Ministry for Primary Industries
Manatū Ahu Matua

Productivity of two species of deepwater sharks, *Deania calcea* and *Centrophorus squamosus* in New Zealand

New Zealand Aquatic Environment and Biodiversity Report No 103

S.J. Parker
M.P. Francis

ISSN 1179-6480 (online)
ISBN 978-0-478-40474-6 (online)

November 2012

New Zealand Government

Growing and Protecting New Zealand

Requests for further copies should be directed to:

Publications Logistics Officer
Ministry for Primary Industries
PO Box 2526
WELLINGTON 6140

Email: brand@mpi.govt.nz
Telephone: 0800 00 83 33
Facsimile: 04-894 0300

This publication is also available on the Ministry for Primary Industries websites at:
http://www.mpi.govt.nz/news-resources/publications.aspx
http://fs.fish.govt.nz go to Document library/Research reports

© Crown Copyright - Ministry for Primary Industries

Table of Contents

Executive Summary

EXECUTIVE SUMMARY

Parker, S.J.; Francis, M.P. (2012). Productivity of two species of deepwater sharks, *Deania calcea* and *Centrophorus squamosus* in New Zealand.

***New Zealand Aquatic Environment and Biodiversity Report No. 103.* 44 p.**

Deepwater sharks are caught in considerable numbers as bycatch in deepwater trawl fisheries targeting hoki (*Macruronus novaezelandiae*), orange roughy (*Hoplostethus atlanticus*), ling (*Genypterus blacodes*), and oreos (family Oreosomatidae), and in bottom longline fisheries targeting ling and ribaldo (*Mora moro*). Eight species of squaloid sharks are commonly captured in New Zealand; shovelnose dogfish (*Deania calcea*), Baxter's dogfish (*Etmopterus granulosusi*), lucifer dogfish (*Etmopterus lucifer*), Owston's or smoothskin dogfish (*Centroscymnus owstoni*), longnose velvet dogfish (*Centroselachus crepidater*), Plunket's shark (*Proscymnodon plunketi*), leafscale gulper shark (*Centrophorus squamosus*), and seal shark (*Dalatias licha*) (Blackwell 2010).

Concern about the productivity, and therefore vulnerability, of deepwater sharks to impacts from fishing has been growing globally as studies show that these species can be long lived, slow to mature, and have few offspring, depressing their ability to recover abundance quickly. Both *D. calcea* and *C. squamosus* are found globally and are relatively common bycatch species in fisheries occurring at depths greater than 500 m, Their life history characteristics are mostly unknown, especially in New Zealand waters, and characterisation of their productivity is necessary to manage potential fishery impacts to their populations.

Fundamental to any analysis of productivity are estimates of longevity, natural mortality and age at reproduction. Ageing techniques for these deepwater elasmobranchs are only just developing and after trialling several methods, Francis & Ó Maolagáin (2004) determined that counting internal bands in cross sections of the trunk of the second dorsal fin spine was the most promising ageing method. Using this ageing method, we estimated age composition, growth functions, maturity ogives, and natural mortality from fin spines and detailed biological information collected from both species during several RV *Tangaroa* trawl surveys (1997–2010), with most collections made during this study. We then conducted a demographic analysis to assess productivity and stock status in order to recommend future monitoring and management options.

Age determination using internal fin spine band counts were problematic with a moderate level of disagreement between readers. No feasible method of validating spine ages was achieved, therefore age-derived biological parameters in this report should be treated with caution.

Demographic analysis confirms that productivity of these species in New Zealand is similar to those estimated in the North Atlantic, although there appear to be significant differences in maximum age for each species compared with North Atlantic data. Overall, both species have life history attributes resulting in very low productivity. In New Zealand trawl surveys, *C. squamosus* are caught too infrequently and sporadically for precise biomass estimates. Although imprecise, biomass trends from the Chatham Rise and Sub-Antarctic trawl surveys suggest a flat or modest increase since the early 1990's in each area for both species.

Because of their vulnerability to exploitation even as bycatch, the relative abundance of these (and other) deepwater shark species should be monitored closely. The two main opportunities to accomplish this are through Observer Programme coverage in the deepwater trawl fisheries where species-level identification can occur over a wide area, and through relative abundance estimates from Chatham Rise and Sub-Antarctic trawl surveys, although only large changes in biomass would be detectable given survey precision. Using demographic analysis or spawning biomass per recruit analysis to set conservative biomass targets will first require an age validation study, and more detailed information on the reproductive biology of these species. Our analysis has highlighted a low occurrence of reproductively active females for both species, and a lack of juvenile (60–100 cm total

length) *C. squamosus* in survey trawl catches. The reasons for these observations are unclear and could have implications for assessing stock status.

