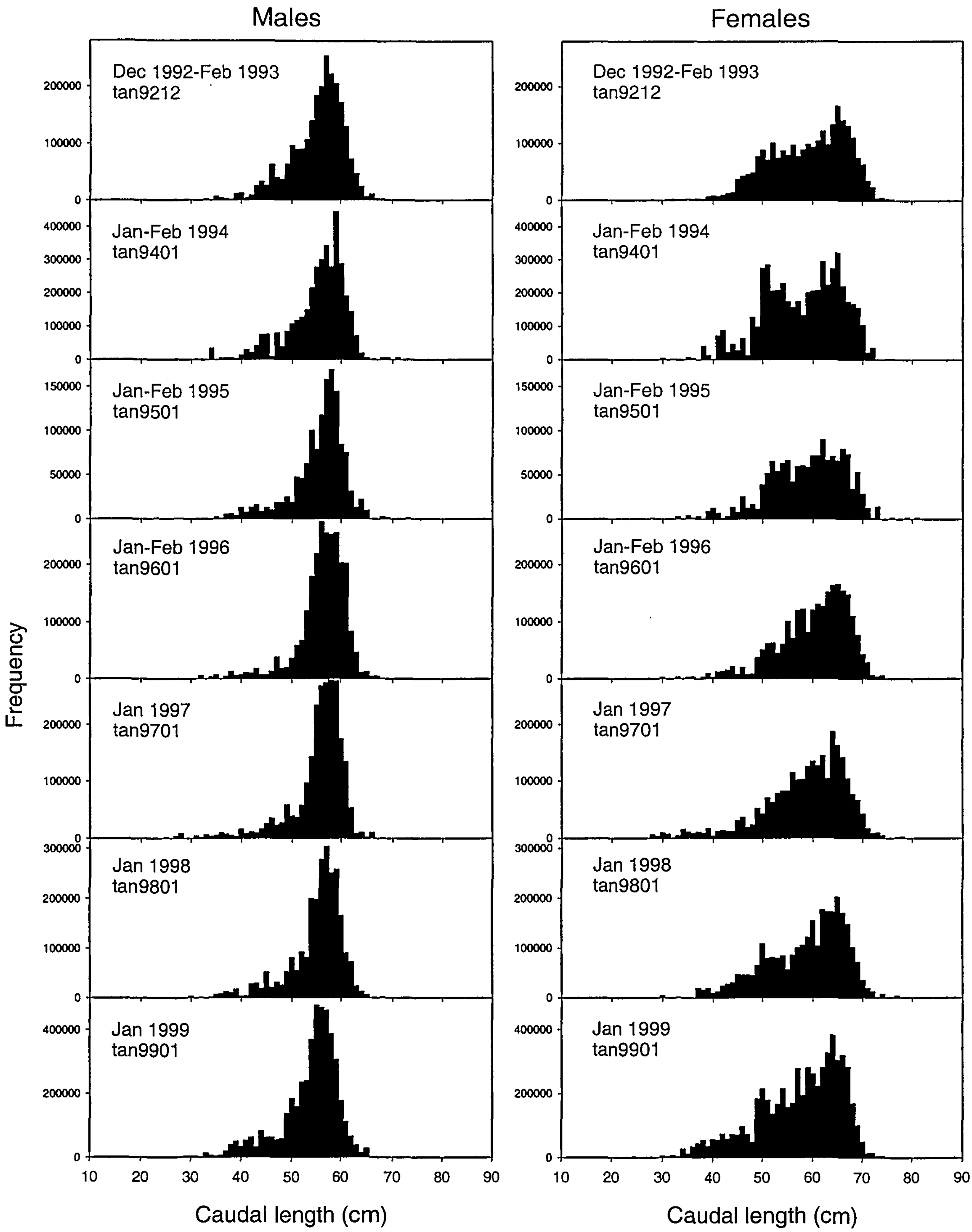
Figure 12: Comparison of growth curves obtained from MULTIFAN analysis of length-frequency data with age estimates obtained from thin sections of dorsal fin spines for Chatham Rise pale ghost sharks. Spine section ages are slightly offset horizontally for clarity.



