



# Growth and reproduction of four deepwater sharks in New Zealand waters

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## EXECUTIVE SUMMARY

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The Ministry for Primary Industries (MPI) is developing a risk assessment framework to identify the nature and extent of risks to chondrichthyan populations. This project aims to fill some of the knowledge gaps for some of the high-risk, non-Quota Management System species to reduce the level of uncertainty in the risk assessments of those species, and to provide information on their productivity that can then be used as inputs into future quantitative risk assessments. The species included in this study were seal shark (*Dalatias licha*), Owston's dogfish (*Centroscymnus owstonii*), longnose velvet dogfish (*Centroselachus crepidater*), and Plunket's shark (*Scymnodon plunketi*). Specimens and data were collected aboard commercial fishing vessels and research vessels, and integrated with existing data and specimens held by NIWA.

All species except seal shark were aged by counting growth bands on their dorsal fin spines, either on the external surface or internally following thin sectioning near the spine tip. All four species were also aged by estimating the number of micro-increments deposited in their eye lenses between birth and capture, and dividing by 365 (based on an assumption that one micro-increment is formed per day). Sample sizes were mostly small and spine bands were often unclear so the results presented here are regarded as preliminary and uncertain, but are the best available for these species. Age estimates from spines considerably exceeded those from eye lenses. Neither spine ageing nor eye lens ageing has been validated for these species. However, the spine ages are regarded as more plausible, and they indicate that all three species grow slowly, reaching maturity at about 4–5 years for male Owston's dogfish (no estimate was possible for females); 10 and 15 years, respectively, for male and female longnose velvet dogfish; and 33 and 49 years, respectively, for male and female Plunket's shark. Longevity is moderate to high compared with other elasmobranchs, being 11 years for Owston's dogfish, 26 years for longnose velvet dogfish and 53 years for Plunket's shark. Seal sharks lack fin spines and their eye lens ages are regarded as unreliable, so no age estimates were generated for that species. Our estimates of age and longevity for longnose velvet dogfish and Owston's dogfish are probably underestimates.

Estimated total lengths at 50% maturity were 109 cm and 133 cm, respectively, for male and female seal shark, 71 cm and 107 cm for male and female Owston's dogfish, 65 cm and 87 cm for male and female longnose velvet dogfish, and 110 cm and 130 cm for male and female Plunket's shark. For Owston's dogfish and longnose velvet dogfish, the proportion of mature females that were pregnant was low (37% and 21%), suggesting there may be a resting period of 2–3 years between pregnancies, with a total reproductive cycle length of 3–4 years. We recorded only one pregnant female seal shark and three pregnant Plunket's sharks, so it is unlikely that our samples adequately represent the mature portion of the population for these species. Litter sizes were poorly estimated because of the very small samples of pregnant females. Some reproductive parameters remain unknown, uncertain, or are derived from overseas populations that may differ from those in New Zealand. Uncertainty about these parameters could have a big effect on productivity estimates.

For all species, juveniles made up a significant proportion of the samples, dominating both seal shark and Plunket's shark, and making up almost half of the longnose velvet dogfish and female Owston's dogfish. The only exception was male Owston's dogfish, of which 75% were mature. Samples of all species included likely neonates, based on the estimated sizes at birth. Mature males were generally present in all the main areas sampled, whereas mature female numbers varied among regions.

## 1. INTRODUCTION

One of the major goals of the New Zealand National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks) is to ‘Maintain the biodiversity and long-term viability of New Zealand shark populations based on a risk assessment framework with assessment of stock status, measures to ensure any mortality is at appropriate levels, and protection of critical habitat’ (Ministry for Primary Industries 2013). The Ministry for Primary Industries (MPI) is developing a risk assessment framework to identify the nature and extent of risks to chondrichthyan populations through expert-based and quantitative methods. The first step in that process was in November 2014 when MPI convened an expert panel to conduct a qualitative risk assessment of all New Zealand cartilaginous fishes (Ford et al. 2015). That risk assessment ranked New Zealand’s chondrichthyan species by their perceived risk, and identified gaps in our knowledge of the biological productivity of each species. The present project aims to fill some of the knowledge gaps for some of the high-risk, non-Quota Management System (QMS) species in order to reduce the level of uncertainty in the risk assessments of those species, and to provide information on their productivity that can then be used as inputs into future quantitative risk assessments.

The Overall Research Objective of the present study was: *To estimate basic biological parameters for high risk, high uncertainty chondrichthyans.*

There were three Specific Research Objectives:

1. *To collect (from observers and/or research trawls, or other sources) and store specimens for selected chondrichthyan species.*
2. *To test the efficacy of potential ageing techniques on a subset of specimens for each species collected.*
3. *To process specimens for ageing and other biological parameters, reliant on the outcome of Objectives 1 and 2 and in consultation with MPI.*

The species included in this study were three rays and five sharks (with MPI three-letter species codes):

1. Common electric ray, *Tetronarce nobiliana* (ERA)
2. Blind electric ray, *Typhlonarke aysoni* (BER, TAY)
3. Blind electric ray, *Typhlonarke tarakea* (BER, TTA)
4. Carpet shark, *Cephaloscyllium isabellum* (CAR)
5. **Seal shark, *Dalatias licha* (BSH)**
6. **Longnose velvet dogfish, *Centroselachus crepidater* (CYP)**
7. **Plunket’s shark, *Scymnodon plunketi* (PLS)**
8. **Owston’s dogfish, *Centroscymnus owstonii* (CYO)**

These eight species all fall within the top 11 non-QMS elasmobranch species having the greatest risk in the qualitative risk assessment (Ford et al. 2015). In this report, we deal with the last four species listed (in bold) above; the remaining four species are covered by Francis et al. (2018).

All eight species are caught as unintended bycatch by trawlers, and to a lesser extent by other fishing methods, around New Zealand. Specimens and data were collected to estimate age, growth, longevity, length and age at maturity, and reproductive parameters (including, where possible, gestation period, fecundity, and length at birth). Collections were made by observers aboard commercial fishing vessels, and by scientists aboard research vessels. These new specimens and data were integrated with existing data and specimens held by NIWA.

## 2. METHODS

### 2.1 Specimen and data collection

Deepwater chondrichthyans are not target species on the trawl or acoustic surveys carried out by NIWA, but total length and weight data by sex have been collected for them opportunistically over many voyages. Since 2008–09, macroscopic maturity stage data have also been collected for certain species when time and staff experience permitted. The maturity scale used (Appendix 1) was developed by M. Francis and W. Lyon as a unified version of a number of more species-specific scales used previously in shallow water (e.g., for *Squalus acanthias*). Males were scored on a 3-stage scale (immature, maturing and mature) based on the condition of the claspers. Females were scored on a 6-stage scale (immature, maturing, mature, gravid I and II, post-partum) based on the state of development of the ovaries and oocytes, the presence of ovulated eggs or embryos in the uterus, and condition of the uterus walls. Further female reproductive data have been collected opportunistically since 2013 to aid interpretation of the reproductive cycle of different species. This included counts of mature (yolky) oocytes in the ovaries, maximum diameter of those oocytes, uterus and oviducal gland width, and counts and length measurements of embryos.

Size and reproductive data for the four shark species collected during research surveys were extracted from the MPI *trawl* database, and data collected by observers were extracted from the *COD* database. While the observer sampling covered a wider spatial range than the trawl surveys, length observations were often unsexed and none were staged, so results presented here are based on trawl survey data only. For each species, we determined the total length structure and sex ratio of the sampled population in the main survey series, which were carried out on the east coast of the North Island, the Chatham Rise, the Campbell Plateau, the west coast of the South Island, and the Challenger Plateau. Smaller samples were collected from other areas such as Cook Strait and Northland. This provided information on the maximum sizes for each sex, and the spatial occurrence of neonates and juveniles in the different survey areas. The presence of neonates, particularly in large numbers, and over multiple years, may indicate nursery areas (Heupel et al. 2007). The spatial distribution of pregnant females may similarly provide some indication of pupping grounds. The proportion of mature females in a population that are pregnant may be used as an indicator of the duration of the reproductive cycle. For example, if 33% of mature females are gravid at one time, that might indicate that each female produces one litter every three years. Information on counts of eggs and/or pups observed in pregnant females was also collated, although such observations were very limited for some species.

The maturity-stage data from all areas were combined to estimate maturity ogives by sex. Males were considered mature (developing to reproduce in the current annual period) if they were scored as stage 3 and females were mature if they were scored as stages 3–6. The proportion of mature individuals within each 2 cm length class was modelled as a logistic function of length using a binomial distribution with logit link. The parameters of the regression were used to calculate the length at 50% maturity ( $L_{50}$ ):

$$\text{Proportion mature} = \alpha + \beta * \text{total length (binomial GLM with logit link)}$$

$$L_{50} = -(\alpha / \beta)$$

Existing, archived ageing material included a few dorsal fin spines for the species of interest: 36 longnose velvet dogfish, 9 Plunket's shark, and 1 Owston's dogfish. For the collection of new samples for ageing, the project proceeded in two phases. Phase 1 consisted of the collection of small numbers of specimens of each species, and experimental processing of various hard parts to determine the best structure and technique for revealing growth bands. Phase 2 consisted of the collection of larger samples of the most useful ageing structures, and processing and ageing those samples using the best technique(s). In Phase 1, specimens were collected mainly by scientists during research voyages on RVs *Tangaroa* and *Kaharoa*. In Phase 2, MPI observers, in addition to scientists, were requested to collect larger numbers of specimens. Most specimens and new data were collected between April 2015 and August 2017. Most specimens came from around the South Island and adjacent plateaux (Chatham Rise, Campbell Plateau). In the rest of this report, results from both Phase 1 and Phase 2 are combined, but most of the ages came from Phase 2 samples.

Hard parts tested for suitability for ageing during Phase 1 were vertebrae, fin spines and eye lenses. Seal shark lacks spines so only vertebrae and eye lenses were tested for that species. In Phase 2, both fin spines and eye lenses were used for estimating the ages of shark specimens. Spines were usually removed from sharks at sea, and further cleaned in NIWA's ecology containment laboratory using aseptic techniques.

All analyses were conducted using the statistical software R (R Development Core Team 2008).

## **2.2 Vertebrae**

Band counts on vertebrae are widely used for age estimation in elasmobranchs, with vertebrae viewed either whole or following sectioning to about 0.5 mm thickness, and sometimes stained to enhance band clarity. However, vertebrae of deepwater sharks are poorly calcified and typically do not have visible growth bands.

A block of 3–7 vertebrae was dissected from each specimen and frozen. In the laboratory, vertebral blocks were defrosted, a few of the largest visible vertebrae were removed, and physically trimmed of connective tissue and residual neural and haemal arches. The vertebral centra were then bleached for about 15 minutes in sodium hypochlorite to remove connective tissue. Whole, half and thick-sectioned vertebrae were examined under reflected and transmitted light.

Selected frozen whole vertebrae were imaged in a micro-computed tomography (micro-CT) machine Skyscan 1172 at the University of Otago, Dunedin. Micro-CT uses X-ray technology to produce image slices through objects, which can be reconstructed into virtual, 3-dimensional images that can be rotated and viewed in any orientation (Geraghty et al. 2012). The settings used for the micro-CT scanner were: source voltage 40 kV, image pixel size 17.34  $\mu\text{m}$ , no filter, rotation step 0.40°, frame averaging on=4, random movement on=4. The scanning time for each sample was about 30 minutes. Data files were post-processed with ImageJ (Abramoff et al. 2004), using associated 3D plugin routines that provided both serial sections and video animations for further analysis.

## **2.3 Fin spines**

Dorsal fin spines have often been used for ageing squaloid sharks (Tovar-Ávila et al. 2008; Cailliet 2015). The second (posterior) dorsal fin spine is preferred for ageing purposes as it is usually larger, and is less often damaged or eroded, than the first (anterior) dorsal fin spine. Second dorsal fin spines were excised from the shark by cutting downwards between the spine and fin into the dorsal musculature as far as the vertebral column. The cut was then continued anteriorly and upwards to pass under the base of the spine. The spine base is uncalcified, very soft and fragile, and is easily damaged if the cut does not go all the way down to the vertebral column.

Spines were immersed in boiled water for about 15 minutes, after which the internal cartilaginous 'plugs' were easily removed and the spines dried. Spines were stained in a 1% KOH-saturated alizarin solution using initial time intervals of three hours, one day and one weekend (Irvine 2004). An extra sample of dissected spines was pre-etched in 0.1M EDTA for 20 minutes, then stained in the same KOH/alizarin solution. Spines were viewed under reflected, transmitted or polarised white light, and either dry or immersed in water. Some spines were thick-sectioned (about 0.4 mm thickness) at three distances from the spine tip (2–8 mm) to identify the best location at which to count internal growth bands. Sections that are too close to the tip or too far from the tip may not include all the bands (Irvine 2004). Sections were examined under a compound microscope using differential interference contrast.

One reader (M. Francis) carried out an initial 'familiarisation' read of all spines while knowing the lengths of the specimens. At two later dates, the same reader made additional blind readings of all spines, without knowing the lengths of the specimens. These last two readings were averaged to generate a mean age estimate for each specimen. Ideally, we would have used a second reader to enable estimation of between-reader variability. However, because of the number of species covered by both parts of this project, and the time-consuming nature of the methodology testing in Phase 1 and specimen

preparation, it was only practical to use one reader. Consequently, results presented here are regarded as provisional and they require further corroboration and validation.

Spine readings 1 and 2 were plotted against each other to check for consistency of age estimates. Small sample sizes meant that statistical analyses were not warranted. Growth curves were fitted to the length-at-mean-age data using the R package FSA (version 0.1.7), which fits non-linear curves using the R package nlstools. A two-parameter von Bertalanffy growth model was used because three-parameter models did not converge as a result of the small sample sizes and lack of aged juveniles. Two-parameter models force the growth curve through the known or estimated length at birth instead of estimating a third parameter (the theoretical age at zero length,  $t_0$ ):

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-Kt})$$

where  $L_t$  is the expected length at age  $t$  years,  $L_0$  is the length at birth,  $L_\infty$  is the asymptotic maximum length,  $K$  is the Brody growth coefficient, and  $t$  is the fish age in years. The data were visually inspected for growth differences between males and females, and separate male and female growth curves were fitted for Plunket's shark.

## 2.4 Eye lenses

Eye lenses grow within a fluid/gel filled capsule, in much the same way that fish otoliths grow. Hence, they may continue to grow independently of body size after somatic growth has ceased. This potentially provides a structure from which age estimates can be obtained. Ageing may involve measuring lens weight or diameter and identifying modal peaks and troughs that may represent year classes (Crivelli 1980; Douglas 1987; Siezen 1989; Francis & Ó Maolagáin 2001). An alternative technique, trialled in cephalopods but not, as far as we are aware, in fishes, is to enumerate micro-increments present in the eye lens cores (Baqueiro Cárdenas et al. 2011; Rodríguez-Domínguez et al. 2013). This method relies on the assumption that the lens micro-increments are deposited daily.

Both eye lenses were removed whole by scientists and observers at sea, and stored frozen until preparation. After defrosting, the crystalline eye lens cores were removed, blotted dry, the diameter of one randomly chosen core was measured with a digital micrometer, and selected cores were embedded in epoxy, and then cut in half with a diamond saw. Half lenses were adhered onto microscope slides with thermoplastic resin, and ground and polished until micro-increments became visible under a compound microscope using transmitted light. Because of the large number of micro-increments visible under high magnification, and the fact that it was rarely possible to see increments across the entire lens section, counting a full complement of increments on each section was impractical. Instead, digital images were taken of increments, and average increment width measurements were made at a range of different distances between the focus and the lens margin using calibrated ImageJ software. The number of increments used to estimate average increment width depended on how many were visible at a particular location: it ranged from 6 to 40 increments (mean 16.0), but was usually 10–40 (88% of measurements). The lens cores used for age estimation are hereafter referred to as eye lenses.

Lens-based age estimates were derived by estimating the number of increments laid down between birth and death as follows:

1. A linear regression was fitted to a plot of eye lens diameter versus total length (TL).
2. The linear regression was extrapolated backwards to the length at birth to produce an estimate of the lens diameter at birth. The values of length at birth used were: seal shark 37 cm TL (Section 3.4.1), Owston's dogfish 28 cm TL (Section 3.5.1), longnose velvet dogfish 30 cm TL (Section 3.6.1), and Plunket's shark 30 cm TL (Section 3.7.1).
3. Lens diameter at birth was halved to give the estimated lens radius at birth.
4. Lens diameters at death (i.e., when sampled) were corrected for 'shrinkage' during sectioning (see Section 3.2) and halved to give lens radius at death.
5. Exponential curves were fitted to plots of  $\log(\text{increment width})$  versus  $\log(\text{distance from lens focus})$  and used to predict increment width at any given distance from the focus:

$$\log_{10}(\text{increment width}) = a - b * \exp(-c * (\log_{10}(\text{distance from focus})))$$



6. The number of increments formed between birth and death was estimated by numerical integration of the exponential curve derived in step 5, between the radius at birth and the radius at death, using the R function *integrate*.
7. The age of each fish at death was calculated by dividing the number of increments estimated in step 6 by 365 (assuming one increment is formed per day).

### 3. RESULTS

#### 3.1 Specimens

Large sample sizes of length and weight were available in the research trawl and observer databases for all four shark species, and good sample sizes of reproductive stage were available for seal shark, Owston's dogfish and longnose velvet dogfish (Table 1).

A total of 28 seal sharks, 25 Owston's dogfish, 45 longnose velvet dogfish and 60 Plunket's shark were sampled for hard parts (Table 2). Most sampled animals provided fin spines and/or eye lenses, but a few were missing length or sex data, so slightly fewer animals were available for ageing. Average eye lens increment widths were measured for a subsample of sharks at several locations across the lens (Table 2). Eye lens diameters were measured for larger samples of lenses, and converted into estimated ages using the fitted relationships between increment width and distance from the focus.

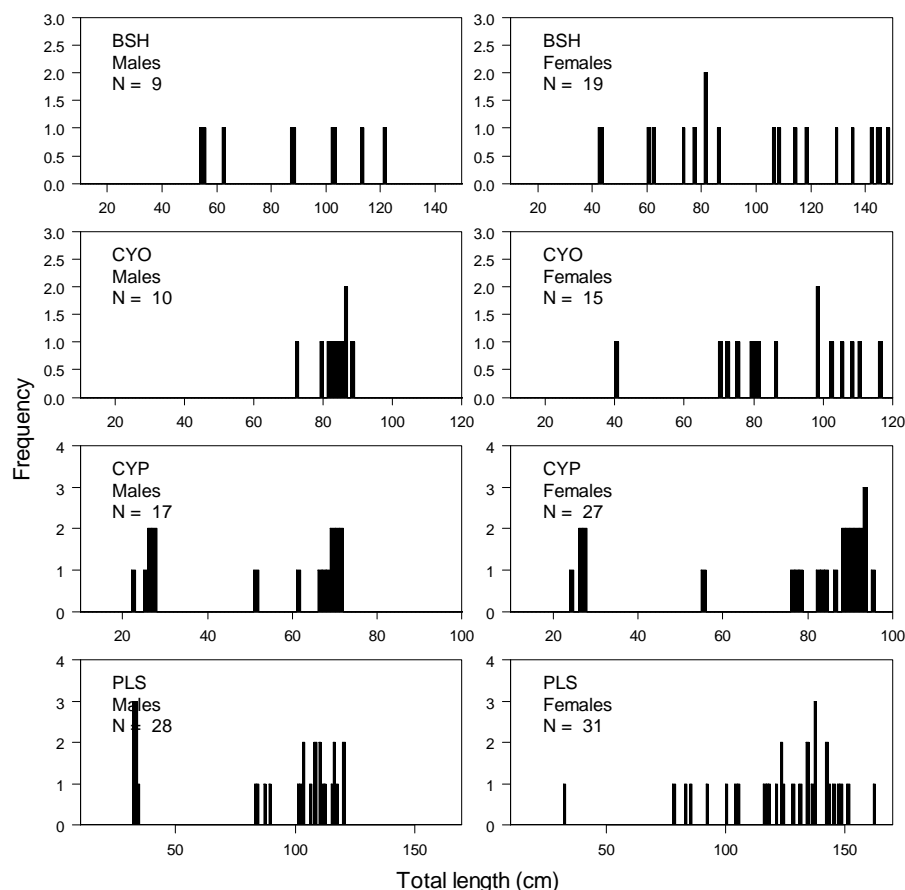
The sampled sharks included both sexes, and generally covered a broad length range that included juveniles and adults; however, most Owston's dogfish were adults (Figure 1). Nevertheless, the small sample sizes mean that our samples are unlikely to be representative of the populations of each species.