1. INTRODUCTION

Deepwater sharks are caught in considerable numbers as bycatch in trawl fisheries and some bottom longline fisheries in the New Zealand Exclusive Economic Zone (NZ EEZ). Eight species of squaloid deepwater sharks are commonly captured in deepwater trawl and longline fisheries in New Zealand: shovelnose dogfish (*Deania calcea*), Baxter's dogfish (*Etmopterus granulosus*), lucifer dogfish (*Etmopterus lucifer*), Owston's dogfish (*Centroscymnus owstoni*), longnose velvet dogfish (*Centroselachus crepidater*), Plunket's shark (*Proscymnodon plunketi*), leafscale gulper shark (*Centrophorus squamosus*), and seal shark (*Dalatias licha*) (Blackwell 2010). Reported catches of all species combined are about 2500 t per year (Blackwell & Stevenson 2003, Blackwell 2010), but this likely under-estimates the total catch as many sharks are discarded and not recorded (Blackwell & Stevenson 2003, Blackwell 2010). Although historical trawl survey data within the NZ EEZ suggested that the catches of most deepwater sharks have been reasonably stable (Blackwell & Stevenson 2003, Blackwell 2010), abundance off the New South Wales shelf and in North Atlantic waters appear to have declined dramatically, especially *Centrophorus* species (Graham et al. 2001, Clarke et al. 2002a,b, Jones et al. 2005). Several recent studies have highlighted the potential vulnerability of deepwater sharks to fishing mortality (Musick et al. 2001, Simpfendorfer & Kyne 2009). Both *D. calcea* and *C. squamosus* are found globally and are relatively common bycatch species in fisheries occurring at depths greater than 500 m (Blackwell 2010, Figure 1). Their life history characteristics are mostly unknown, especially in New Zealand waters, and characterisations of their productivities are necessary to manage potential fishery impacts to their populations (Ministry of Fisheries 2008b).

The development and application of a precise and reliable age estimation method is fundamental to any study of fish population dynamics. The most common applications of age data are the derivation of growth curves and estimation of growth rates. Other important applications are the estimation of age at maturity and recruitment to the fishery, longevity, population age structure, natural and fishing mortality rates, and recruitment strength and variability. The ability to estimate fish ages is thus a requirement for quantitative fish stock assessment modelling and for monitoring population responses to exploitation. In the absence of a quantitative stock assessment model that allows current and reference biomasses and sustainable yields to be estimated, information on age at maturity, longevity, and natural mortality can still provide important information on the ability of a species to withstand fishing exploitation. In sharks, age at maturity has been shown to be a particularly important indicator of productivity (Au & Smith 1997), but these data do not yet exist for even the most commonly caught deepwater shark species in the NZ EEZ.

The feasibility of estimating ages of these two species and seal shark was investigated using samples collected during research trawl surveys of the Chatham Rise and Sub-Antarctic plateau during 2002–03 (Francis & Ó Maolagáin 2004). These species lack a strongly calcified vertebral column, so vertebral aging is not feasible, but it was concluded that *D. calcea* and *C. squamosus* could be aged using transverse thin sections of dorsal fin spines viewed under transmitted white light. Preliminary results from Francis & Ó Maolagáin (2004) suggested that New Zealand *D. calcea* and *C. squamosus* grow at similar rates and have similar longevities to conspecifics in the north-east Atlantic Ocean, reaching about 35 and 70 years respectively (Clarke et al. 2002a,b). However, further developmental work was recommended, especially an examination of larger sample sizes, development of a standardised fin spine preparation and interpretation protocol, and independent age validation.

In this project, we collected and aged fin spines from larger numbers of each species to estimate life history characteristics such as growth, maturity, longevity, and natural mortality. Other quantities such as proportions-at-age distributions and total mortality estimates are calculated to provide indicators of the productivity of these species in New Zealand waters. The knowledge gained on the life-history characteristics of these species is then integrated in a demographic analysis to provide an initial assessment of the risk to these species of over-exploitation in New Zealand waters. We then make recommendations on how to monitor these and other deepwater shark species.

(a) Shovelnose dogfish (*Deania calcea*)

(b) Leafscale gulper shark (*Centrophorus squamosus*)

Figure 1: (a) Shovelnose dogfish and (b) leafscale gulper shark. In the New Zealand EEZ, leafscale gulper shark typically reach about 140 cm in total length and 20 kg or more. Shovelnose dogfish are much less stocky, reaching about 120 cm in total length and 8 kg in weight. (data source: *trawl* fisheries research database; photographic credits: NIWA.)

This project comprised a single objective with five key activities:

Specific objective one:
*To determine the growth rate, age at maturity, longevity and natural mortality rate of shovelnose dogfish (*Deania calcea*) and leafscale gulper shark (*Centrophorus squamosus*).*

Key activities:

(i) collect *D. calcea* and *C. squamosus* fin spines;
(ii) prepare and read *D. calcea* and *C. squamosus* fin spines;
(iii) analyse data;
(iv) recommend appropriate methods to monitor stock status; and
(v) investigate the feasibility of validating *D. calcea* and *C. squamosus* age estimates.