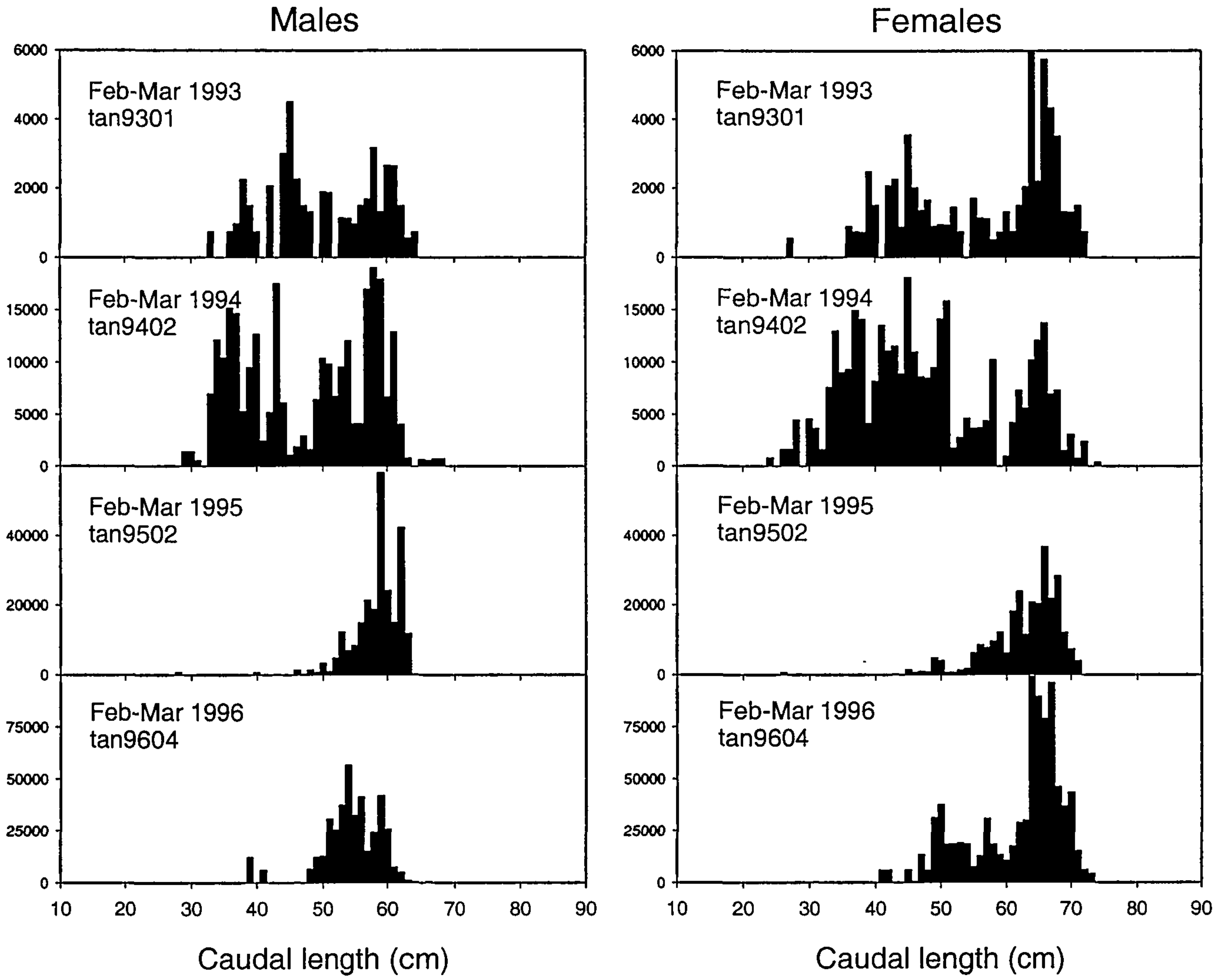
Appendix 1: Scaled length-frequency distributions of dark ghost shark from *Kaharoa* trawl surveys of the east coast of South Island.