**Table 1: Sample sizes for biological data collected for four deepwater shark species.**

Species	Sexed length records	Length-weight records	Maturity stages	Additional reproductive data
Seal shark	1 347	1 085	548	32
Owston's dogfish	3 330	2 297	1 241	97
Longnose velvet dogfish	17 444	10 635	5 124	459
Plunket's shark	599	490	223	13

**Table 2: Number of specimens of four shark species used for ageing. NA = not available.**

	Total specimens	Dorsal fin spines	Eye lens increment	Eye lens diameters	Eye lens ages
			widths		
Seal shark	28	NA	11	28	28
Owston's dogfish	25	8	9	20	20
Longnose velvet dogfish	45	25	12	33	33
Plunket's shark	60	16	15	49	49

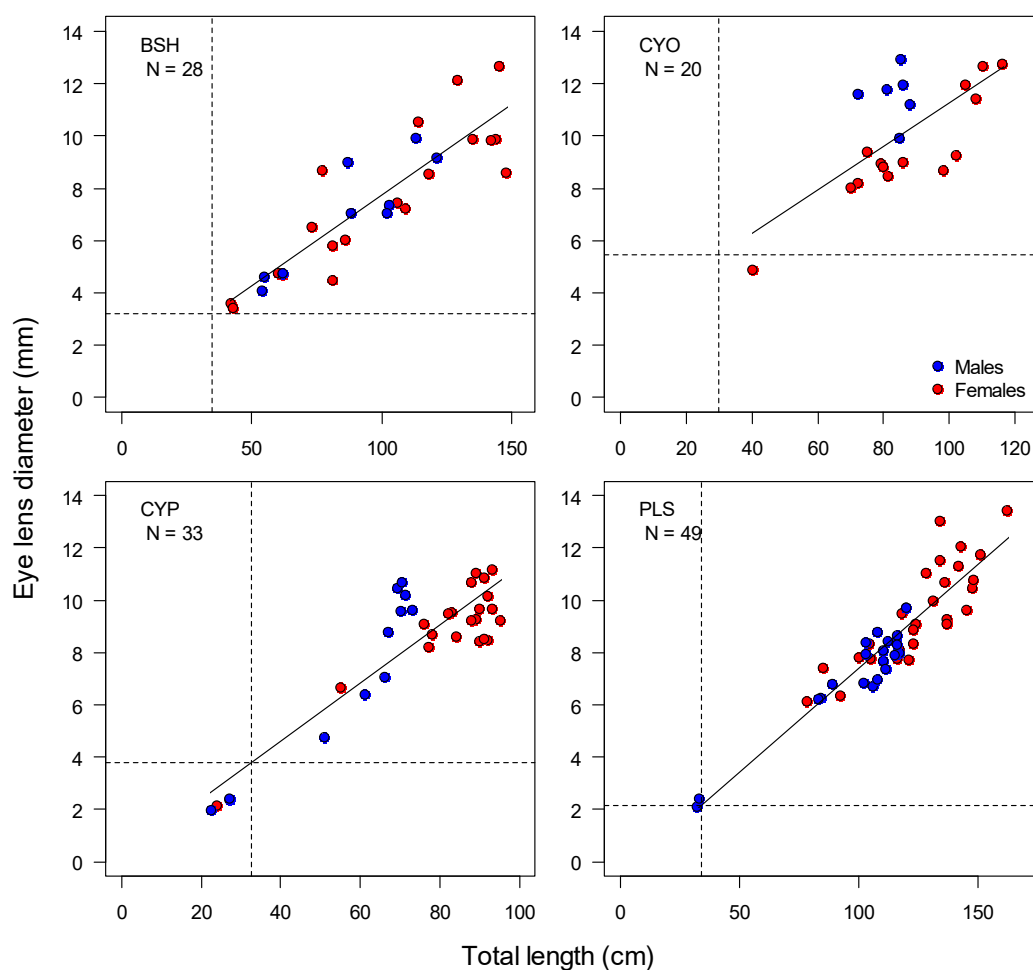


**Figure 1: Length-frequency distributions of the specimens collected for ageing during the present study. BSH, seal shark; CYO, Owston's dogfish; CYP, longnose velvet dogfish; PLS, Plunket's shark. Sample sizes are slightly smaller for longnose velvet dogfish and Plunket's shark than indicated in Table 2 because a few specimens lacked length or sex data.**

### 3.2 Eye lens increments

Fish eye lenses are spherical and are composed of concentric protein layers (Fernald 1985). Lens diameter was positively correlated with TL for all four shark species (Figure 2). There was considerable variability among fish, which for Owston's dogfish and longnose velvet dogfish was related to gender. However, we used a single regression relationship for both sexes combined in subsequent analyses (Table 3). Estimated lens diameters at birth were 1.85–5.27 mm for the four species (Table 3).

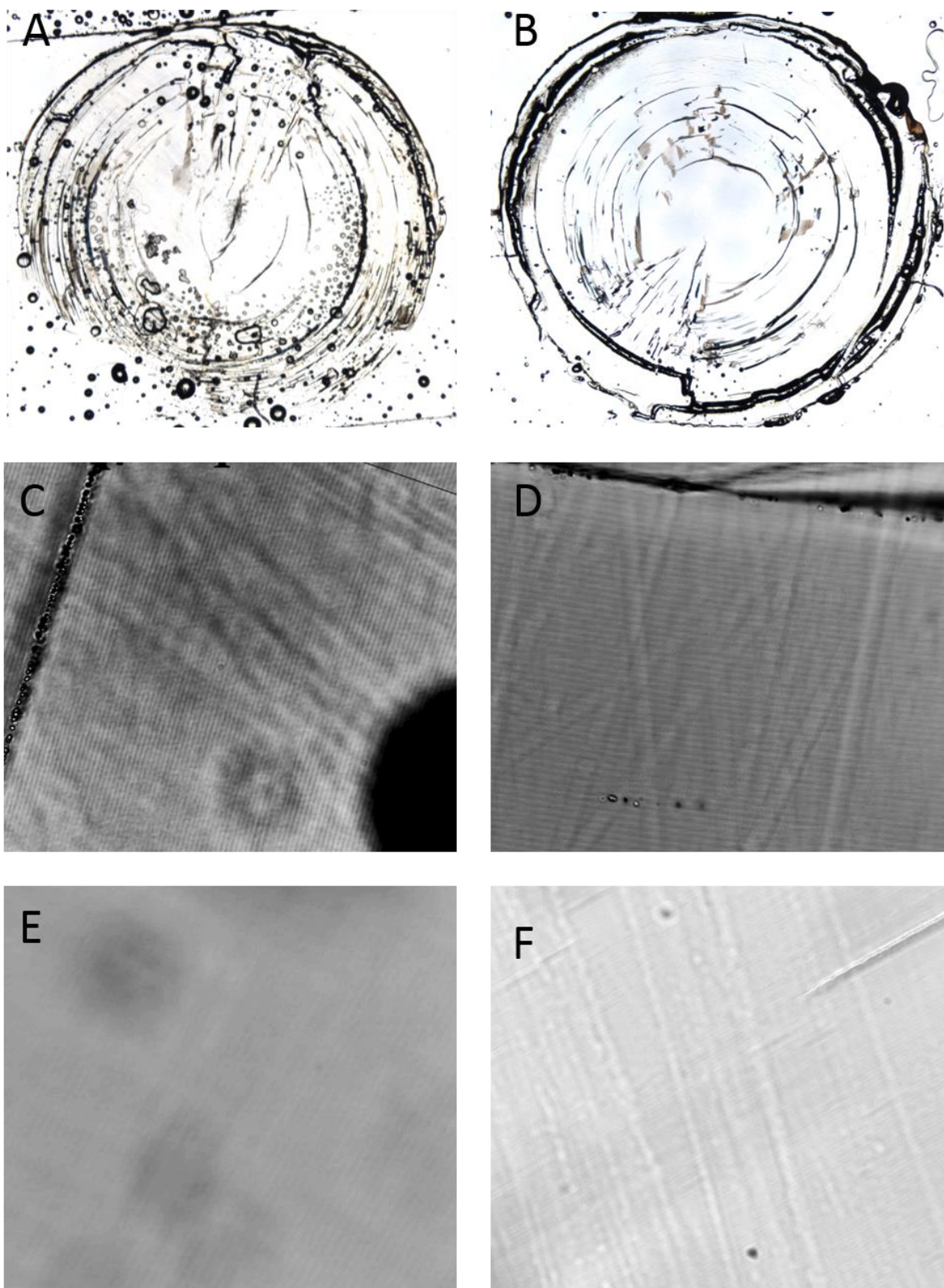
The concentric layers in the eye lens are not strongly bound, and some of the layers 'fractured' apart because of the physical stress involved in sectioning and grinding (Figure 3A–C). Major fracture zones were apparent around the entire lens, but much shorter partial fractures were often only apparent at high magnification. There was no reduction in increment width before or after the fractures (Figure 3F), so they do not appear to represent zones of reduced increment growth that might occur in periods of slow somatic growth, such as during winter. We assumed that no increments were 'lost' at fracture zones. The same is not true for the outer surface of the lens. Before sectioning, the gelatinous outer surface was gently blotted dry to facilitate subsequent embedding in resin. Microscopic examination of the outer edge of sections indicated that the gelatinous surface layer comprised delicate sheets of newly formed or forming micro-increments that were broken or lost during sectioning. We could not estimate the number of micro-increments that were lost this way, but we believe it was a few percent or less of the total number of increments. No correction was made for the resulting underestimation of increment counts.



**Figure 2: Relationship between eye lens diameter and total length.** BSH, seal shark; CYO, Owston's dogfish; CYP, longnose velvet dogfish; PLS, Plunket's shark. The vertical dashed line is the estimated length at birth, and the horizontal dashed line is the eye lens diameter at birth calculated by backwards extrapolation of the regression line. Linear regression parameters are provided in Table 3. CYP and PLS specimens near or to the left of the vertical dashed line were near-term embryos.

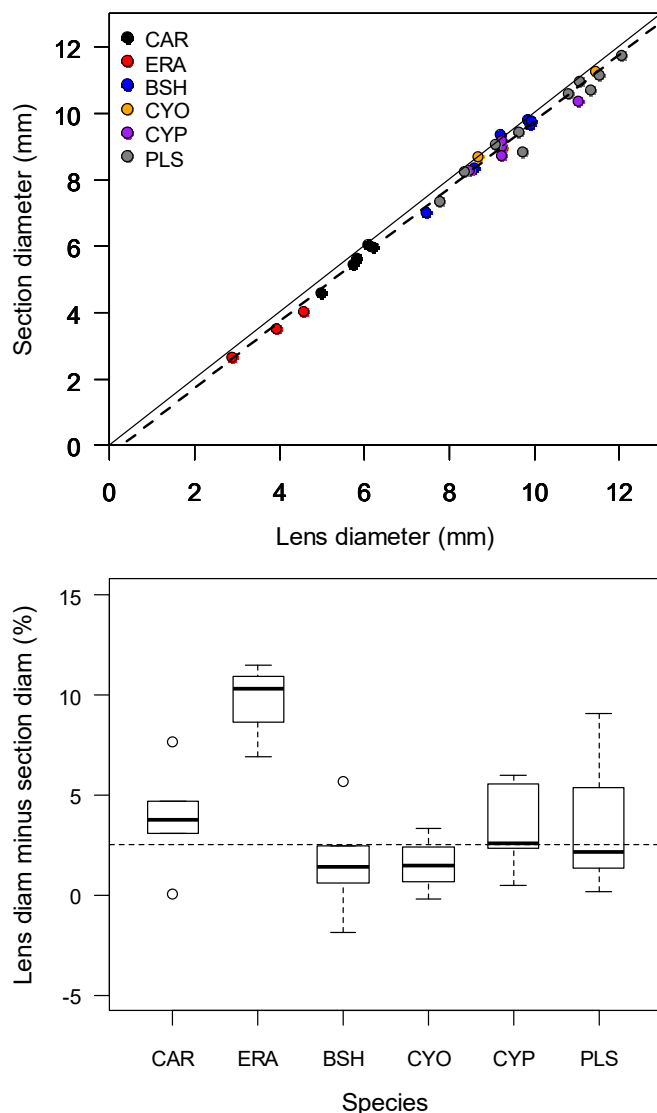
**Table 3: Eye lens core measurements for seal shark (BSH), Owston’s dogfish (CYO), longnose velvet dogfish (CYP) and Plunket’s shark (PLS). Regression parameters are also provided for the linear regressions fitted to the data in Figure 2, and the curves fitted to the data in Figure 5 using the equation  $\log_{10}(\text{increment width}) \sim a - b * \exp(-c * (\log_{10}(\text{distance from focus})))$ .**

	Species			
	BSH	CYO	CYP	PLS
Length at birth (cm)	37	28	30	30
Lens diameter at birth (mm)	3.35	5.27	3.50	1.85
Standard error (mm)	0.50	1.22	0.48	0.44
Lens radius at birth (mm)	1.67	2.64	1.75	0.92
Lens maximum diameter (mm)	12.68	12.92	11.19	13.44
Linear regression parameters from Figure 2				
<i>a</i>	0.780	2.942	0.179	-0.537
<i>b</i>	0.069	0.083	0.111	0.079
<i>R</i> <sup>2</sup>	0.759	0.455	0.790	0.840
Non-linear regression parameters from Figure 5				
<i>a</i>	0.5426	0.7134	0.6418	0.5451
<i>b</i>	0.0001	0.0064	0.0029	0.0005
<i>c</i>	-2.4271	-1.2416	-1.4371	-1.8024
<i>R</i> <sup>2</sup>	0.861	0.810	0.822	0.734



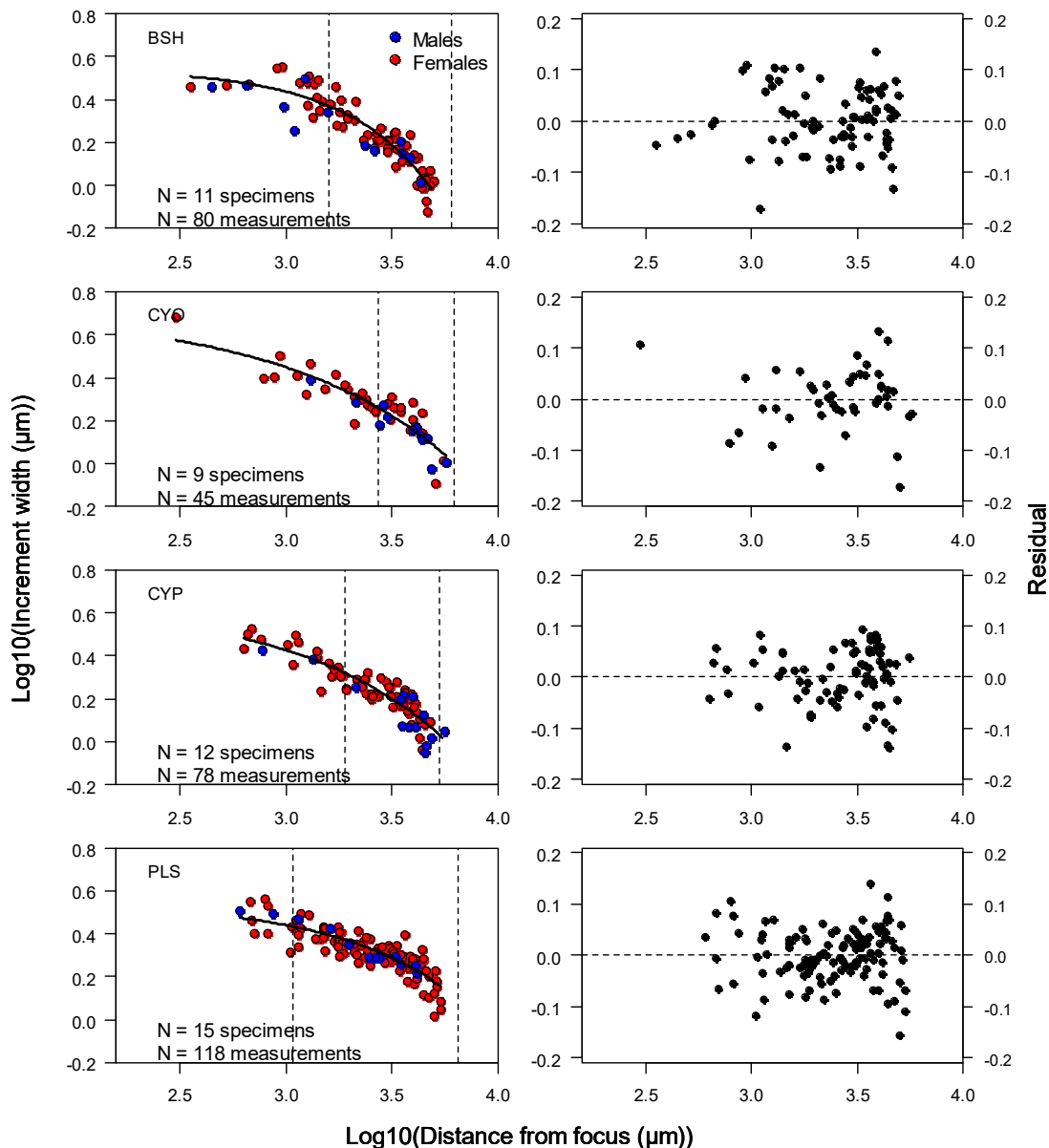
**Figure 3: Whole-lens sections (A, B) and high magnification images of eye lens micro-increments (C–F) in deepwater sharks. A: Seal shark BSH 8, 108 cm TL female, lens diameter 7.2 mm. B: Owston’s dogfish CYO 24, 84 cm TL male, lens diameter 9.9 mm. C: Seal shark BSH 7, 129 cm TL female, increments ca. 1.7  $\mu\text{m}$  wide. D: Plunket’s shark PLS 9, 147 cm TL female, increments ca. 2.3  $\mu\text{m}$  wide. E: Longnose velvet dogfish CYP 19, 76 cm TL female, increments ca. 2.1  $\mu\text{m}$  wide. F: Owston’s dogfish CYO 25, 81 cm TL male, increments ca. 1.4  $\mu\text{m}$  wide.**

Nevertheless, we observed ‘shrinkage’ of the eye lens between the whole and sectioned states (Figure 4). Shrinkage was consistent across the six species analysed in this study and by Francis et al. (2018), and because each species was represented by only a few specimens, and each species had different sized eye lenses, we combined all species when estimating the amount of shrinkage (Figure 4). The slope of the relationship between section diameter and whole-lens diameter was not significantly different from 1 ( $1.001 \pm 0.017$ , estimate  $\pm 1$  standard error), and section diameters were 0.263 mm ( $\pm 0.148$  mm) smaller than whole diameters overall. Whole-lens diameters were subsequently converted to section diameters using this regression for analyses and plots involving comparisons of distances measured on lens sections. Median shrinkage across all species was 2.5%, and the four species considered in this report were all close to that value (Figure 4). Lens shrinkage probably results from a combination of the loss of the newly formed outer layer of increments, and artefacts of the sectioning process.



**Figure 4: Top: Relationship between eye lens core diameter and eye lens section diameter for the same specimens. Bottom: Percentage differences between section diameter and lens diameter. The central black bar is the median, the box spans the first to third quartiles, and the whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box. CAR, carpet shark; ERA, common electric ray; BSH, seal shark; CYO, Owston’s dogfish; CYP, longnose velvet dogfish; PLS, Plunket’s shark. The horizontal dashed line indicates the median shrinkage across all six species (2.5%).**

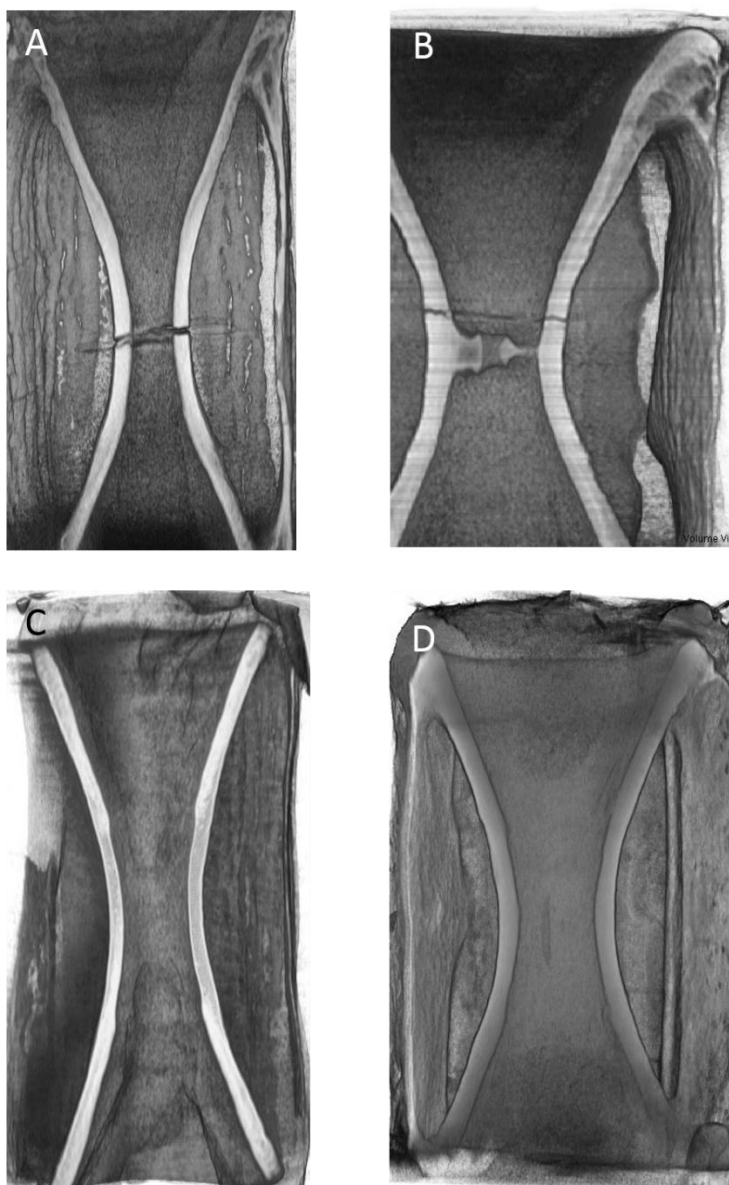
Micro-increment widths declined between the focus and the outer margin (Figure 5). Mean increment width varied between 0.84  $\mu\text{m}$  and 3.55  $\mu\text{m}$  for seal shark, 0.81  $\mu\text{m}$  and 4.79  $\mu\text{m}$  for Owston's dogfish, 0.92  $\mu\text{m}$  and 3.37  $\mu\text{m}$  for longnose velvet dogfish, and 1.04  $\mu\text{m}$  and 3.64  $\mu\text{m}$  for Plunket's shark. The parameters of the exponential curves fitted to the data in Figure 5 are shown in Table 3. Residuals plots showed that the curves fitted the data reasonably well, although there was considerable variability.