This report first describes the sample collection and basic biological data summaries for the two species. It then evaluates the age determination process, summarizes the age-related biological data, and estimates growth and reproductive parameters. Finally demographic data are presented and options for future stock monitoring and assessment discussed.

2. METHODS

2.1 Fin spine collection

No archival collection of *D. calcea* and *C. squamosus* fin spines exists within the Ministry for Primary Industries (formerly Ministry of Fisheries) collection of structures for fish age estimation, and no new specimens have been collected since the modest pilot study by Francis & Ó Maolagáin (2004). Our sampling effort focused on the Chatham Rise and Sub-Antarctic plateau because of the relatively high occurrence of these species and the regularity of trawl surveys there (Blackwell 2010). All fin spines were collected from the catch using a random sampling scheme, so that the specimens collected would be a random sample from the catch at length.

Following Francis & Ó Maolagáin (2004), we collected the second dorsal fin spine from each sampled shark. The second dorsal fin spine is usually used in preference to the first in age determination of these species (e.g., Clarke et al. 2002a, 2002b, Francis & Ó Maolagáin 2004, Irvine et al. 2006), as it is usually larger and less damaged than the first. Spines were frozen and length, weight, sex, and reproductive state data were recorded following Francis & Duffy (2005) for each shark from which a fin spine was collected. The maturity scale used is given in Appendix I.

2.2 Fin spine preparation

Growth bands formed in the external enamel layer of fin spines have been used to age shallow water squaloid sharks, notably *Squalus acanthias* (Holden & Meadows 1962, Ketchen 1975, Soldat 1982). However, in deepwater squaloid sharks, this enamel layer is not complete. It is usually reduced to three longitudinal ribs, and does not extend down the entire spine. For this reason, and because of the poor definition of enamel bands, the external enamel layer has not been used to age deepwater sharks (Clarke et al. 2002a, 2002b, Clarke & Irvine 2006). However, transverse sections taken through the spine reveal growth bands in the dentine layers.

Spines grow by deposition of new cones of dentine inside the older cones (Holden & Meadows 1962, Soldat 1982). The first band in the inner trunk layer (the region between the lumen and the trunk primordium) of dentine originates at the trunk primordium by deposition of material along the lumen surface by odontoblasts (Figure 2, Clarke et al. 2002a, 2002b). New material is also added to the external surface by odontoblasts covering the portion of the spine embedded under the skin, but this material is not present in the exposed portion of the spine (Clarke et al. 2002b). Thus the full growth history is only apparent in the inner trunk layer. Sections taken too close to the spine tip do not contain the most recently deposited cones, and sections taken too close to the base do not contain the earliest cones. The best sectioning location is near where the lumen of the spine becomes constricted and occluded (Tanaka 1990, Clarke et al. 2002a, 2002b). This location moves further from the spine tip as the shark ages through deposition of new dentine along the lumenal surface, so the optimal location for the section moves with age (Holden & Meadows 1962).

Spines were cleaned in hot water, air dried for one week, and embedded in clear epoxy resin (Araldite K142). Thick (0.5 mm) sections were cut with a dual-bladed, precision diamond wafering saw (Struers Accutom 2). One side of each section was polished using a graduated series of carborundum polishing papers, and then glued to a glass microscope slide using thermoplastic cement. The other side of the section was similarly polished until growth zones became visible under a dissecting microscope at low power. The target thickness of the final section was 0.3–0.4 mm. Multiple transverse sections were made at different distances from the tip of each spine to locate the section with the smallest lumen for age estimation.

2.3 Growth band interpretation

Each section was viewed under a compound microscope at 40–100× magnification using transmitted light. Growth band counts were initiated at the trunk primordium (Clarke et al. 2002a, 2002b) proceeding inwards towards the lumen (Figure 2). Following Francis & Ó Maolagáin (2004), the outermost band of the inner trunk layer was omitted from the counts because it was assumed to be produced before or near birth. All fin spines were read “blind” by a single reader, that is, the reader had no knowledge of fish length or sex during reading. The number of fully-formed growth zones present and a five-point “readability” score was recorded for each spine. Terminology is as described in a glossary developed recently for fin spine studies (Clarke & Irvine 2006). One reader determined ages for all spines. A second reader determined ages independently for a random subset of 100 spines for each species. As documentation, the ageing protocol was developed in detail and provided in Appendix II.

Within- and between-reader variability in fin spine readings was quantified following Campana et al. (1995). A subsample of approximately 100 fin spines was randomly selected from the set of all fin spines prepared for each species (n = 200 in total) and read by a second experienced reader for comparison.