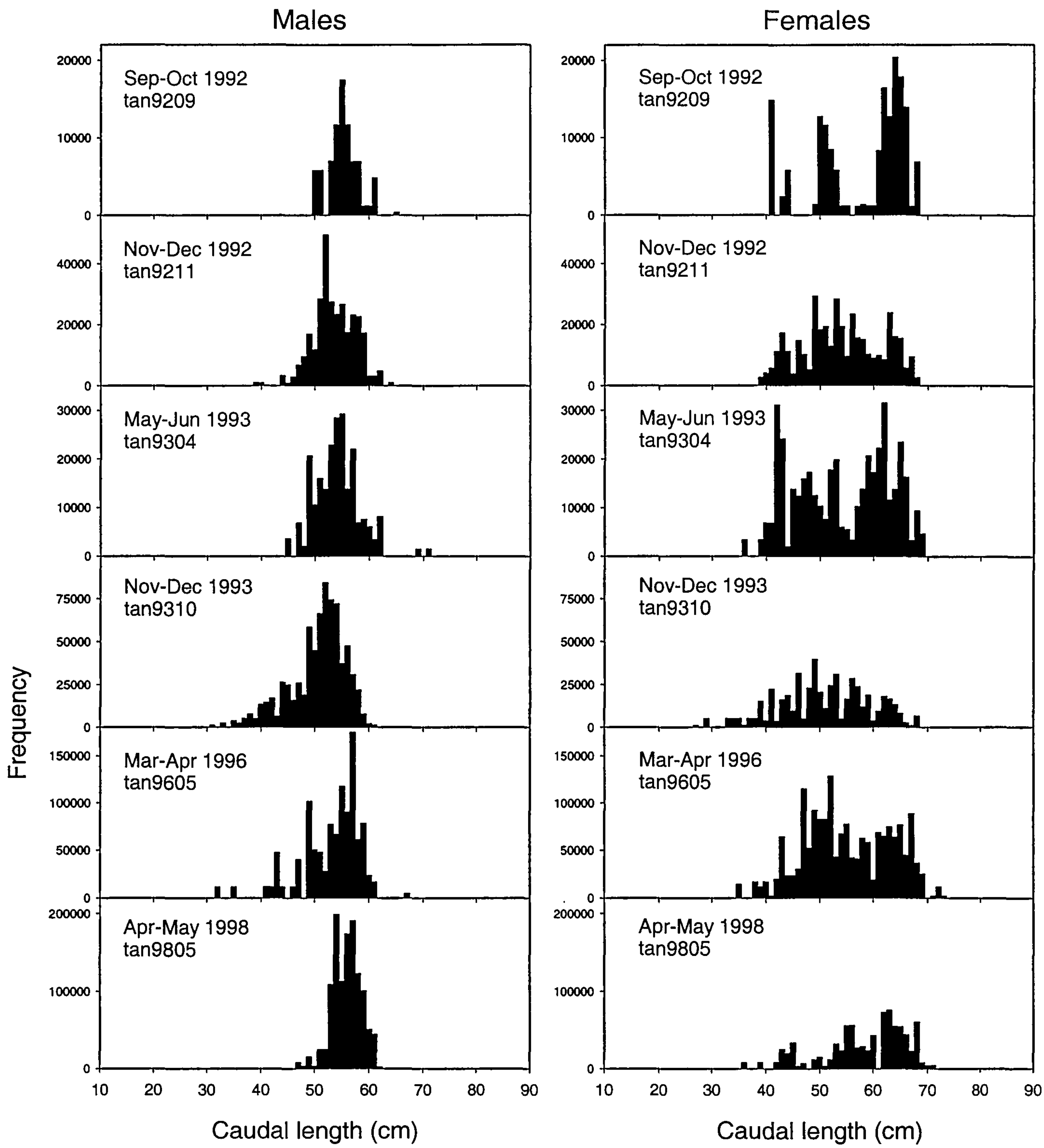
Appendix 1: Scaled length-frequency distributions of dark ghost shark from *Kaharoa* trawl surveys of the west coast of South Island.