**Figure 5: Relationship between average width of eye lens micro-increments and the distance from the lens focus for four deepwater sharks. Non-linear regression curves were fitted to the data using the equation  $\log_{10}(\text{increment width}) \sim a - b * \exp(-c * (\log_{10}(\text{distance from focus})))$ . Residuals are plotted in the right panels, and regression parameters are provided in Table 3. Vertical dashed lines in the left panels indicate the estimated radius of the lens core at birth (left line) and the maximum lens radius observed (right line). BSH, seal shark; CYO, Owston's dogfish; CYP, longnose velvet dogfish; PLS, Plunket's shark. The distance from the focus of one longnose velvet dogfish measurement slightly exceeded the maximum lens radius because of the use of different measurement techniques: the distance from the focus was measured on a section under a microscope, and the lens radius was measured on a whole-lens core with callipers.**

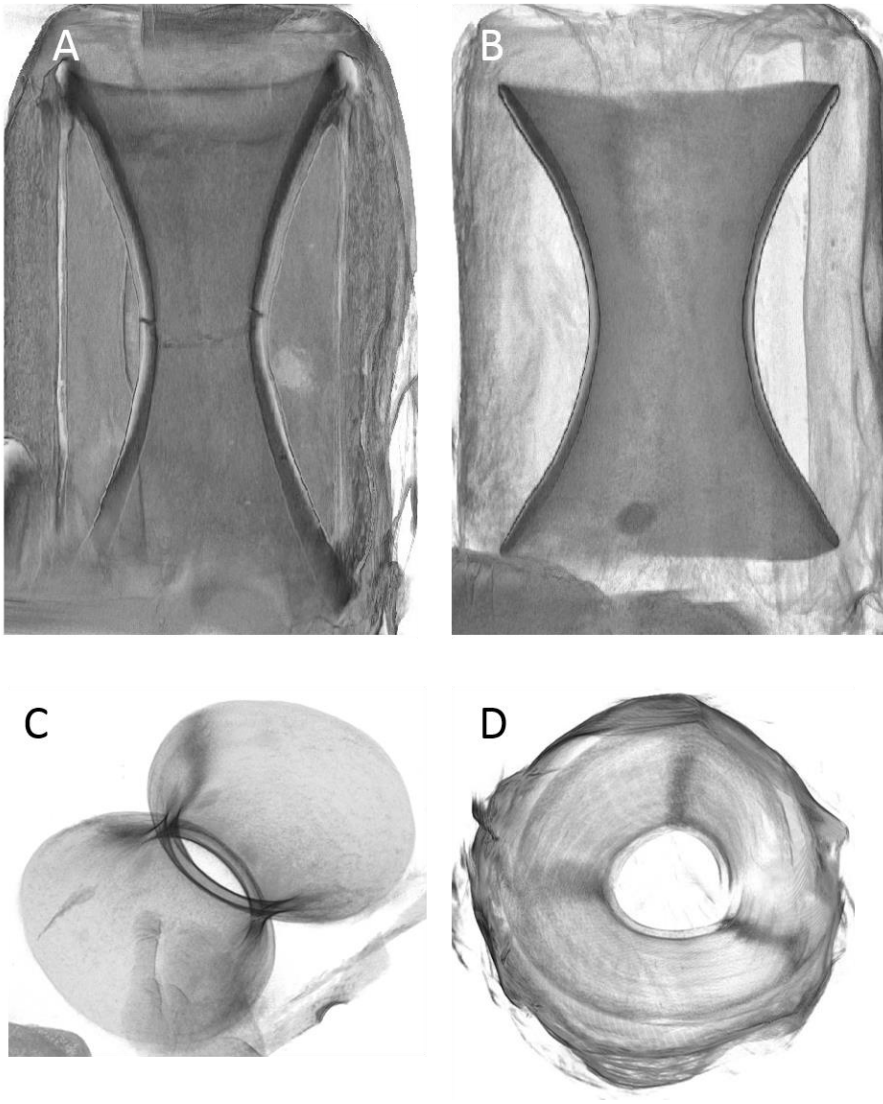
### 3.3 Micro-CT scans

Micro-CT scans of vertebrae from the four deepwater shark species are shown in Figures 6–7. Growth bands were not visible in most specimens, but there were a few exceptions. Seal sharks sometimes exhibited lines in the corpus calcareum that may represent growth bands (Figure 6B, top-right corner), and wavy lines in the intermedialia, whose significance is unknown (Figure 6A, left and right sides of image; Figures 6B and C, right side of images). Bands were rarely visible in the other species, although indistinct bands were sometimes visible on the centrum cone of Plunket’s sharks when viewed from the focus (Figure 7D). Nevertheless, micro-CT imaging has utility in revealing the structure of hard parts and the presence or absence of growth bands in preliminary studies using small samples of animals. The banding pattern seen in seal shark vertebrae warrants further investigation to determine whether the bands are related to age.



**Figure 6: Micro-CT scans of vertebral centra. A: Seal shark BSH 6, 118 cm TL female. B: Seal shark BSH 7, 129 cm TL female. C: Seal shark BSH 8, 108 cm TL female. D: Owston’s dogfish CYO 24, 84 cm TL male.**





**Figure 7: Micro-CT scans of vertebral centra. A: Longnose velvet dogfish CYP 18, 90 cm TL female. B: Plunket's shark PLS 13, 92 cm TL female. C: Plunket's shark PLS 10, 85 cm TL female. D: Plunket's shark PLS 11, 104 cm TL female.**

### 3.4 Seal shark (BSH)

#### 3.4.1 Introduction

This species has a global distribution, occurring in the Atlantic, western Mediterranean, Pacific and Indian oceans. It is widespread around New Zealand, from North Cape as far south as the Campbell Plateau, occurring both in midwater and demersal from 300 to 1000 m (Last & Stevens 2009; McMillan et al. 2011b; Roberts et al. 2015). There are reports of this species being caught in shallow waters from 20 to 90 m on the continental shelf of Europe and Georges Bank (Castro 2011), and in New Zealand it is reported from surface longlines over deepwater, and set nets on the shelf (MPI Observer Database).

Several studies of the biology of this species have been conducted from populations in the eastern Atlantic and Mediterranean (Appendix 2). Around the Azores, da Silva (1988) sampled 2753 individuals from both handlines (mainly larger, adult females) and nets (mainly adult males). The length range was 98–132 cm for males, and 119–162 cm for females. The author noted the absence of juveniles, despite smaller hook sizes used in the fishery, proposing that the nurseries were in deeper or unexplored waters. Of the 67 females examined (TL = 123–156 cm), 87% were ‘ovulated’ (i.e., large, yolked eggs were found in the ovary), had eggs or embryos in the uterus, or were recently post-partum. The remaining individuals were considered to be mature but resting. The number of eggs per female was 10–18, litter size was 10–14, and a gestation period of two years was estimated, with a birth size of 42 cm.

Other reports have estimated a much smaller birth size of 30 cm (Bigelow & Schroeder 1948), with free-swimming specimens reported from as small as 32 cm in the western Mediterranean (Capapé et al. 2008), 36 cm off Southern Africa (Bass et al. 1976), and 39–46 cm off the west coast of Ireland (Henderson et al. 2003) and Scotland (Neat et al. 2015).

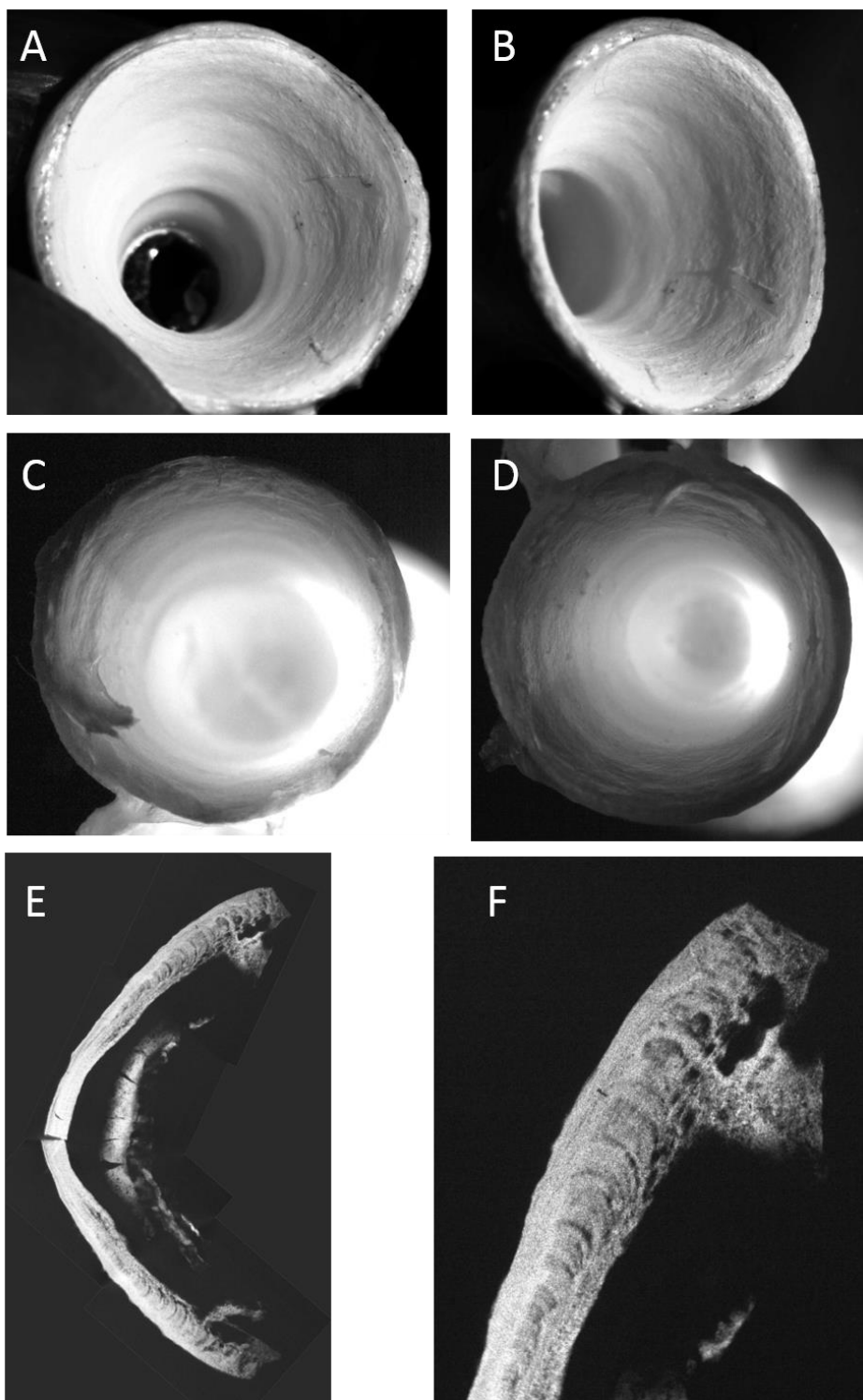
Reported litter sizes are 1–16 pups. Litters from the Mediterranean are usually around 6–8 pups (Tortonese 1956; Bini 1976; Bauchot 1987; Capapé et al. 2008), with 7 pups reported from a 136 cm female from the Bay of Biscay (Quéro et al. 1987) and 15 from Taiwan (Chen 1963). Bass et al. (1976) found no pregnant females from South African waters, but reported ovarian egg counts of 10–20 with diameters of 70–90 mm. Several of these studies found evidence of seasonality in the reproductive cycle. Length at maturity has been estimated as 77–121 cm for males and 117–159 cm for females (Bass et al. 1976; Bauchot 1987), although mature females as small as 96 cm have been observed in the Adriatic (Blasdale et al. 2009).

In Australia, Daley et al. (2002) noted that catches around Tasmania were dominated by juveniles, but adult males up to 117 cm and females up to 151 cm were caught there and in New South Wales waters. The size range of mature males was 113–117 cm, and 127–151 cm for females. The largest immature male was 109 cm. Four pregnant females were collected with litter sizes ranging from 7–11, with an average of 9. Embryo size was measured from 38–43 cm, with neonates found in catches measured at 39–42 cm. The authors concluded a size at birth of 40 cm for populations around Australia. Both pregnant and resting females had resting ovaries with small eggs (3–8 mm), suggesting a non-continuous breeding cycle.

The maximum reported size for this species is 170–180 cm, based on two historic European records (Castro 2011), but most recent studies, including this one, have found a maximum size of 150–160 cm.

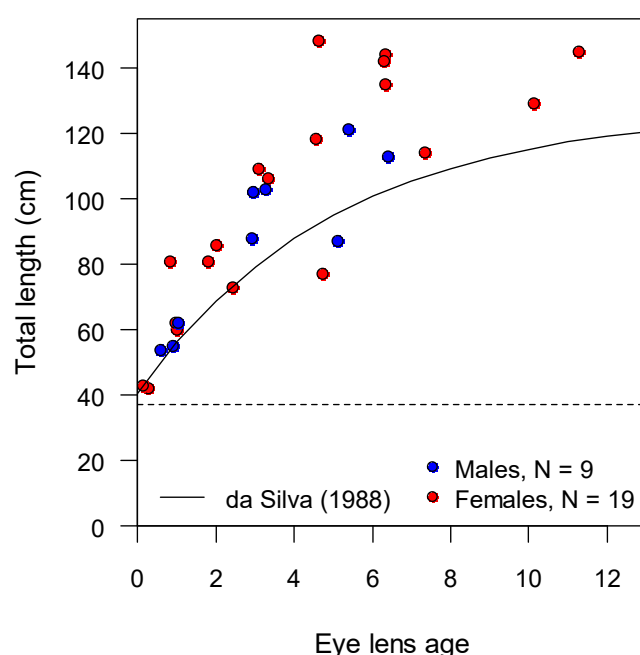
#### 3.4.2 Age and growth

Some seal shark vertebrae displayed bands on the surface of their centra cones when viewed under reflected and transmitted white light (Figure 8A–D). Faint bands were also occasionally visible in the corpus calcareum in X-rayed thick sections (Figure 8E–F). However, band patterns were inconsistent both within and between specimens, and between whole specimens and X-rayed sections, and we could not confidently age seal sharks from their vertebrae. However, the band patterns show some promise, and an ageing protocol using seal shark vertebrae could potentially be developed with further experimentation.



**Figure 8: Images of whole seal shark vertebrae viewed under reflected and transmitted white light (A–D), and thick sectioned vertebrae that were X-rayed (E–F). A, B: BSH 8, 108 cm TL female. C: BSH 49\_2004, 74 cm TL female. D: BSH 61\_2004, 136 cm TL female. E, F: BSH 14\_2004, 143 cm TL female. F is an enlarged image of the upper part of E.**

Eye lens age estimates were positively correlated with TL, and there was no apparent difference in the relationship between the two sexes (Figure 9). Eye lens age estimates were routinely much lower than ages derived from other hard parts (spines, vertebrae) in other species we have examined and the former may not be a good indicator of age (see Section 4: Discussion). The only other estimate of growth for seal shark of which we are aware came from modal decomposition of the lengths of 1005 male sharks caught by ‘bottom net’ (presumably set net) in the Azores Islands (da Silva 1988). The growth curve from that study suggested slower growth than was implied by our eye lens age estimates (Figure 9). However, the Azores growth curve may itself have overestimated the actual growth rate because modal decomposition methods tend to underestimate the number of modes present, because modes tend to merge in older fish. Furthermore, the Azores dataset contained no juveniles under about 100 cm TL to constrain the early part of the growth curve and allow the determination of the true ages of the sharks in the identified modes (da Silva 1988).

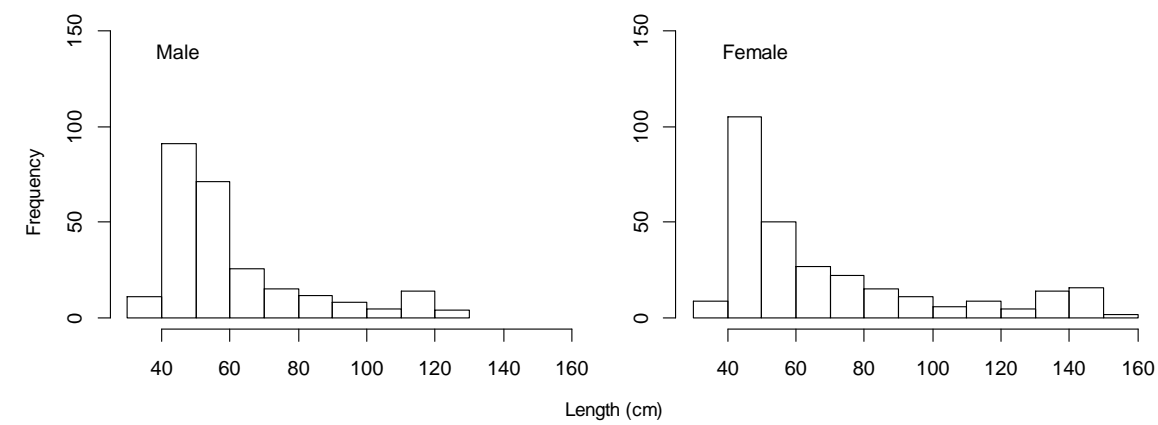


**Figure 9: Plot of shark length versus eye lens growth estimates for seal shark. The dashed line is the estimated length at birth. The solid line shows a growth curve based on length-frequency modal analysis of male seal sharks from the Azores Islands (da Silva 1988).**

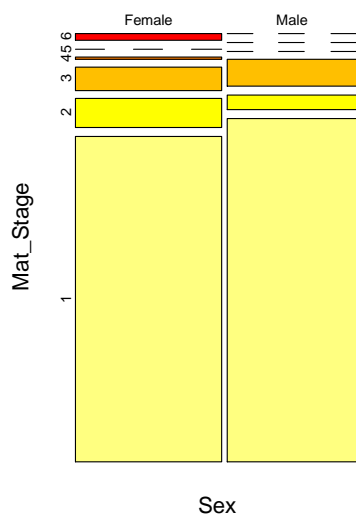
### 3.4.3 Reproduction

Seal shark reproductive data from the 1985–86 *Wanaka* research trawl survey around North Island were reported by King and Clark (1987). In a sample of 134 sharks, they recorded mature males of 95–129 cm TL, and mature females of 132–145 cm, with the latter having an average of 12 ovarian eggs. More recent data from the research trawl database provided a much larger sample, having biological data (sex and/or weight) for 1098 sharks. The length ranges of males and females were 35–126 cm and 37–153 cm, respectively (Figure 10). For both sexes, there was a modal peak at 40–50 cm, with a second smaller peak at 110–120 cm for males and 140–150 cm for females. Maturity-stage data were collected for 257 females, and 291 males. Most specimens caught were immature, with only 22 mature females and 18 mature males representing 7–8% of the samples (Figure 11). The length ranges of mature specimens were 81–122 cm and 119–152 cm for males and females, respectively. The largest immature male was 123 cm and the largest immature female was 141 cm. Fifteen females longer than 120 cm were recorded as stage 1 or 2, but they may have been resting mature females. If four females longer than 140 cm are assumed to be mature, the  $L_{50}$  for females was estimated to be 132.6 cm (95% c.i.: 126.8–136.9 cm) (Figure 12). For males, the  $L_{50}$  was estimated to be 108.8 cm (95% c.i.: 102.6–115.9 cm). These size-

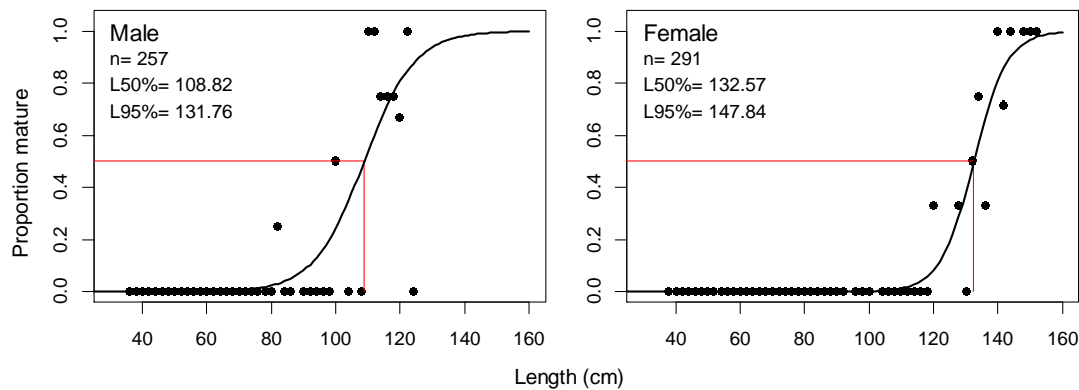
at-maturity estimates from the New Zealand population are similar to those reported by Daley et al. (2002) from Australian waters.



**Figure 10: Length-frequency distribution for male and female seal shark collected from trawl surveys around New Zealand.**



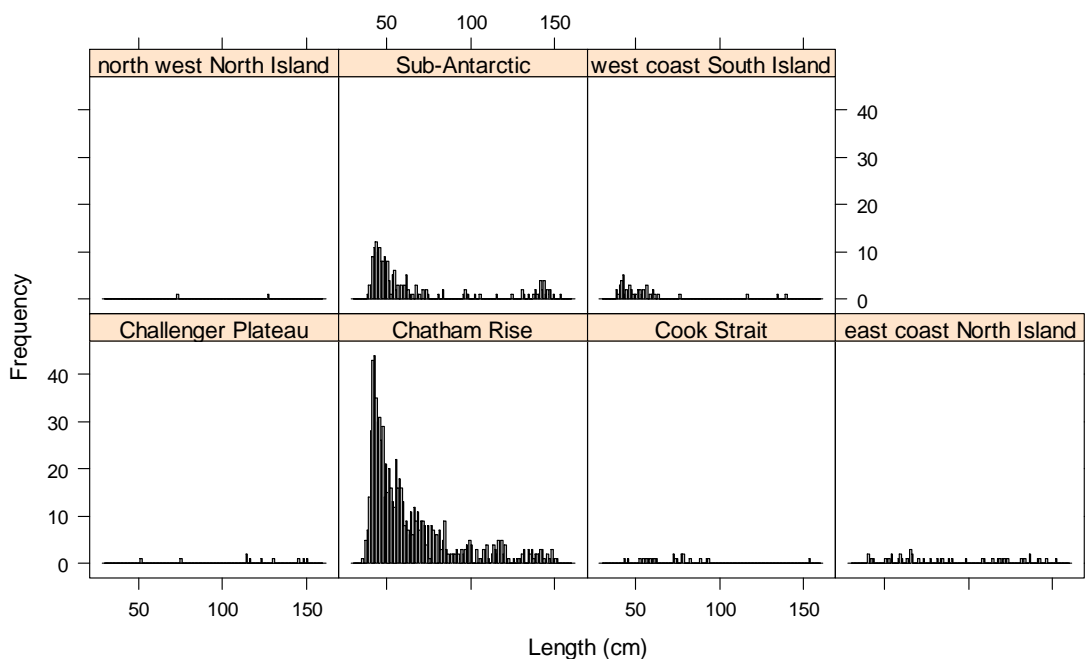
**Figure 11: Proportional distribution of seal shark maturity stages by sex. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**



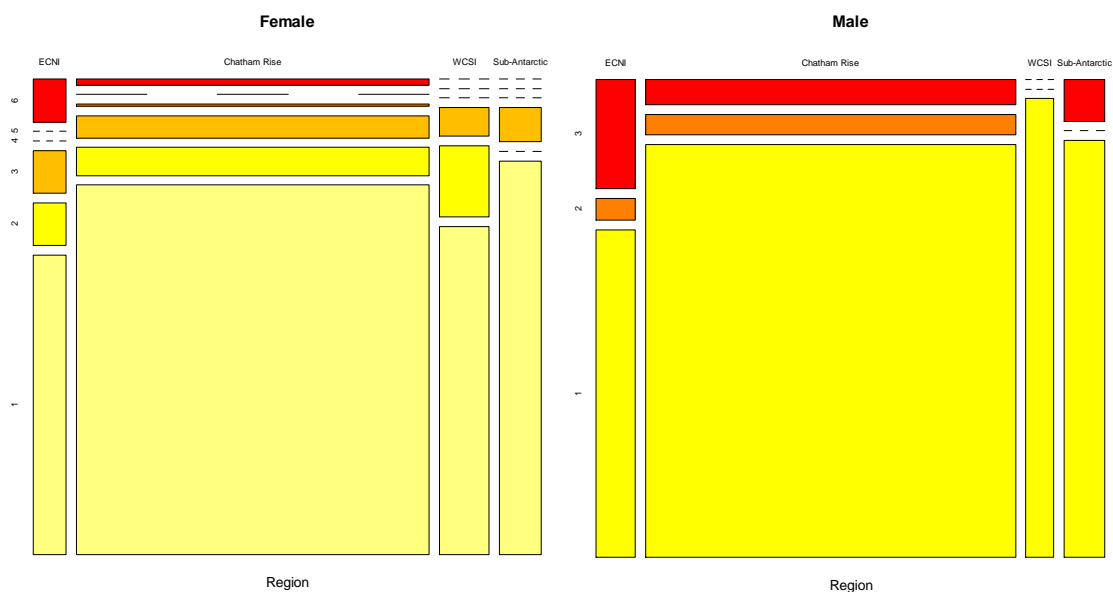
**Figure 12: Length-at-maturity ogives for male (left) and female (right) seal shark. The red line indicates the  $L_{50}$ .**

Most mature females sampled were stage 3, having large yolky eggs ready for ovulation (Figure 11). Only two egg counts were recorded (5 and 23 ovarian ova), with maximum ovum diameter ranging from 29–50 mm ( $n=4$ ). Only one pregnant stage 4 female was recorded from the Chatham Rise, and there were no stage 5 females with uterine embryos. The smallest free-living specimens were 35 cm, and two specimens of about 37–39 cm had unhealed umbilical scars. The length at birth appears to be 35–40 cm, which agrees with the range reported by Daley et al. (2002) from Australia.

Figures 13–14, Table 4 and Appendix 3 summarise the spatial patterns in population structure among the areas sampled. Records of assumed neonates (less than 40 cm TL) came mainly from the northern Chatham Rise, but also from the Sub-Antarctic region and the west coast of the South Island. Immature and mature fish were found in almost all areas sampled; mature males were only absent from the west coast South Island survey. The proportion of mature males and females was highest in the east coast North Island.



**Figure 13: Length-frequency distributions of seal sharks sampled from different regions around New Zealand.**



**Figure 14: Proportional distribution of seal shark maturity stages by sex and region. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**

**Table 4: Size composition and sex ratio (female:male) of seal sharks sampled in different regions.**

Area	Depth range (m)	Male TL (cm)		Female TL (cm)		Sex ratio
		n	Range	n	Range	
North-west North Island	937–984	0		2	74–128	–
East coast North Island	600–1 160	24	42–123	22	40–152	0.9:1
Challenger Plateau	338–1 114	2	52–117	8	76–151	–
Cook Strait	322–514	3	52–72	14	45–153	–
Chatham Rise	363–1 203	322	35–126	458	37–151	1.4:1
West coast South Island	263–871	20	38–117	29	38–139	1.4:1
Sub-Antarctic / Campbell Plateau	425–982	56	41–115	125	38–153	2.2:1

### 3.5 Owston's dogfish (CYO)

#### 3.5.1 Introduction

Owston's dogfish has a global distribution, having been recorded from the central and southern Atlantic, eastern Pacific, southern Japan, eastern Indian Ocean, and southern Australia. It occurs all around New Zealand, from off North Cape, to the Campbell Plateau (Anderson et al. 1998; Last & Stevens 2009; McMillan et al. 2011b; Roberts et al. 2015). This species inhabits continental slopes and seamounts between about 500 m and 1400 m, although they are also frequently caught in the surface-longline fishery for tuna and swordfish to the west of the South Island (McMillan et al. 2011c; Anderson 2013).

The biology of Owston's dogfish (summarised in Appendix 2) was studied from collections from central Japan (Yano & Tanaka 1988). Male TL was 35–88 cm, with the smallest mature male at 67 cm, and  $L_{50}$  estimated as 70–75 cm. Female lengths ranged from 50 to 116 cm, with the smallest mature female at 95 cm and  $L_{50}$  was estimated to be about 100 cm. Counts of mature eggs in ovaries ranged from 20 to 28, with a mean of 25.7 ( $n=19$ ), and litter sizes ranged from 16 to 28, with a mean of 22 ( $n=21$ ). Pregnant females were caught in shallower water (100–300 m), although no females with full-term pups or neonates (estimated to be around 30–35 cm) were recorded, suggesting that pupping grounds may be elsewhere. Sampling was carried out across different months, but no defined breeding season was observed and the authors suggested a reproductive cycle of at least two years.

In Australian waters, Owston's dogfish occurs south of 30°S, from central New South Wales to Shark Bay, Western Australia, including Tasmania (Last & Stevens 2009). In NSW waters, the length ranges of males and females were 28–88 cm and 25–113 cm, respectively, but juveniles less than 70 cm TL dominated catches (Daley et al. 2002). In Tasmania, the sample ( $n=160$ ) comprised mainly adult males (up to 96 cm) and larger females (up to 120 cm), with few smaller fish. Males were estimated to mature around 75 cm (the smallest mature male was 73 cm and largest immature male was 79 cm). Mature females ranged from 82 to 120 cm, with the smallest pregnant female measuring 89 cm and the largest immature female 103 cm. Only two pregnant females were recorded, with litter sizes of 5 and 13. Free-swimming neonates were as small as 25–30 cm, while the maximum embryo size was 32 cm. Daley et al. (2002) observed that reproduction was non-continuous with ovaries in pregnant and spent females having a maximum ovum diameter of 7 mm. Using a smaller sample size from the same area, Irvine (2004) found that the size range of mature males was 69–85 cm and 100–116 cm for females. The smallest shark was 58 cm, and no pregnant females or neonates were found, but a mean ovarian egg count of 12 (range 8–19,  $n=8$ ) was reported.

#### 3.5.2 Age and growth

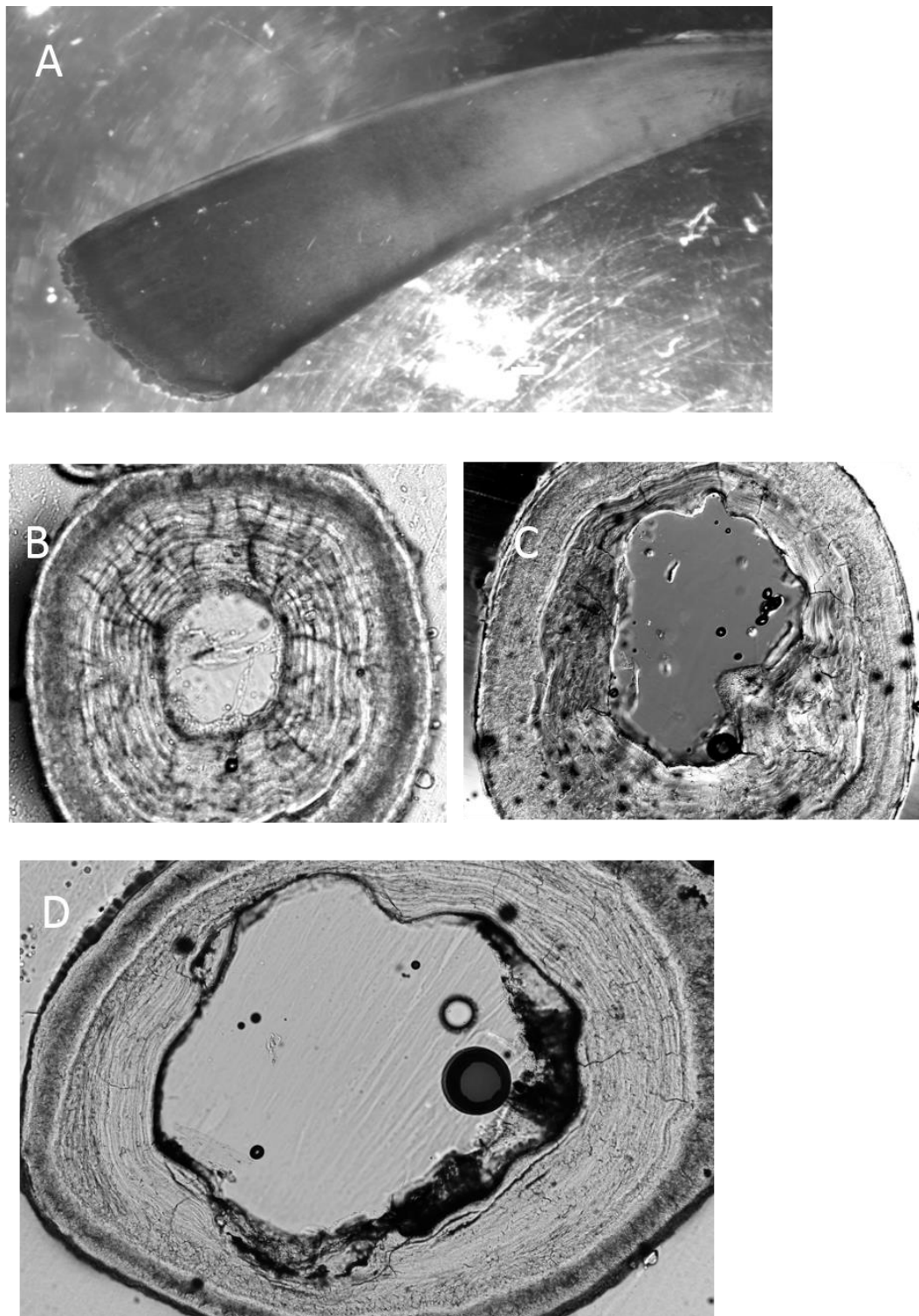
Owston's dogfish spines had no or very faint growth bands on the exterior surface when examined under a variety of lighting conditions, with or without staining (Figure 15A). We therefore used thick sections cut 3–6 mm from the spine tip for counting internal growth bands (Figure 15B–D), and those counts were used as age estimates. These bands were often clear enough to be counted easily, but were sometimes indistinct.

The repeat readings of Owston's dogfish spines produced similar results, although the second reading was greater than the first reading for the three oldest sharks (Figure 16A). Greatest mean ages recorded were 11.5 years for males and 10.0 years for females (Table 5), however our sample size was very small, so these values probably underestimate maximum age. The sample size and length range of specimens were both too small to produce a plausible von Bertalanffy growth curve (Figure 16C), but we provide growth curve parameters in Table 5.

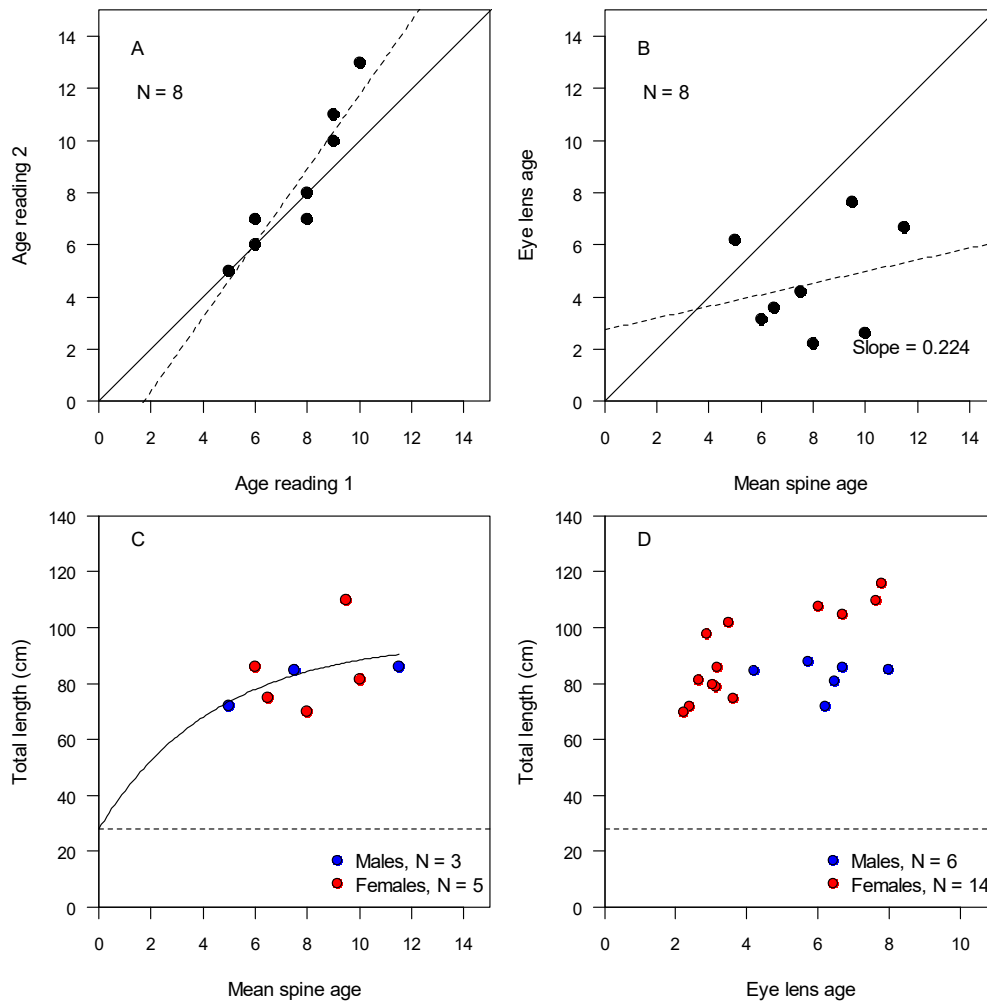
Eye lens age estimates were positively correlated with TL, but there was considerable variability (Figure 16D), and males and females had different relationships. This probably reflects the greater length attained by females than males. Eye lens age estimates were uncorrelated with mean spine age ( $R^2 = -0.1$ ), and there was poor agreement between the two estimates: lens age estimates were much lower than spine band estimates (regression slope = 0.224). If lens micro-increments are formed daily, with



365 comprising one year of growth, then each spine band represents only 0.22 years; conversely, if spine bands are formed annually, micro-increments are formed every 4.5 days.



**Figure 15: Images of stained whole (A) or sectioned (B–D) Owston’s dogfish dorsal fin spines. A: CYO 41, 82 cm TL male. B: CYO 254, 102 cm TL female. C: CYO 255, 98 cm TL female. D: CYO 42, 79 cm TL male.**



**Figure 16: Age and growth estimates for Owston's dogfish. A: Comparison of spine age readings 1 and 2. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. B: Comparison of eye lens age estimate and mean spine age. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. C: Plot of shark length versus mean spine age with fitted von Bertalanffy growth curve. The dashed line is the estimated length at birth. D: Plot of shark length versus eye lens age. The dashed line is the estimated length at birth.**

**Table 5: Growth and maturity estimates for seal shark (BSH), Plunket's shark (PLS), Owston's dogfish (CYO), and longnose velvet dogfish (CYP). Growth parameters for longnose velvet dogfish were estimated separately for the two sexes. The first two rows are the von Bertalanffy growth parameters (no  $t_0$  parameter was estimated because the growth curve was forced through the length at birth).**

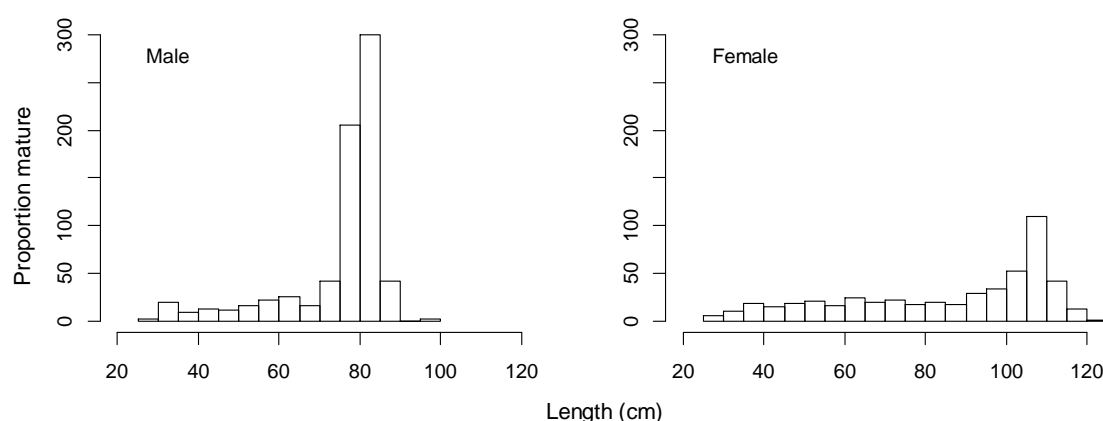
	Species				
	BSH	PLS	CYO	CYP male	CYP female
$L_{inf}$		173.8	95.6	73.6	92.2
$K$		0.024	0.224	0.164	0.170
Maximum age of males (yr)		42.0	11.5	17.0	
Maximum age of females (yr)		53.0	10.0		26.5
Length at 50% maturity males (cm)	108.8	110.0	71.0	65.0	
Length at 50% maturity females (cm)	132.6	130.0	107.0		87.0
Age at 50% maturity males (yr)		33.2	4.5	9.9	
Age at 50% maturity females (yr)		48.6	NA		14.7

### 3.5.3 Reproduction

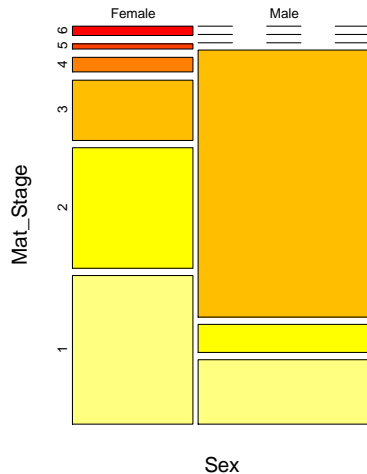
Owston's dogfish reproductive data from the 1985–86 *Wanaka* research trawl survey around North Island were reported by King and Clark (1987). They reported mature males from 71 to 93 cm, mature females from 98 to 121 cm, and an average of 17 ovarian eggs in mature females. More recent data from fisheries trawl surveys provided 2297 records of sexed Owston's dogfish, with 1241 of these assessed for maturity. The length ranges were 28–125 cm ( $n=1327$ ) and 26–148 cm ( $n=970$ ) for males and females, respectively. Some individuals less than 30 cm may have been unborn embryos aborted during capture. It is likely that a few large sharks in the database (more than 100 cm for 10 males and more than 125 cm for four females) were mistakes or species misidentifications, and they were excluded.

Figure 17 shows the adjusted length-frequency distributions for males and females from all surveyed regions. The male population was dominated by a modal peak at 75–85 cm, representing mature adults, which made up 75% of those that were staged for maturity (Figure 18). Juveniles made up 17% of the male sample. The female modal peak was 100–110 cm (Figure 17). From those staged for maturity, there was a more even spread between juveniles (41.5%), maturing (32.5%) and mature individuals (26%) (Figure 18). From a sample size of 727 sharks, the male  $L_{50}$  was estimated as 71.6 cm (95% c.i.: 69.6–72.3 cm) (Figure 19). The smallest mature male was 61 cm, and the largest immature male was 95 cm. The female  $L_{50}$  was estimated as 106.3 cm (95% c.i.: 104.8–107.9 cm,  $n=514$ ), which is larger than reported elsewhere, but the size range of mature females was broad (85–122 cm). The largest immature female recorded was 118 cm. It is possible that at least some of the larger females (longer than 110 cm) may have been mature but resting, and mistakenly classed as maturing (stage 2).

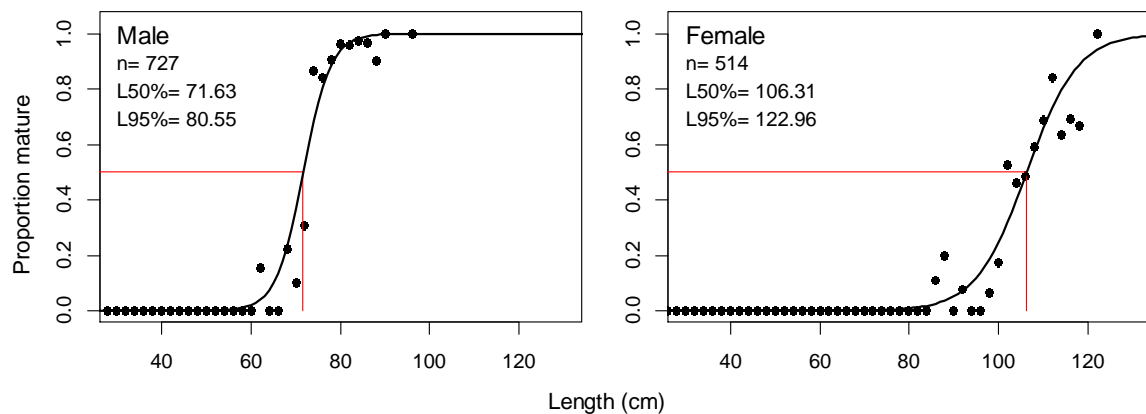
Based on a length at maturity of 71 cm TL, males are estimated to reach maturity at 4.5 years (Table 5). The female age at maturity is undefined as the female length at maturity of 107 cm TL exceeds the value of  $L_{\infty}$  in the fitted von Bertalanffy growth curve.