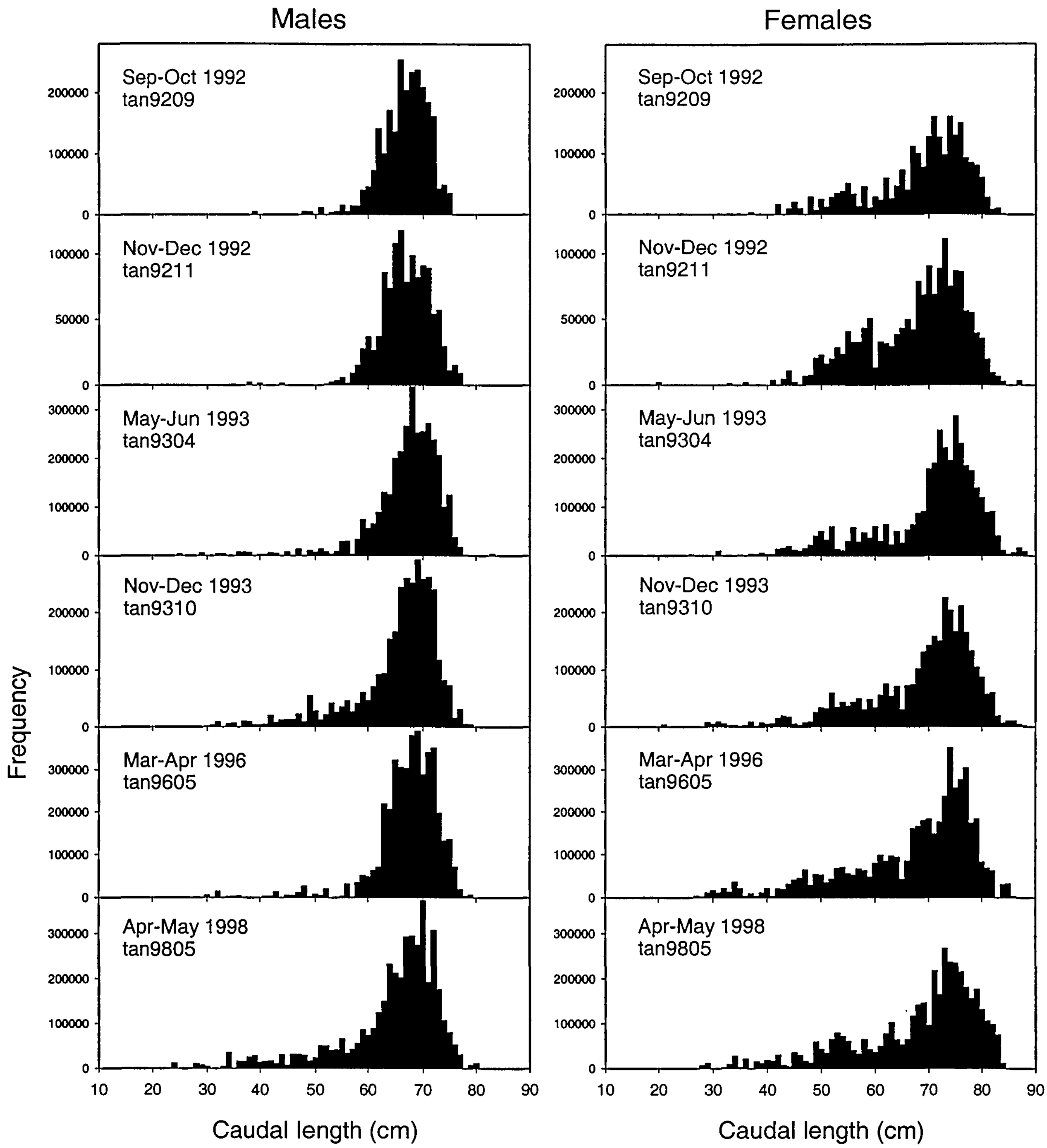
Appendix 1: Scaled length-frequency distributions of dark ghost shark from *Tangaroa* trawl surveys of the Chatham Rise.



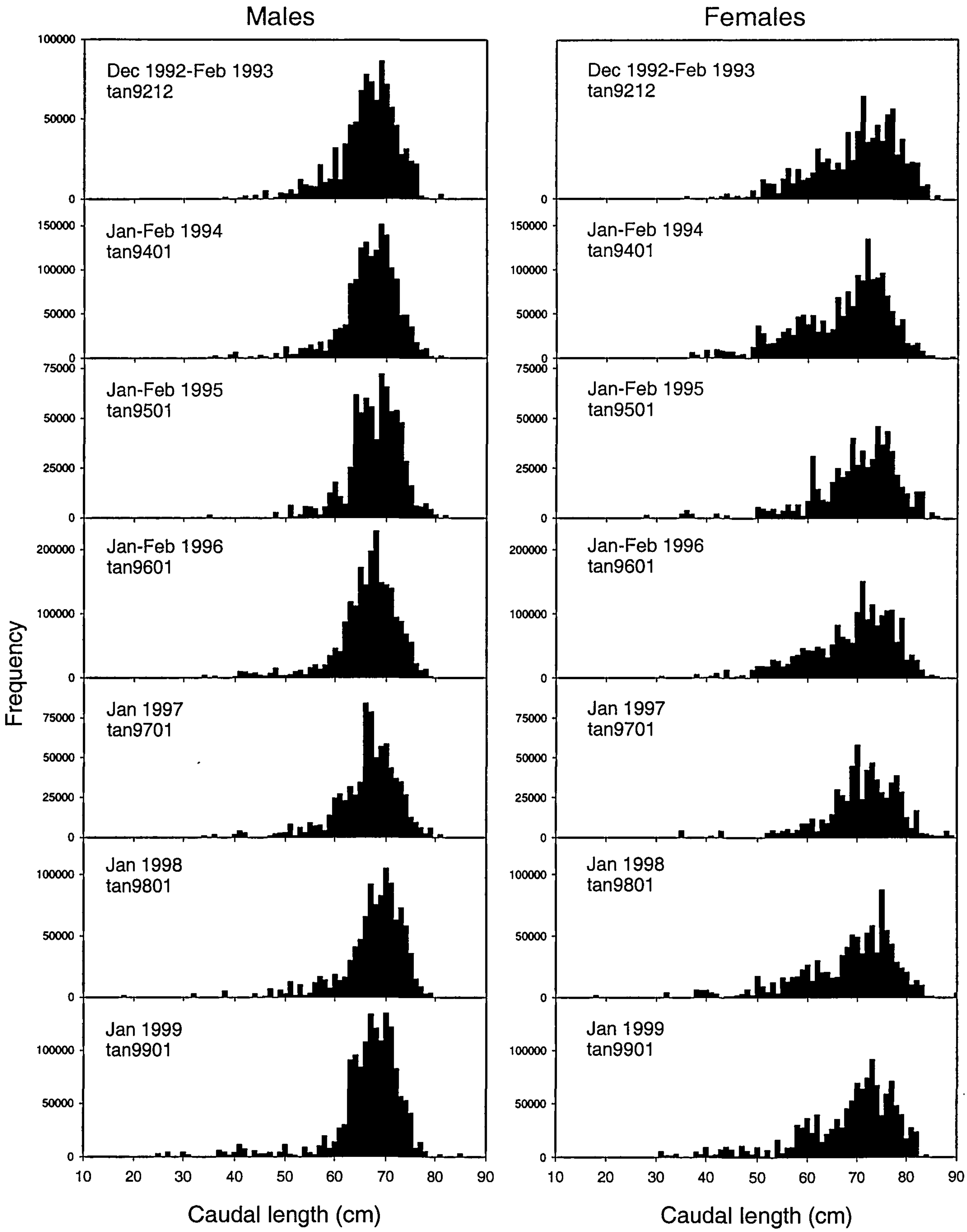
Appendix 1: Scaled length-frequency distributions of dark ghost shark from *Tangaroa* trawl surveys of the Stewart-Snares Shelf.



Appendix 1: Scaled length-frequency distributions of dark ghost shark from *Tangaroa* trawl surveys of Southland and the Campbell Plateau.



Appendix 1: Scaled length-frequency distributions of pale ghost shark from *Tangaroa* trawl surveys of Southland and the Campbell Plateau.



Appendix 1: Scaled length-frequency distributions of pale ghost shark from *Tangaroa* trawl surveys of the Chatham Rise.