**Figure 17: Length-frequency distribution for male and female Owston's dogfish collected from trawl surveys around New Zealand.**

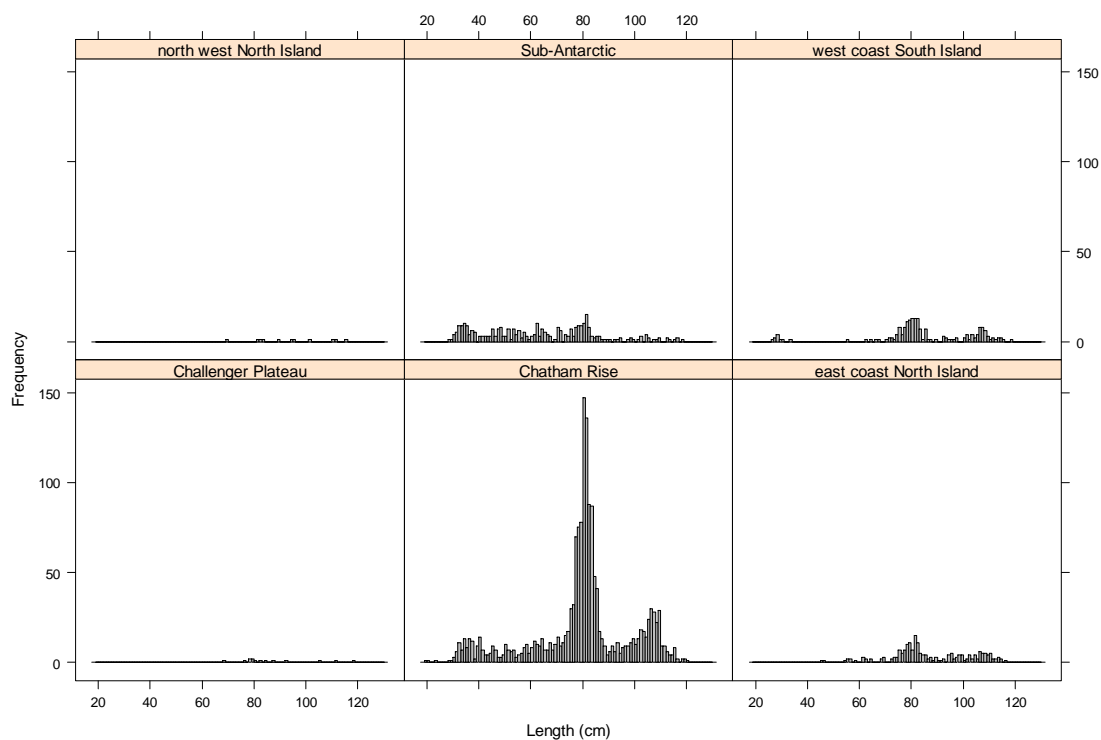


**Figure 18: Proportional distribution of Owston's dogfish maturity stages by sex. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**

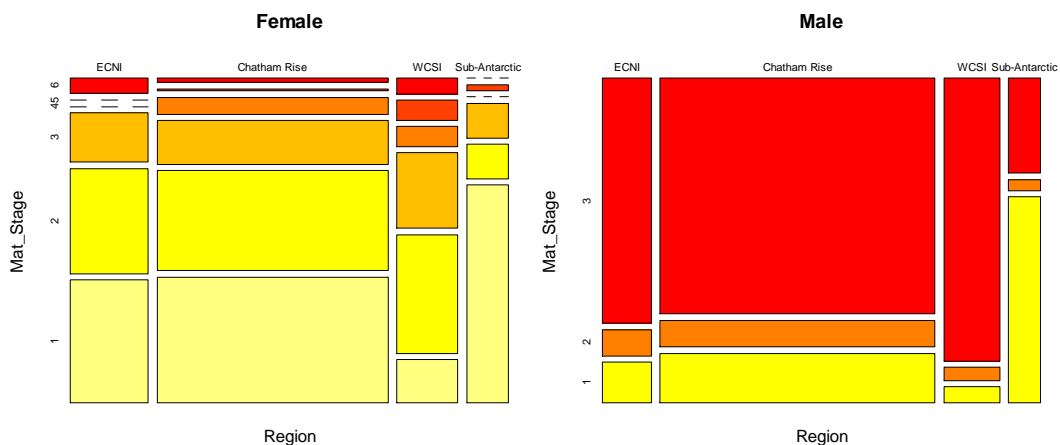


**Figure 19: Length-at-maturity ogives for male (left) and female (right) Owston's dogfish. The red line indicates the  $L_{50}$ .**

At a regional level, mature males were particularly abundant on the Chatham Rise and the west coast South Island, where they outnumbered females in the sample (Figures 20–21, Table 6, Appendix 3). Although neonates and juveniles were found in all regions sampled, they dominated the Sub-Antarctic sample, while mature females were much less commonly caught there. Pregnant females were recorded from the northern Chatham Rise, west coast of the South Island, and the Sub-Antarctic, and made up 5.6% of females overall and 22% of mature females. The average number of ova in the ovaries was 19 (range 7–30,  $n=25$ ), with litter sizes ranging from 7 to 20, with an average of 15 ( $n=6$ ). Information on embryo lengths was limited to four litters from a recent survey on the west coast of the South Island. Lengths ranged from approximately 10 cm and 16–17 cm for two litters, up to 29–31 cm from the other two litters. All embryos had visible egg sacs. In the *trawl* database, assumed free-swimming individuals were as small as 26 cm, but these may have been pups aborted during capture.



**Figure 20: Length-frequency distributions of Owston's dogfish sampled from different regions around New Zealand.**



**Figure 21: Proportional distribution of Owston's dogfish maturity stages by sex and region. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**

**Table 6: Size composition and sex ratio (female:male) of Owston's dogfish sampled in different regions.**

Area	Depth range (m)	Male TL (cm)		Female TL (cm)		Sex ratio
		n	Range	n	Range	
North west North Island	923–1 180	6	69–96	5	95–116	0.8:1
East coast North Island	600–1 487	92	45–98	108	47–116	1.2:1
Challenger Plateau	733–1 114	3	68–61	3	106–119	1:1
Chatham Rise	448–1 285	948	31–94	617	28–120	0.6:1
West coast South Island	715–979	113	28–90	75	26–122	0.7:1
Sub-Antarctic / Campbell Plateau	622–922	159	30–87	159	28–118	1:1

## 3.6 Longnose velvet dogfish (CYP)

### 3.6.1 Introduction

The longnose velvet dogfish is globally widespread in the Atlantic, Pacific and Indian Oceans (Last & Stevens 2009; Ebert et al. 2013). In New Zealand waters, it ranges from the Norfolk Ridge in the north to the Campbell Plateau in the south, including Chatham Rise and Challenger Plateau (Anderson et al. 1998; McMillan et al. 2011a). It has been recorded in New Zealand from 100–1450 m, but is most commonly caught between 700–1200 m (Anderson et al. 1998).

The biology of longnose velvet dogfish is summarised in Appendix 2. Daley et al. (2002) reported that the longnose velvet dogfish population off NSW was dominated by juveniles with a peak around 30–50 cm and very few over 60 cm TL. In contrast, research and commercial catch data from Tasmania showed two peaks representing adult males (around 75 cm) and adult females (around 90 cm) with few juveniles. Daley et al. (2002) estimated that females matured at 82 cm and males at 62 cm. Irvine and Irvine et al. (2004; 2006) used commercial catches from south-eastern Australia and Tasmania to estimate male maturity at 6–11.5 years with an  $L_{50}$  of 64 cm, and female maturity at 17–22 years with an  $L_{50}$  of 84 cm.

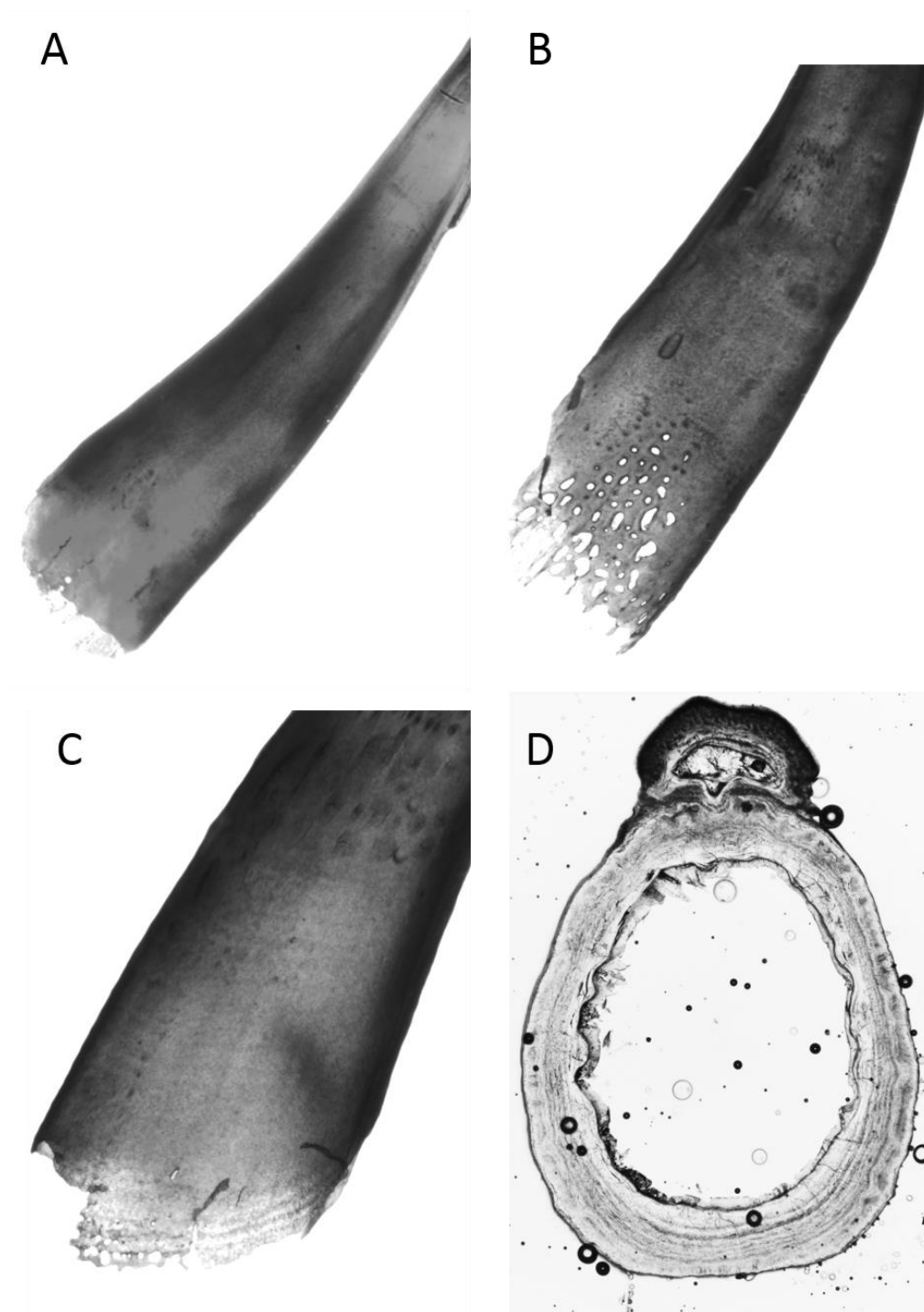
Several studies in the north-east Atlantic, off the coast of Scotland and Ireland, have reported that maturity is reached at smaller sizes. Clarke et al. (2001) reported  $L_{50}$  for females as 68 cm ( $n=331$ ) and for males as 52 cm ( $n=137$ ), while Moore et al. (2013) reported 75 cm ( $n=100$ ) and 57 cm ( $n=73$ ), respectively. The maximum TL reported by Clarke et al. (2001) was similar to that in the Southern Hemisphere (99 cm for females and 92 cm for males). Moore et al. (2013) reported lower values (87 cm and 76 cm for females and males, respectively), but they came from a small sample from one survey. However, the length distributions in both north-east Atlantic studies were similar, and were dominated by adults, with few juveniles found; the female modal peak was around 80 cm, and the male modal peak around 63 cm, with few specimens reported above 90 cm.

### 3.6.2 Age and growth

Longnose velvet dogfish spines had highly variable degrees of external banding patterns. Many had no visible bands (Figure 22A), some had faint indistinct bands (Figure 22B), and a few had faint but distinct bands on the lower two-thirds of the spine but none on the upper one-third (Figure 22C). We were therefore unable to use spine bands for ageing this species. Instead, we used thick sections cut 3–6 mm from the spine tip for counting internal growth bands (Figure 22D), and those counts were used as age estimates. These bands were often clear enough to be counted easily, but were sometimes indistinct.

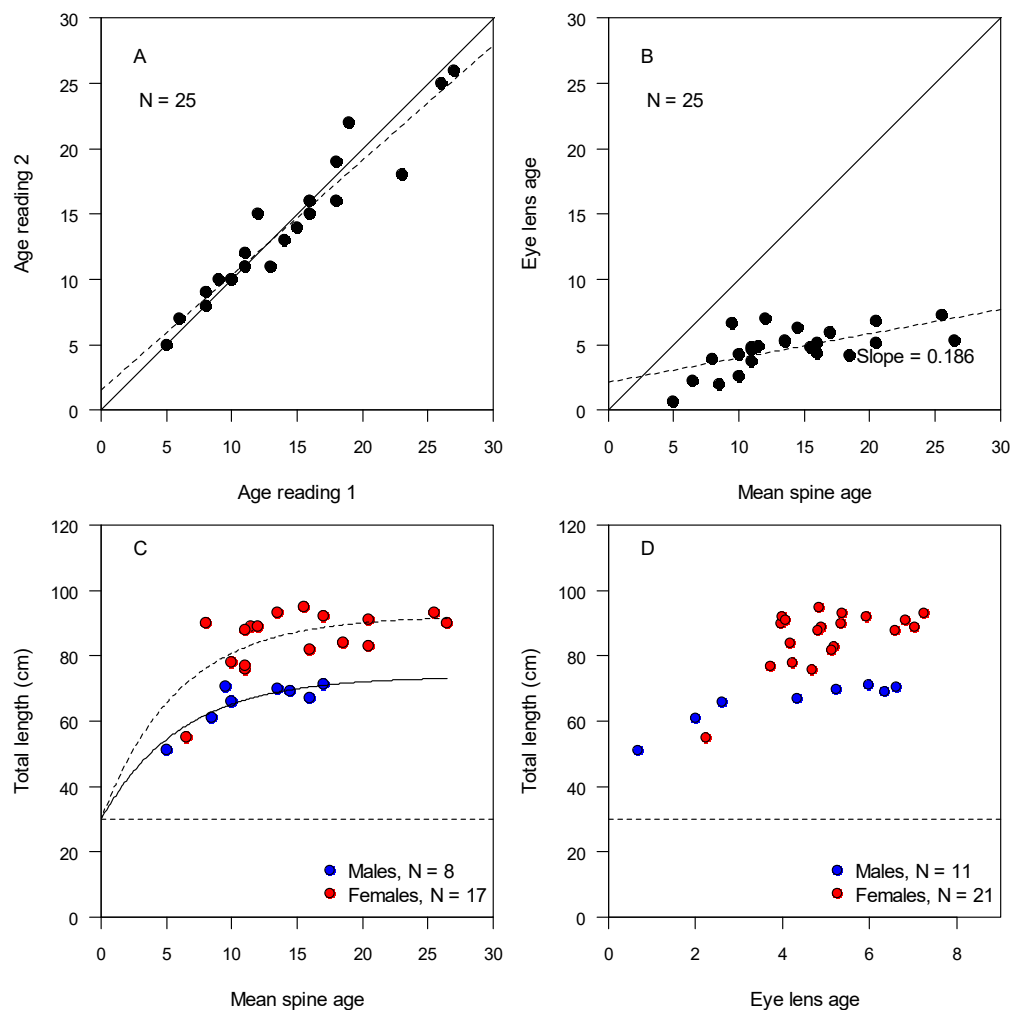
The repeat readings of longnose velvet dogfish spines produced similar results, indicating good count repeatability (Figure 23A). Greatest mean ages recorded were 17.0 years for males and 26.5 years for females (Table 5), however our sample size was small, so these values probably underestimate maximum age. There was a clear divergence between males and females in the relationship between length and spine age, so we fitted separate von Bertalanffy growth curves by sex (Figure 23C) and provide growth parameters by sex in Table 5.

Eye lens age estimates were positively correlated with TL (Figure 23D), and males and females had different relationships. This probably reflects the greater length attained by females than males. Eye lens age estimates were correlated with mean spine age ( $R^2 = 0.36$ , Figure 23B), but there was poor agreement between the two estimates: lens age estimates were much lower than spine band estimates (regression slope = 0.186). If lens micro-increments are formed daily, with 365 comprising one year of growth, then each spine band represents only 0.19 years; conversely, if spine bands are formed annually, micro-increments are formed on average every 5.4 days.



**Figure 22: Images of stained whole (A–C) or sectioned (D) longnose velvet dogfish dorsal fin spines. A: CYP 272, 61 cm TL male. B, D: CYP 37, 86 cm TL female. C: CYP 34, 68 cm TL male.**





**Figure 23: Age and growth estimates for longnose velvet dogfish. A: Comparison of spine age readings 1 and 2. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. B: Comparison of eye lens age estimate and mean spine age. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. C: Plot of shark length versus mean spine age with fitted von Bertalanffy growth curves for males and females. The dashed line is the estimated length at birth. D: Plot of shark length versus eye lens age. The dashed line is the estimated length at birth.**

### 3.6.3 Reproduction

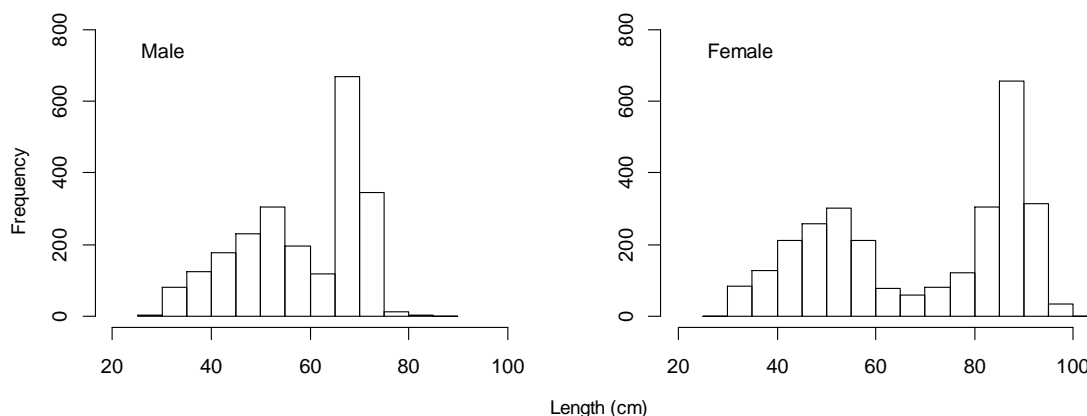
Over 5000 maturity records have been collected since 2009 on research trawl surveys of the Chatham Rise, Campbell Plateau (Sub-Antarctic), west coast South Island, and east coast North Island, as well as some limited sampling during a fishing industry orange roughy survey to west Northland, and a hoki survey in Cook Strait.

Juveniles accounted for nearly half of the female sample, sub-adults 26%, and mature adults 27% (Figures 24 and 25). Fewer than 300 mature females (9% of the total female sample, 37% of mature females) were gravid, with only 58 having visible embryos (stage 5) (Figure 25). Just over half of the males were juveniles, 10% sub-adults, and nearly 40% mature males (Figures 24 and 25).

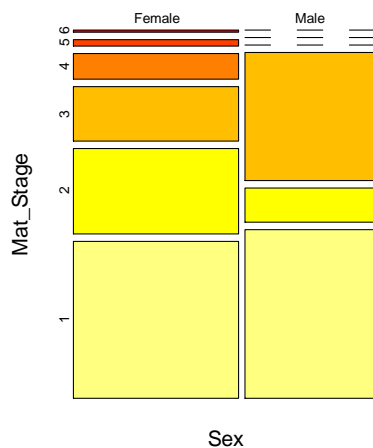
Female lengths ranged from 30 to 102 cm, and males from 29 to 82 cm (Figure 24). Length-at-maturity ogives for female longnose velvet dogfish were fitted for all records of maturity, and for a subset of the records for which additional morphological data had been collected to verify maturity stage. Both datasets provided similar estimates of  $L_{50}$ : 86 cm (95% c.i.: 84.9–86.7 cm) for the subset, or 87 cm (95% c.i.: 86.5–87.4 cm) for the larger dataset presented in Figure 26. From the larger dataset, the smallest mature female was 73 cm TL and the largest immature female was 96 cm. A length-at-maturity ogive fitted to all male data produced an estimated  $L_{50}$  of 65.4 cm (95% c.i.: 64.9–65.7 cm) (Figure 26).

From the North Island *Wanaka* trawl series, King and Clark (1987) noted the length range of mature females was 81–102 cm, and 62–73 cm for males. Their smallest mature male was 60 cm, and largest immature specimen was 76 cm. The  $L_{50}$  estimates from the present study suggest a larger size at maturity, particularly for females, than in other Pacific regions.

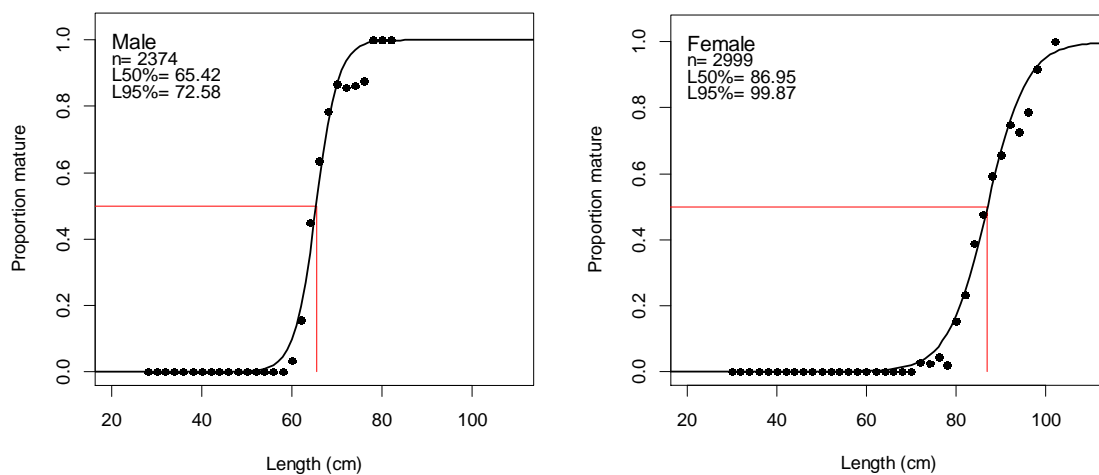
Based on a length at maturity of 65 cm TL, males are estimated to reach maturity at 9.9 years (Table 5). At a length at maturity of 87 cm, females are estimated to reach maturity at 14.7 years.



**Figure 24: Length-frequency distribution for male and female longnose velvet dogfish collected from trawl surveys around New Zealand.**



**Figure 25: Proportional distribution of longnose velvet dogfish maturity stages by sex. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**



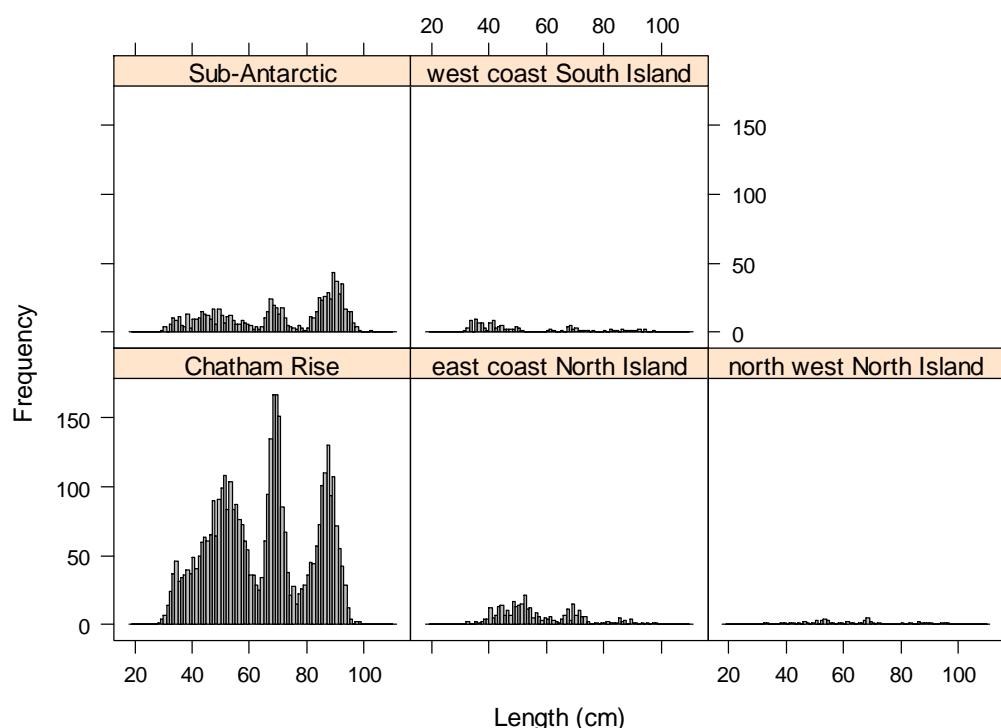
**Figure 26: Length-at-maturity ogives for male (left) and female (right) longnose velvet dogfish. The red line indicates the  $L_{50}$ .**

The median ovarian egg count was 11 ( $n=32$ ), with a range of 5–20. Four uterine egg counts of 6–8 were recorded. The median embryo count was 8 ( $n=8$ ), with a range of 2–10. Embryo length ranged from 2 to 31 cm. The smallest (assumed) free-living individuals were 28 cm TL. Thus, the size at birth was probably about 30 cm TL. Other records of litter sizes include Garrick’s (1959a) description of an 89.5 cm pregnant female with four pups caught off Kaikoura. King and Clark (1987) recorded an average of seven ovarian eggs and a birth size of 28–30 cm from around the North Island. Daley et al. (2002) observed eight pregnant females with pup counts ranging from 3 to 9, and an average of 6, around southern Australia.

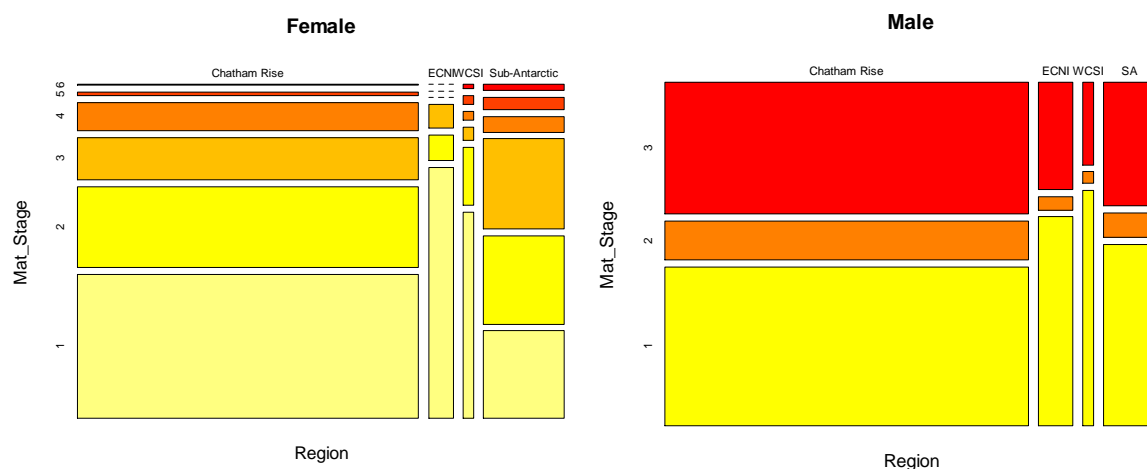
The overall length distributions of both sexes were dominated by the Chatham Rise sample, and showed modal peaks at 50–55 cm, which encompasses juveniles and sub-adults, and a second peak at 85–90 cm for females, and 65–70 cm for males, representing the mature adult population (Figures 24 and 27, Appendix 3). Mature and immature individuals were also found in all other regions although a greater proportion of juveniles were collected from the east coast North Island and west coast South Island surveys (Figures 27 and 28, Table 7). In contrast, mature females made up a greater proportion of the catches from the Sub-Antarctic surveys: 40% of females were mature compared with 25% on the Chatham Rise and fewer in other regions. This is consistent with the study by Francis et al. (2016), which found a larger median length for females in Sub-Antarctic surveys than on the Chatham Rise,

and a higher ratio of females to males (nearly 2:1) compared with a more even ratio elsewhere (Table 7).

A total of 297 gravid females (239 stage 4 and 58 stage 5) were recorded across 99 stations from all the main survey regions except the east coast North Island (Figure 28). Nearly 40% of these pregnant females were caught either singly or with 1–2 other pregnant females. In a small number of samples, 10 or more pregnant females were caught together (the maximum was 25 in one trawl).



**Figure 27: Length-frequency distributions of longnose velvet dogfish sampled from different regions around New Zealand.**



**Figure 28: Proportional distribution of longnose velvet dogfish maturity stages by sex and region. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**

**Table 7: Size composition and sex ratio (female:male) of longnose velvet dogfish sampled in different regions.**

Area	Depth range (m)	Male TL (cm)		Female TL (cm)		Sex ratio
		n	Range	n	Range	
Chatham Rise	114–1 246	1 846	28–80	2 211	29–98	1.2:1
West coast South Island	710–965	56	31–73	67	32–97	1.2:1
North west North Island	843–1 179	28	32–73	29	33–97	1.0:1
East coast North Island	600–1 451	172	35–74	164	32–98	0.9:1
Sub-Antarctic / Campbell Plateau	620–996	272	30–82	529	30–102	1.9:1

In the Northern Hemisphere, Nolan and Hogan (2003) reported that 17.5% of the females sampled in the north-east Atlantic were pregnant, with pup counts ranging from 1 to 9. They and other authors noted that there appears to be no defined breeding season. Daley et al. (2002) observed a non-continuous reproductive cycle with no seasonal trends in maximum ovum diameter or gonadosomatic index in Australia. The length of gestation is unknown, but a number of authors have suggested that follicle development, gestation and a resting phase would likely result in a reproductive cycle of two or more years (Irvine et al. 2006; Simpfendorfer & Kyne 2009). Irvine et al. (2006) estimated a maximum productivity of 102 offspring per lifetime, assuming an annual fecundity of three pups and a maximum 34 years of active reproduction, based on their ageing study from south-east Australia. Simpfendorfer and Kyne (2009) calculated an intrinsic rebound potential of 0.0133–0.0230, and a population doubling time of 3–52 years for this species, based on the information from Irvine et al. (2006). These estimates were in the middle of the range of the deepwater cartilaginous species assessed.

### 3.7 Plunket's shark (PLS)

#### 3.7.1 Introduction

Plunket's shark is found in the southern Indo-Pacific, from ridges off the coast of Mozambique in the western Indian Ocean, south-western and eastern Australia, including Tasmania, the Norfolk Ridge, Lord Howe Rise, and around New Zealand (including the Chatham Rise, Challenger and Campbell Plateaux) (Anderson et al. 1998; Last & Stevens 2009; McMillan et al. 2011a; Ebert et al. 2013). Previously placed in the genera *Proscymnodon*, *Scymnodon* and *Centroscymnus*, the correct generic assignment is currently uncertain. It is caught from 200 to 1550 m, but most commonly between 500 and 1000 m (Anderson et al. 1998; McMillan et al. 2011a). Early New Zealand accounts by Garrick (1959b) described large numbers (estimated 300–400 per month) of this species being taken by long-line in the Kaikoura region, but it is currently considered uncommon (Paul 2003), with a bycatch from deepwater line and trawl fisheries, mainly the orange roughy and oreo trawl fisheries (Anderson 2013).

Few biological data have been recorded for this species (summarised in Appendix 2). Compagno (1984) reported mature males from 100 to 131 cm TL and females from 129 to 170 cm, an average ovarian egg count of 36, and a birth length of 32–36 cm. Garrick (1959b) examined adult, juvenile and late embryo museum specimens from Kaikoura and Cook Strait. The adults included a 119 cm male, and females between 130 and 141 cm (n=3). The juveniles and late embryos ranged from 31 to 34 cm (n=3), with another juvenile at 52 cm. That paper also referred to two pregnant females examined by previous authors, one of which was carrying 36 embryos, the other at least two embryos that were considered not far off birth (33 and 34 cm).

Daley et al. (2002) collected 112 specimens from research and commercial catches in eastern Bass Strait and Tasmania between 700 and 1000 m. Females ranged from 66 to 154 cm (n=67), and males from 52 to 133 cm (n=45). The size at first maturity for females was estimated at about 140 cm (34 mature specimens), with the smallest, pre-ovulatory female being 137 cm and the largest immature specimen 143 cm. No pregnant females were recorded, but 7–27 developing ova were counted in mature females, with a maximum egg diameter of 80 mm. The authors noted that 60% of mature females had resting

ovaries with small (3–11 mm diameter) ova, suggesting a non-continuous reproductive cycle with a long resting phase. For males, the size at first maturity was estimated at about 108 cm (36 mature specimens), with the smallest mature male measuring 108 cm and the largest immature male 106 cm.

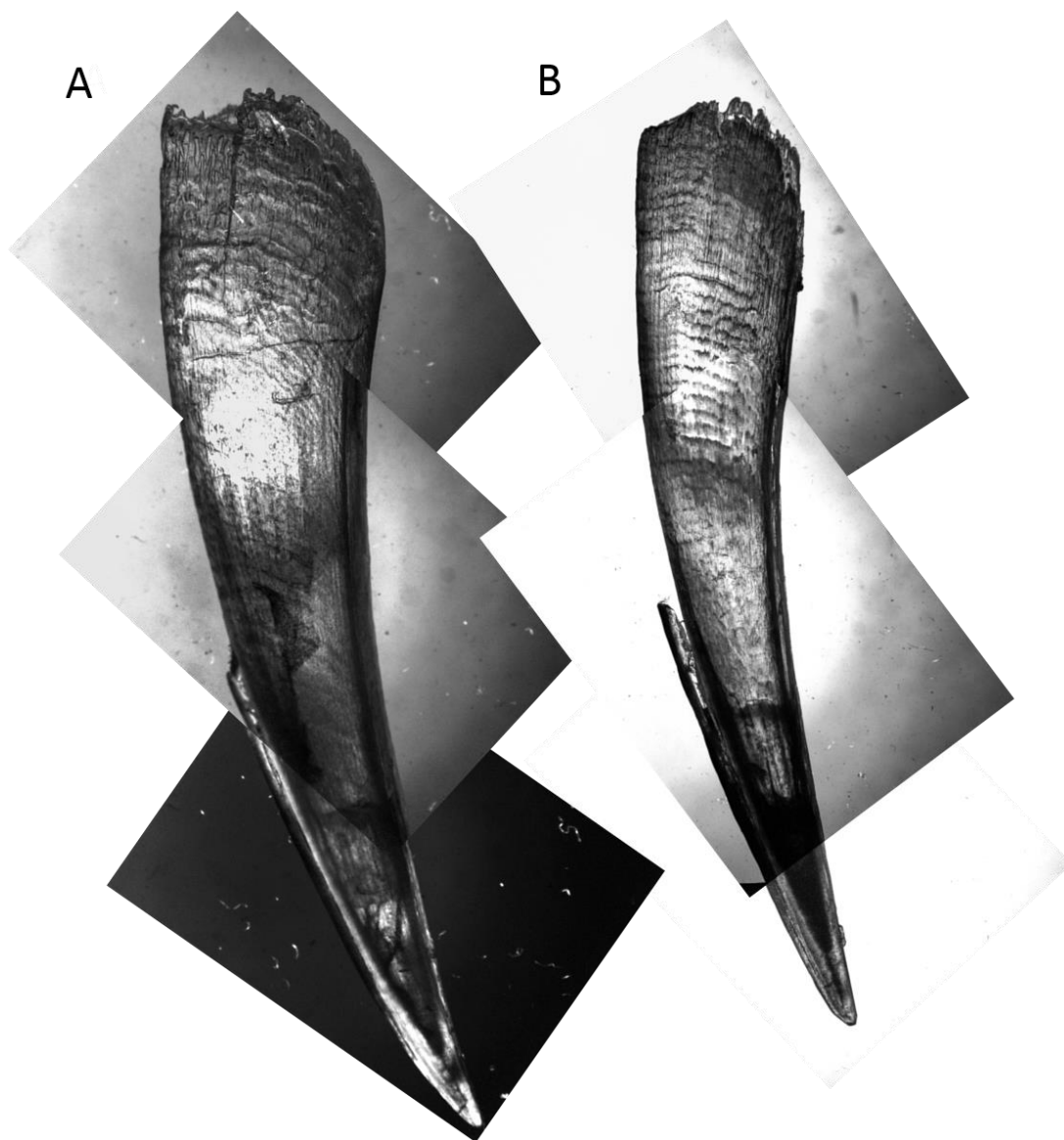
Irvine (2004) collected 66 specimens from commercial catches around Tasmania. The size range of females was 65–155 cm, although most were larger than 100 cm. Fourteen of the 37 females were mature; the smallest mature specimen was 117 cm, and the largest immature specimen was 143 cm. Irvine estimated that females matured at around 132 cm. The mean ovarian fecundity was 28 ( $n=9$ , range 19–43), with a maximum ovum diameter of 24–66 mm. That study did not find any pregnant females, although three post-partum individuals were observed with undeveloped oocytes of less than 6 mm diameter. The size range of males was 111–129 cm, with 27 of the 29 examined classed as mature; the smallest mature male was 111 cm, and largest immature specimen was 112 cm. Although no records of embryo counts from pregnant females were recorded, Irvine (2004) used a litter size of 17 to estimate annual fecundity for this species as 8.5 or 5.6, depending on whether a 2- or 3-year reproductive cycle is assumed.

### 3.7.2 Age and growth

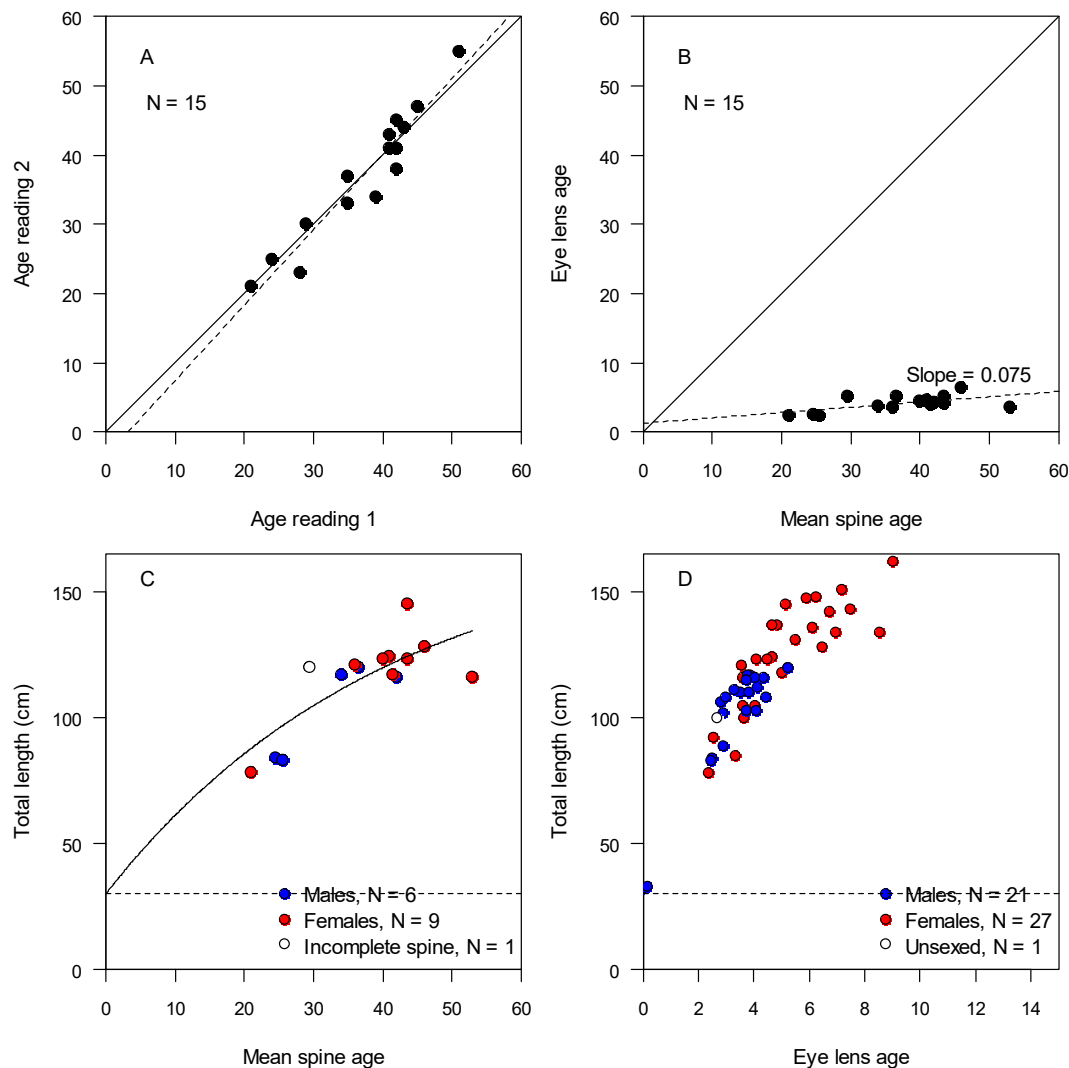
Etched and stained Plunket's shark spines viewed under polarised light usually had distinct and readily counted external bands on the lower two-thirds (Figure 29). Bands were usually less distinct and sometimes not apparent on the upper one-third (the part of the spine laid down in young, faster-growing sharks). We therefore used external spine bands for ageing this species.

The repeat readings of Plunket's shark spines produced similar results, indicating good count repeatability (Figure 30A). Greatest mean ages recorded were 42.0 years for males and 53 years for females (Table 5), however our sample size was small, so these values probably underestimate maximum ages. There was no clear divergence between males and females in the relationship between length and spine age, so we fitted a single von Bertalanffy growth to both sexes (Figure 30C, Table 5).

Eye lens age estimates were positively correlated with TL (Figure 30D). Eye lens age estimates were correlated with mean spine age ( $R^2 = 0.28$ , Figure 30B), but there was poor agreement between the two estimates: lens age estimates were much lower than spine band estimates (regression slope = 0.075). If lens micro-increments are formed daily, with 365 comprising one year of growth, then each spine band represents only 0.075 years; conversely, if spine bands are formed annually, micro-increments are formed on average every 13.3 days.



**Figure 29: Image montages of stained and etched Plunket's shark dorsal fin spines viewed under polarised light. A: PLS 181, 121 cm TL female. B: PLS 191, 117 cm TL female.**



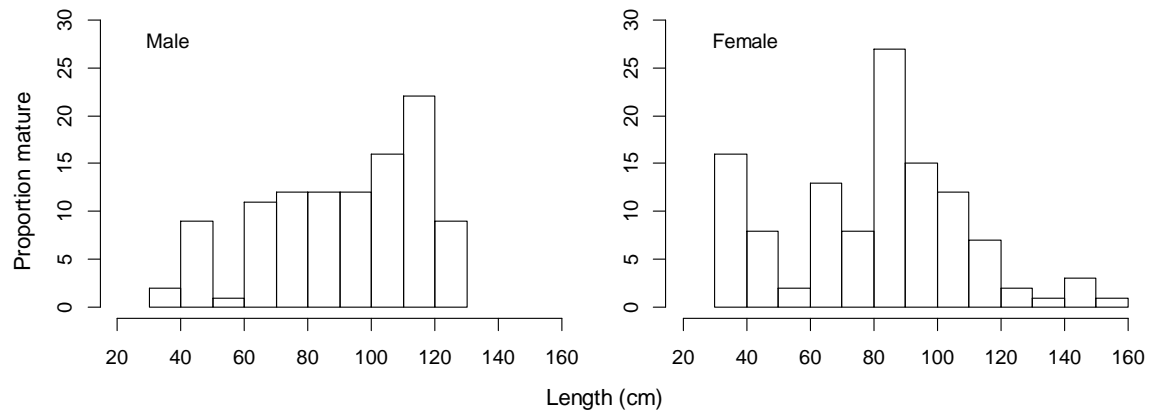
**Figure 30: Age and growth estimates for Plunket's shark. A: Comparison of spine age readings 1 and 2. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. B: Comparison of eye lens age estimate and mean spine age. The solid line is the 1:1 line and the dashed line is a linear regression fitted to the data. C: Plot of shark length versus mean spine age with fitted von Bertalanffy growth curve. The dashed line is the estimated length at birth. D: Plot of shark length versus eye lens age. The dashed line is the estimated length at birth.**

### 3.7.3 Reproduction

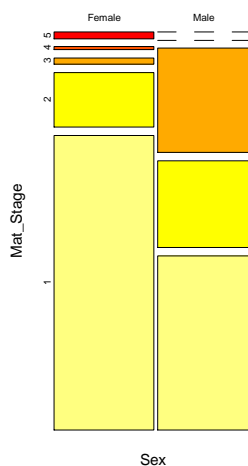
There were 497 biological records of this species in the research trawl database, ranging from 29 to 150 cm TL. Of these, 223 had associated maturity-stage data. Most were immature (95% of females and 70% of males) (Figures 31 and 32, stages 1–2). The largest immature female was 126 cm, the smallest mature female was 114 cm (one mature female at 106 cm was considered too small to be mature), and the largest mature female was 150 cm (Figure 33). Of the six mature females recorded, three were gravid, representing fewer than 3% of the total female sample. The  $L_{50}$  for females was estimated as 128.5 cm (95% c.i.: 119.5– $\infty$ ). A greater proportion of the males sampled was mature (nearly 30%), and the modal peak for males was larger than for females, at 110–120 cm (Figure 31). The largest immature male was 103 cm, with mature males ranging from 103 cm to 128 cm ( $n=31$ ). The male  $L_{50}$  was estimated as 109.5 cm (95% c.i.: 106.3–112.2 cm). These values are similar to those reported from Australian populations.



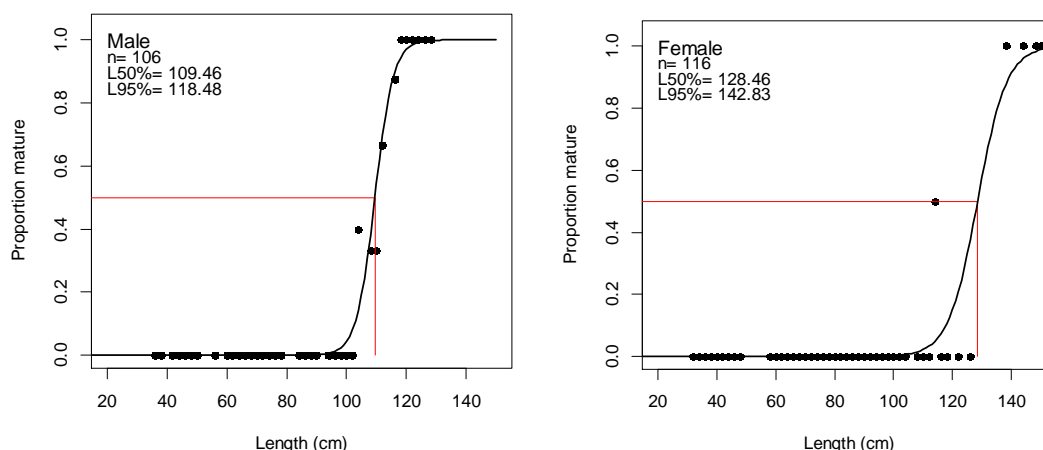
Based on a length at maturity of 110 cm TL, males are estimated to reach maturity at 33.2 years (Table 5). At a length at maturity of 130 cm, females are estimated to reach maturity at 48.6 years.



**Figure 31: Length-frequency distribution for male and female Plunket's shark collected from trawl surveys around New Zealand.**



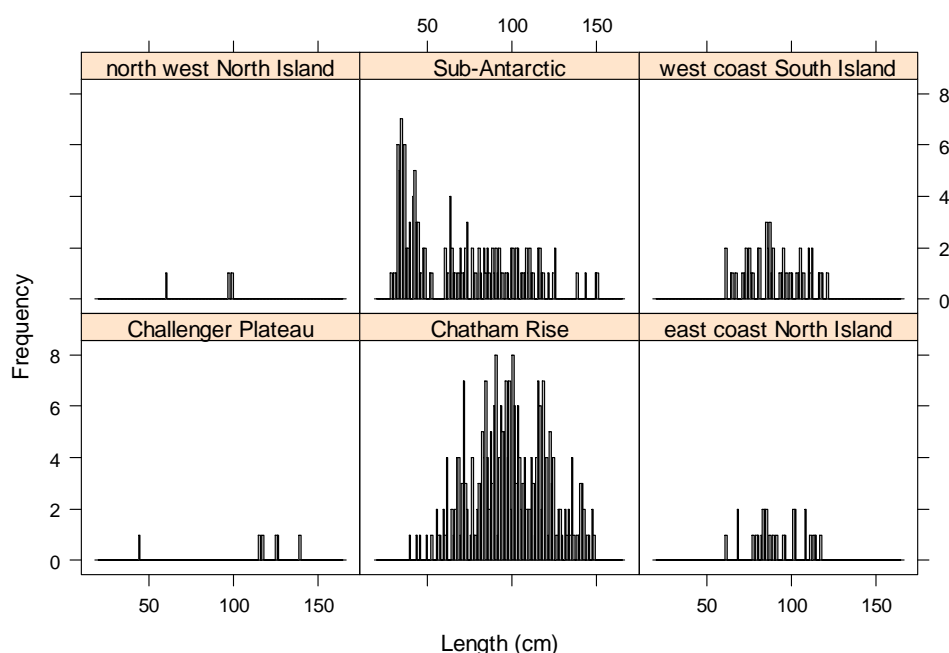
**Figure 32: Proportional distribution of Plunket's shark maturity stages by sex. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**



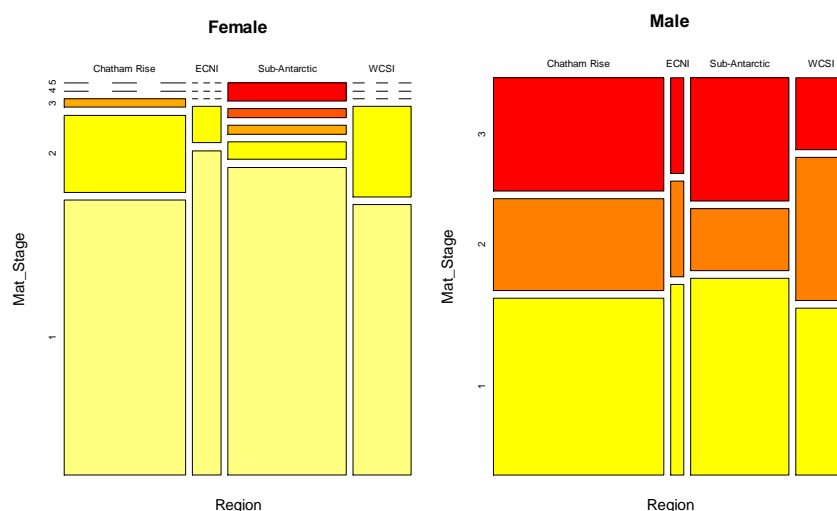
**Figure 33: Length-at-maturity ogives for male (left) and female (right) Plunket's shark. The red line indicates the  $L_{50}$ .**

One ovarian egg count of 28 was reported from a 139 cm female caught on Puysegur Bank (Sub-Antarctic), and one pup count of 23 was also recorded from that area.

Figures 34–35, Table 8 and Appendix 3 summarise the spatial patterns in population structure among the areas sampled. Plunket's sharks were recorded from the Chatham Rise, Sub-Antarctic (Campbell Plateau), the west coast of South Island, the middle-east coast of North Island and west coast of Northland. Females outnumbered males in all areas, with a modal peak at 80–100 cm, and only 5% of the female sample were mature. A significant number of Plunket's shark under 50 cm TL were recorded, particularly at Puysegur Bank in the Sub-Antarctic region (Figure 34). A number of sharks in the birth range reported by Compagno (1984) were caught. Gravid females were also only recorded in this area (Figure 35).



**Figure 34: Length-frequency distributions of Plunket's shark sampled from different regions around New Zealand.**



**Figure 35: Proportional distribution of Plunket's shark maturity stages by sex and region. Stages 3–6 indicate mature animals (see Appendix 1 for details). The width of each bar is proportional to the sample size.**

**Table 8: Size composition and sex ratio (female:male) of Plunket's shark sampled in different regions.**

Area	Depth range (m)	Male TL (cm)		Female TL (cm)		Sex ratio
		n	Range	n	Range	
Chatham Rise	400–1 170	110	45–133	156	39–149	1.4:1
West coast South Island	524–915	19	61–117	31	61–121	1.6:1
North west North Island	937–1 179	1	60	2	98–100	2:1
East coast North Island	632–1 170	6	61–118	22	68–114	3.5:1
Challenger Plateau	790–1 114	2	118–127	4	45–140	2:1
Sub-Antarctic / Campbell Plateau	419–1 015	57	29–126	78	30–150	1.4:1

## 4. DISCUSSION

The sample sizes available for estimating age and growth in this study were small, despite having a lengthy sampling period. The number of specimens was further impacted by attrition as a result of occasional species misidentification by observers, missing length and/or sex data, damage of specimens during preparation, and an inability to count bands on vertebrae and some spines. A particular concern is that we were unable to count external spine growth bands for longnose velvet dogfish and Owston's dogfish, and therefore resorted to counting the internal bands seen in thick transverse spine sections. Irvine (2004) has shown that external bands are routinely more numerous than internal bands in the spines from larger individuals of several squaloid dogfish species. External bands are more likely to be reliable indicators of age than internal bands, given that the former are more consistent than the latter with radiometric dates in at least one species (longnose velvet dogfish) (Fenton 2001; Irvine 2004; Irvine et al. 2006). Thus, our band counts for longnose velvet dogfish and Owston's dogfish probably underestimate the age of larger animals.

The use of eye lens micro-increments to estimate age has, to our knowledge, only been reported previously for cephalopods (Baqueiro Cárdenas et al. 2011; Rodríguez-Domínguez et al. 2013), so its application to elasmobranchs here (and in our companion study, Francis et al. (2018)) is unique. The technique relies upon an assumption that the micro-increments are formed daily, in an analogous way to daily formation of micro-increments in teleost otoliths. The only known attempt to validate the daily

formation of eye lens micro-increments, in reared (known-age) juvenile *Octopus maya*, found no correlation between age and the number of increments (Rodríguez-Domínguez et al. 2013). Thus, eye lens ageing has yet to be established as a valid tool.

In this study, we found large differences between age estimates from fin spines and eye lenses, with the former exceeding the latter by factors of about five for longnose velvet dogfish and Owston's dogfish and 13 for Plunket's shark. Similarly, our companion study (Francis et al. 2018) found vertebral age estimates exceeded lens age estimates by factors of five for carpet shark and six for common electric ray. Since neither eye lens ageing nor spine ageing has been validated for the species in the present study, we cannot say which, if either, is correct. However, the spine ages are regarded as more plausible for the following reasons:

1. Spine ageing is well established as an ageing tool for elasmobranchs, and band counts have been validated as being formed annually in some, mostly shallow-water, species (Cailliet & Goldman 2004; Cailliet 2015).
2. Eye lens micro-increment ageing has not yet been validated for any animal, and was proven invalid for reared *Octopus maya*.
3. The ages at maturity estimated from spine bands were 4.5 years for male Owston's dogfish, 9.9 and 14.7 years for male and female longnose velvet dogfish, and 33.2 and 48.6 years for male and female Plunket's shark (Table 5). If the eye lens ages for these species were correct, the ages at maturity would reduce to 1 year for male Owston's dogfish, 1.8 and 2.7 years for male and female longnose velvet dogfish, and 2.5 and 3.7 years for male and female Plunket's shark. Such low ages at maturity are implausible for deepwater elasmobranchs, which are widely believed to be slow growing and later maturing.

This does not mean that eye lens ageing should be abandoned as an ageing tool. If there is a constant relationship, or even a quantifiable size-dependent relationship, between the number of micro-increments deposited in lenses and an animal's age, then eye lens diameters may provide a useful estimate of age. A good way to quantify the relationship would be to count micro-increments in newborn sharks or rays and, at a later date, known-age animals from the same cohort. This could most easily be tested in a shallow-water elasmobranch. For example, 0+ rig are born in Porirua Harbour in spring and emigrate the following autumn–winter at an age of 5–7 months (Francis & Francis 1992; Francis 2013). Differences in increment counts for 0+ rig captured in spring and autumn would provide a quick test of whether increments are formed daily or with some other periodicity. Another test could involve the injection of a fluorescent chemical that is deposited in the eye lenses of tagged and released sharks or rays. Recapture of those animals would enable the estimation of the number of micro-increments formed between injection and recapture. This procedure would be analogous to the injection of oxytetracycline into teleosts for validating otolith growth band formation, but would use a different chemical (one that bonds to protein instead of calcium, and one that does not affect the vision of sharks and rays).

The only previous study of growth in seal shark was based on modal decomposition of length data for males from the Azores Islands, rather than direct ageing of individuals (da Silva 1988). The growth curve from that study suggested relatively fast growth, with males reaching 100 cm TL in about 6 years and a maximum age of about 13 years; however, that study probably overestimated the growth rate and underestimated longevity (Section 3.4.2). The eye lens age estimates presented here are probably also unreliable, given the poor correspondence between eye lens ages and vertebral- or spine-derived ages for other species discussed above. We are therefore unable to provide age-at-maturity, longevity or growth-rate estimates for this species.

The remaining three deepwater shark species have all been aged in south-eastern Australia (Irvine 2004; Irvine et al. 2006), providing a useful comparison for our results (Table 9). Important caveats when making such comparisons include: lack of validation of ageing techniques; use of internal spine band counts in the present study for Owston's dogfish and longnose velvet dogfish; and small sample sizes

leading to incomplete sampling of the population and underestimation of longevity. Preliminary conclusions may nevertheless be proposed:

- Age at maturity is poorly known for Owston's dogfish in either location.
- Longevity of Owston's dogfish was greater in Australia than in our study, probably because we used internal band counts, which underestimate age.
- Age at maturity of longnose velvet dogfish was similar in both locations (~10 years for males and 15–20 years for females).
- Longevity of longnose velvet dogfish was twice as high in Australia (34 years for males and 54 years for females) than in our study (17 and 26 years, respectively), probably because we used internal band counts, which underestimate age.
- Plunket's shark age at maturity estimates were considerably higher in our study (33 years for males and 48 years for females) than in Australia (20–25 and 30–35 years, respectively).
- Plunket's shark longevity was higher in our study (42 years for males and 53 years for females) than in Australia (32 and 39 years, respectively).

Although the ageing results presented here, and by Irvine and Irvine et al. (2004; 2006), are highly uncertain because of the caveats mentioned above, it appears that all three species are long-lived, that longnose velvet dogfish matures at a moderately high age, and that Plunket's shark matures at a high age (summarised in Table 10). These characteristics suggest that the productivity of all three species is low. This is consistent with a recent study, based on the growth parameters of Irvine and Irvine et al. (2004; 2006), that found that longnose velvet dogfish had a population doubling time of 22–52 years and Plunket's shark had a doubling time of 37–109 years (depending on assumptions about reproductive output) (Simpfendorfer & Kyne 2009). Plunket's shark was the least productive of the species included in that study, and longnose velvet dogfish was in the middle of the range of species examined. However, to put these deepwater sharks into a wider context, Simpfendorfer and Kyne (2009) noted that: 'Deepsea cartilaginous fishes [i.e., the species included in their study] have rates of population increase that are on average less than half those of shelf and pelagic species, and include the lowest levels observed to date. Population doubling times indicate that once a stock has been depleted, it will take decades, and potentially centuries, before it will recover.'

**Table 9: Comparison of age-at-maturity and longevity estimates between the present study and those of Irvine and Irvine et al. (2004; 2006) in south-eastern Australia.**

Species	Sex	Age at maturity		Maximum age	
		This study	SE Australia	This study	SE Australia
Owston's dogfish	Male	4	–	11	24
	Female	–	–	10	29
Longnose velvet dogfish	Male	10	9	17	34
	Female	15	20	26	54
Plunket's shark	Male	33	20-25	42	32
	Female	48	30-35	53	39

**Table 10: Summary of new age, growth and reproductive parameters obtained during the present study. Some of these values are uncertain or have known biases (see text for details).**

	Species				
	BSH	PLS	CYO	CYP male	CYP female
$L_{inf}$	NA	173.8	95.6	73.6	92.2
$K$	NA	0.024	0.224	0.164	0.170
Maximum age of males (yr)	NA	42.0	11.5	17.0	NA
Maximum age of females (yr)	NA	53.0	10.0	NA	26.5
Length at 50% maturity males (cm)	108.8	110.0	71.0	65.0	NA
Length at 50% maturity females (cm)	132.6	130.0	107.0	NA	87.0
Age at 50% maturity males (yr)	NA	33.2	4.5	9.9	NA
Age at 50% maturity females (yr)	NA	48.6	NA	NA	14.7
Length of female reproductive cycle (yr)	NA	NA	3–4	NA	3–4
Litter size (range)	NA	23–36	7–20	NA	6–8

Reproductive parameters derived in this study are shown in Table 10, although caution is required in their use because of caveats mentioned in previous sections. Large maturity-stage datasets have been obtained for longnose velvet dogfish and Owston’s dogfish from the areas where regular trawl surveys occur, mainly the Chatham Rise and Sub-Antarctic (Campbell Plateau and Puysegur Bank). Sample sizes were much lower for seal shark and Plunket’s shark, mainly due to their relatively low abundance in trawl surveys. Ovarian egg counts, pup counts and pup lengths were limited for all four species.

The reported maximum size and size range of mature females from several different areas is summarised in Appendix 2. For the most extensively sampled species, longnose velvet dogfish, the estimated length at 50% maturity for males (65 cm) agreed well with estimates from Australia, but was longer than estimates from the north-east Atlantic (52–57 cm). For females, the  $L_{50}$  (87 cm) was slightly larger than reported from Australia (82–84 cm) and considerably larger than reported from the north-east Atlantic (68–75 cm). Maximum lengths for this species appear to be similar for New Zealand and Australia, but smaller in the north-east Atlantic. For Owston’s dogfish, the estimated male  $L_{50}$  of 70 cm was similar to those from other studies, whereas for females, the  $L_{50}$  of 107 cm from New Zealand sample was slightly higher than the 100 cm estimated from Japan.

For both longnose velvet dogfish and Owston’s dogfish, the female maturity ogives did not reach an asymptote at which all the females were mature. This was despite having a large sample of mature longnose velvet dogfish, and a reasonably large sample of mature Owston’s dogfish. Assuming the mature portion of the population was adequately sampled, it is possible that some resting mature females (stage 3) were misidentified as maturing females (stage 2). Our maturity scale does not include a stage specifically for resting females, and in any event, resting females may be difficult to distinguish from maturing females.

For the other two species studied, our sample sizes of mature females were much smaller: 22 mature seal shark and six Plunket’s shark (an additional Plunket’s shark had been discounted because it was too small). Despite the limited sample, the  $L_{50}$  estimate for seal shark of 132 cm matched the reported ranges of mature females from elsewhere (Appendix 2). For Plunket’s shark, our female ogive is uncertain, but the range of our mature females, 114–150 cm, was within the range reported elsewhere. For both species, the  $L_{50}$  and size range of mature specimens were similar to those from Australia.

For Owston’s dogfish and longnose velvet dogfish, mature females made up around one-third of the females sampled. The proportion of the female population that were pregnant was much lower: 10% for longnose velvet dogfish, and 5.6% for Owston’s, or 37% and 21% of the mature females,

respectively. Based on these observations, and as suggested by other authors (Daley et al. 2002; Irvine 2004; Simpfendorfer & Kyne 2009), a resting period of 2–3 years may occur between pregnancies, with a total reproductive cycle length of 3–4 years. If resting females were under-reported in our data, the proportion of gravid females could be even lower. For seal shark and Plunket’s shark, mature females made up just 7% and 5% of the sample, respectively, with only one pregnant seal shark female sampled (4% of total female sample) and three pregnant Plunket’s sharks (2.5%). It seems unlikely these samples adequately represent the mature portion of the population for these species.

Egg counts and pup counts for the four species examined were poorly estimated because of the very small samples of pregnant females, but were within the range of estimates from elsewhere (Appendix 2).

Population composition varied among species and to some extent among areas. For all species, juveniles made up a significant proportion of the samples, dominating both seal shark and Plunket’s shark, and making up almost half of the longnose velvet dogfish and female Owston’s dogfish. The only exception was male Owston’s dogfish, for which 75% were mature. Samples of all species included likely neonates, based on the estimated sizes at birth. However, it is possible that some of these records were from near-term pups that were aborted during capture. Neonates were sampled in all four main survey areas for seal shark and longnose velvet dogfish (Campbell Plateau, west coast of South Island, Chatham Rise, and east coast of North Island). Neonate Owston’s dogfish were also found in all areas except the east coast of the North Island, and were particularly common in the Sub-Antarctic region. Neonate Plunket’s shark were only sampled in the Sub-Antarctic. Mature males were generally present in all the main areas sampled, whereas mature female numbers varied among regions. Mature female seal sharks were more common on the east coast of North Island, while mature female longnose velvet dogfish and Plunket’s shark were more common, or only sampled, in the Sub-Antarctic region. Mature female Owston’s dogfish were more common on the west coast South Island than in other sampled regions.

## 5. MANAGEMENT IMPLICATIONS

It is not yet possible to determine current stock status in relation to a limit reference point for New Zealand deepwater sharks. The development of the necessary age-structured population models would require information on stock structure, catch history, biological productivity, age structure of the catch, and an abundance index. Such rigorous information requirements have yet to be met for any New Zealand deepwater sharks, so further research on all of them is required before any comprehensive stock assessments are possible.

However, the vulnerability of deepwater sharks to fishing impacts can be ranked using risk assessment methods that have lower information requirements than a full stock assessment. MPI carried out qualitative risk assessments for all 112 New Zealand chondrichthyans (including the four species covered by the present study) in 2014 and 2017 (Ford et al. 2015; MPI unpublished data). The main inputs for those risk assessments consisted of information on spatial and temporal overlap of fisheries and shark distributions; biological productivity data; and abundance trends (Ford et al. 2015). For most of the commonly caught deepwater sharks, sufficient information was available to carry out the qualitative risk assessment. The 2017 risk ranks for the species from the present study, relative to all 98 non-QMS species that were assessed, were 1 for Plunket’s shark, 3 for seal shark, 9 for longnose velvet dogfish, and 12 for Owston’s dogfish (MPI unpublished data).

The biological productivity of the species studied here was an important driver in determining the relative risk rankings mentioned above. The productivity of most deepwater sharks is at the lower end of the range exhibited by all cartilaginous fishes, leading to international concerns about the potential for overfishing (Kyne & Simpfendorfer 2007; Simpfendorfer & Kyne 2009; Rigby & Simpfendorfer 2015). An important and widely accepted indicator of shark productivity is the intrinsic rebound potential, a measure of how quickly a heavily depleted population will rebound. The metric usually

used to quantify this productivity is the population doubling time (Simpfendorfer & Kyne 2009). Out of 15 species of deepwater sharks analysed by Simpfendorfer and Kyne (2009), New Zealand species comprised 4 of the top 5 species in a ranked list of doubling times; they were Plunket's shark (doubling time = 37 years), leafscale gulper shark (*Centrophorus squamosus*, 40 years), Baxter's dogfish (*Etmopterus granulosus*, 37 years), and shovelnose dogfish (*Deania calcea*, 29–32 years). Longnose velvet dogfish, Owston's dogfish and seal shark were not ranked by Simpfendorfer and Kyne (2009) because of insufficient data.

The present study confirms the low reproductive rate of four species of deepwater sharks, based on their combination of small litter size and the low proportion of females pregnant (the latter being indicative of a multi-year reproductive cycle). Thus, the replacement rate of sharks removed by a fishery is very low. Furthermore, our age and growth estimates, although uncertain and unvalidated, suggest that three species (excluding seal sharks, which could not be aged by conventional methods) have low growth rates and moderate to high ages at maturity, particularly longnose velvet dogfish and Plunket's shark.

A recent indicator-based analysis (Francis et al. 2016) found little evidence of declines in abundance of three of the species studied here (the fourth species, Owston's dogfish, was not included in the indicator study). However, the indicators were often uncertain and monitored some species poorly:

*'Seal shark:* Trawl survey and commercial trawl abundance indicators produced conflicting results. The status of seal shark in FMAs 3–6 is uncertain. The fishery-independent trawl survey indicators suggest that there has been no major change over a long period of time in the abundance of juvenile seal shark. Adult seal sharks are not well monitored by the surveys.

*Longnose velvet dogfish:* Only indicators derived from trawl surveys in FMAs 3–6 were available. No trends were found in any indicators. However, Chatham Rise surveys monitor this species poorly.

*Plunket's shark:* The only indicators available were trawl survey relative biomass, which showed no trends in FMAs 3–6. However both surveys monitor this species poorly.'

Given the low productivity of the deepwater sharks covered by the present report, and the absence of suitable tools for accurately monitoring their abundance, these species should be considered vulnerable to overfishing.

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## APPENDIX 1: Reproductive staging guide for sharks and rays

Stage	Name	Males	Females
1	Immature	Claspers shorter than pelvic fins, soft and uncalcified, unable or difficult to splay open	Ovaries small and undeveloped. Oocytes not visible, or small (pin-head sized) and translucent whitish
2	Maturing	Claspers longer than pelvic fins, soft and uncalcified, unable or difficult to splay open or rotate forwards	Some oocytes enlarged, up to about pea-sized or larger, and white to cream.
3	Mature	Claspers longer than pelvic fins, hard and calcified, able to splay open and rotate forwards to expose clasper spine	Some oocytes large (greater than pea-sized) and yolky (bright yellow)
4	Gravid I	<i>Not applicable</i>	Uteri contain eggs or egg cases but no embryos are visible
5	Gravid II	<i>Not applicable</i>	Uteri contain visible embryos. <i>Not applicable to egg laying sharks and skates.</i>
6	Post-partum	<i>Not applicable</i>	Uteri flaccid and vascularised indicating recent birth

## APPENDIX 2: Size, maturity and reproductive information for four deepwater sharks

Species	Location	TL <sub>max</sub> (cm)	Maturity range TL (cm)	L <sub>50</sub>	Ovarian egg count	Litter size	Size at birth	Reference
Longnose velvet dogfish	New Zealand	♀ 105 ♂ 93	♀ 76–102 ♂ 59–81	♀ 86.9 ♂ 65.4	11 (5–20 n=32)	8 (2–10, n=8)	~30– 31	This study
	New Zealand (North Island)		♀ 81–102 ♂ 62–73		7		28–30	King and Clark (1987); Clark and King (1989)
	Worldwide	90						Compagno (1984)
	SE Australia	♀ 103 ♂ 94	♀ 82–120 ♂ 63–122	♀ ~ 82 ♂ ~ 62		6 (3–9, n=8)	32	Daley et al. (2002)
	SE Australia	♀ 101 ♂ 88	♀ 68–101 ♂ 52–88	♀ 84 ♂ 64	7.6 (4 – 18 n=68)		31	Irvine (2004)
	NE Atlantic	♀ 99 ♂ 92		♀ 68 ♂ 52				(Clarke et al. 2001)
	NE Atlantic	♀ 87 ♂ 76		♀ 75 ♂ 57				Moore et al. (2013)
	NE Atlantic	♀ 87 ♂ 69		♀ 68 ♂ 52	26–117*	1–9		Nolan and Hogan (2003)
Plunket's shark	New Zealand	♀ 150 ♂ 133	♀ 114–150 ♂ 108–126	♀ 128 ♂ 109	28	23	~ 30 cm	This study
	New Zealand		♀ 130–141 ♂ 119			36	33–34	Garrick (1959b)
	SE Australia	♀ 154 ♂ 133	♀ 137–154 ♂ 108–133	♀ 140 ♂ 108	7–27			Daley et al. (2002)
	SE Australia	♀ 155 ♂ 129	♀ 117–155 ♂ 111–129	♀ 132	28 (19–43, n=9)	17 (source not given)		Irvine (2004)
	New Zealand / SE Australia		♀ 129–170 ♂ 100–131		36	32–36		Compagno (1984)
Owston's dogfish	New Zealand	♀ ♂ 99	♀ 75–122 ♂ 51–99	♀ ♂ 106.3 70.7	17 (10–22, n=12)	15 (7–20, n=6)	26–31	This study
	New Zealand (North Island)		♀ 98–121 ♂ 71–93		17			King and Clark (1987); Clark and King (1989)
	Japan	♀ 116 ♂ 88	♀ 95–116 ♂ 67–88	♀ 100 ♂ 70– 75	25.7 (20–28, n=19)	22 (16–28, n= 21)	30–35	Yano and Tanaka (1988)
	Australia	♀ 120 ♂ 96	♀ 82–120 ♂ 73–96	♂ ~ 75		5 & 13	25–35	Daley et al. (2002)
	Australia		♀ 100–116 ♂ 69–85	♀ ♂ ~100	12 (8– 19, n=8)			Irvine (2004)
Seal shark	New Zealand	♀ 153 ♂ 126	♀ 119–152 ♂ 81–122	♀ 132 ♂ 108	5 & 23		35–40	This study
	New Zealand (North Island)	♀ 145 ♂ 129	♀ 132–145 ♂ 95–129		12			King and Clark (1987); Clark and King (1989)
	Australia	♀ 151 ♂ 117	♀ 127–151 ♂ 113–117			9 (n=4, 7– 11)	39–42	Daley et al. (2002)
	Azores, NE Atlantic	♀ 162 ♂ 132	♀ 123–156 ♂ 106–131		10–18	10–14	42	da Silva (1988)
	NW Atlantic				10–16		30	(Bigelow & Schroeder 1948)

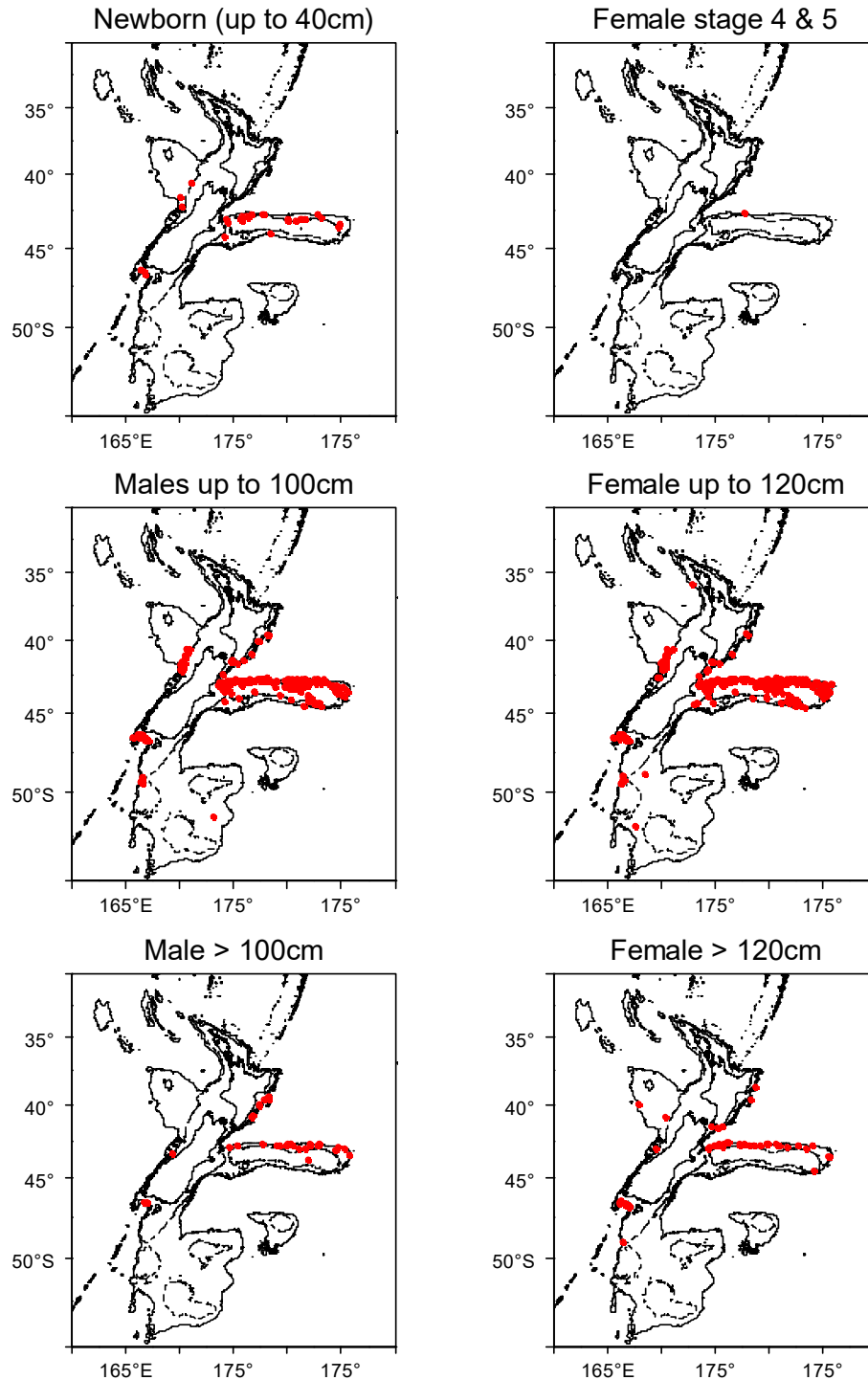
	Bay of Biscay, NE Atlantic	♀ 136				7		(Quéro et al. 1987)
	South Africa	♀ 159 ♂ 121	♀ 134–159 ♂ 105–121		10–20		36	(Bass et al. 1976)
	Mediterranean	♀ 117 ♂ 95	♀ 96–117 ♂ 74–95			3–6	32–39	(Bottaro et al. 2003; Capapé et al. 2008)

\* Counts of ova greater than 1 mm diameter.

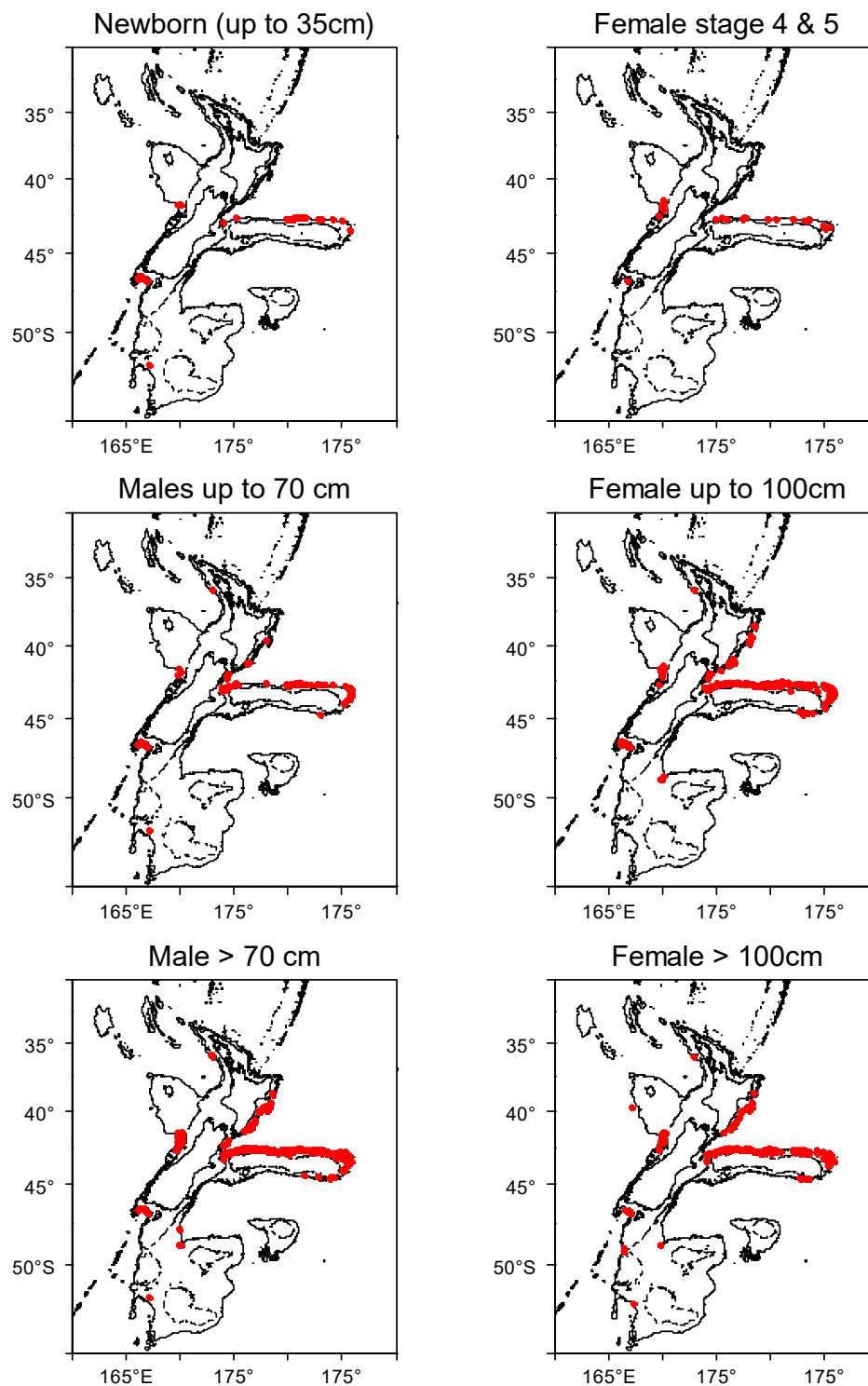
### APPENDIX 3: Spatial distribution of four deepwater sharks by life-history stage

Spatial distribution of neonates (top left), pregnant females (top right), sub-adults (middle) and adults (bottom) around New Zealand, based on data collected on trawl surveys.

Seal shark

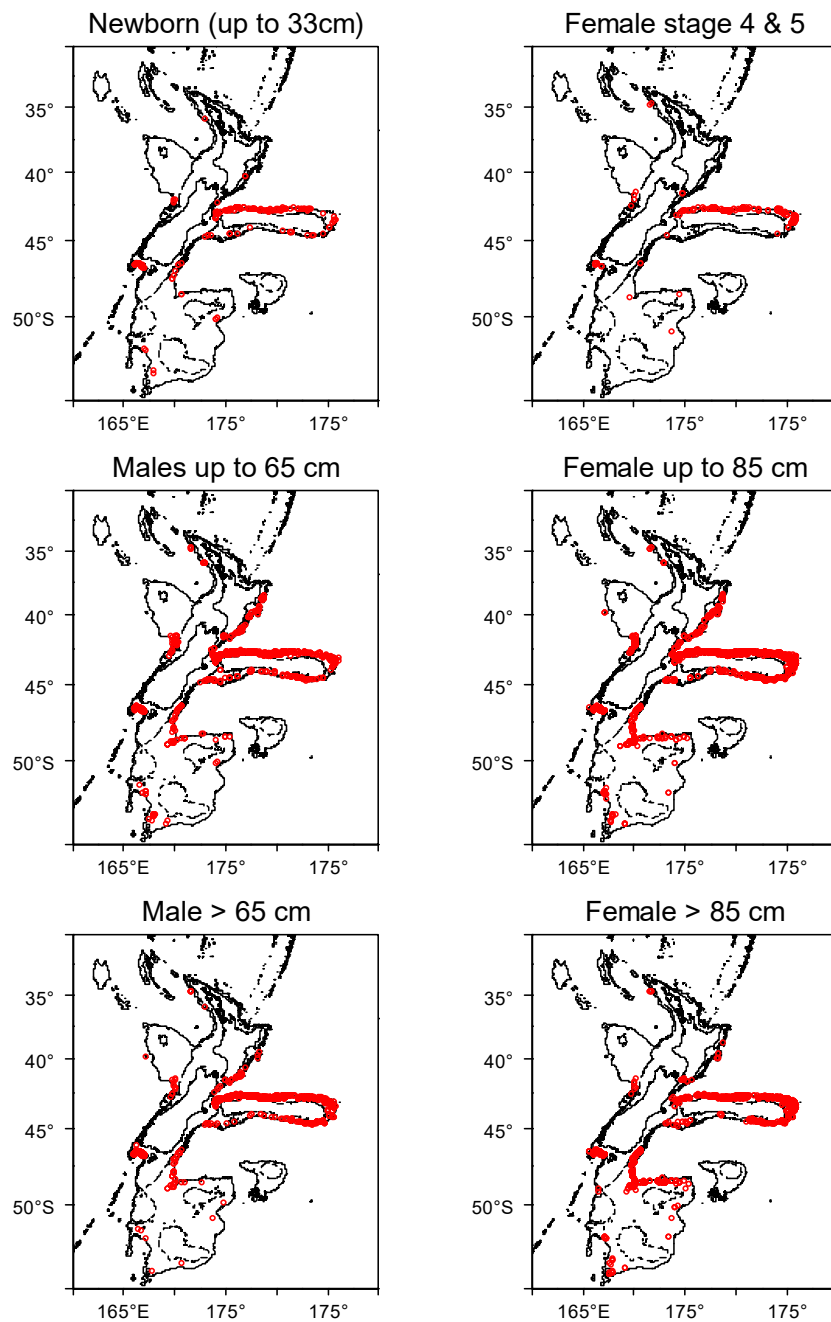


Owston's dogfish



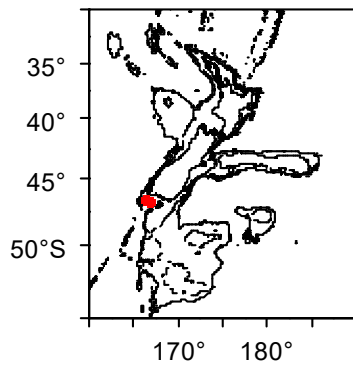


## Longnose velvet dogfish

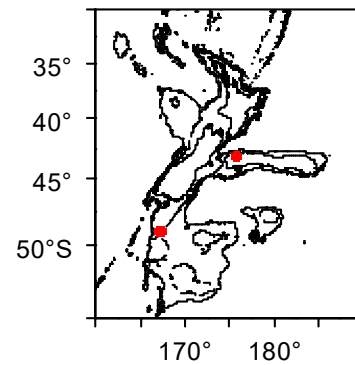


Plunket's shark

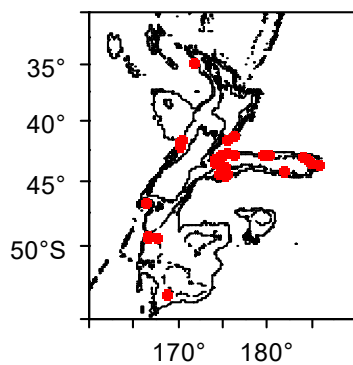
Newborn (up to 36cm)



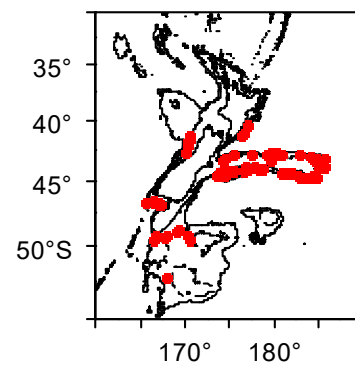
Female stage 4 & 5



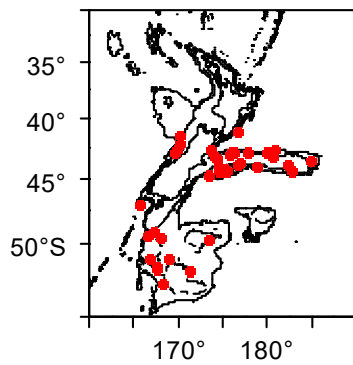
Males 0-100cm



Female 0-130cm



Male > 100cm



Female > 130cm