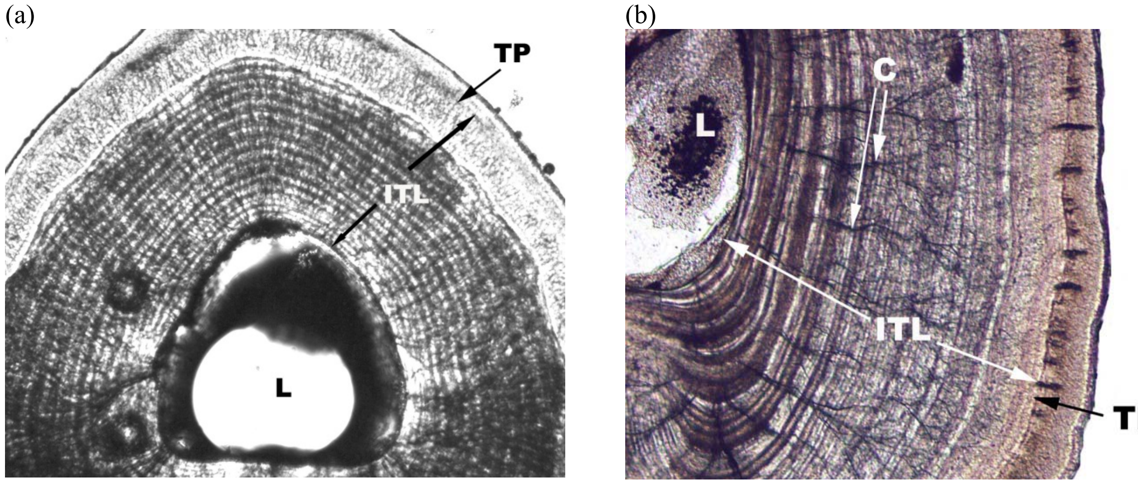

Figure 2: Thick sections from dorsal fin spines of (a) *Deania calcea* (82 cm male) and *Centrophorus squamosus* (b) leafscale gulper shark (102 cm male) illuminated with transmitted white light (from Francis & Ó Maolagáin 2004). L, lumen; TP, trunk primordium; ITL, inner trunk dentine layer; C, canaliculi.

2.4 Life history characteristics

Data from biological samples taken during trawl surveys were used to fit non-linear length-weight regressions to characterise sex-specific growth. The equation fitted was:

$$W = \alpha L^{\beta},$$

where weight =W, total length = L, and α and β are estimated coefficients.

Growth relationships over time were then fitted to age and length data for each sex using the von Bertalanffy growth function:

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

where the length in a given time step (L_t) is a function of the asymptotic size (L_∞), the Brody growth coefficient (k), and the time at L=0 (t_0) (von Bertalanffy 1938).

Age composition was examined using aged samples to generate an age-length key, and translate scaled length distributions for each survey to scaled age distributions using the software Catch-at-age (Bull & Dunn 2002). Aged individuals resulted from only a few of the most recent surveys, and the total numbers of fin spines aged from a given survey was small. Therefore, a single age-length key was developed using all aged samples from each species and applied to the length distributions of each species in each year data were available.

Natural mortality was estimated using Hoenig's (1983) equation of:

$M = -\ln(0.05) / A_{max}$

where natural mortality is the negative log of the proportion of the population reaching a given age, divided by that age; chosen here to be 5% of the population reaching the maximum observed age (A_{max}). Catch curve analysis, to estimate a total population mortality rate of Z (equal to M plus the fishing mortality, F) was conducted using the Chapman-Robson estimation procedure (Robson & Chapman 1961).

Gonad stage for each species was assessed using the criteria developed by Francis and Lyon (unpublished data, Appendix I). For both species, males and females were considered to be mature (developing to reproduce in the current annual period) if they were staged as mature or more advanced (gonad stage greater than 2). If "maturing" individuals are considered immature for the purposes of maturity estimation, the resulting proportions mature by size or age become erratic and the ogive becomes meaningless (see below).

The proportion mature was modelled as a logistic function of length (or age) using a binomial distribution with logit link. The parameters of the regression were used to calculate the length (or age) at 50% maturity ($L_{50\%}$ or $A_{50\%}$),

Proportion mature = $\alpha + \beta$ * length (binomial GLM with logit link)
$L_{50\%}$ or $A_{50\%} = -(\alpha / \beta)$

Several parameters relevant to assessing stock productivity and resiliency can be estimated using standard demographic analysis (Krebs 1985, Simpfendorfer 2004, Brooks et al. 2007). We used the new life history parameters generated in this study to estimate the net reproductive rate (R_0), generation time (G), intrinsic rate of population increase (r), and spawning potential ratio at maximum excess recruitment (SPR_{MER}) for *D. calcea* and *C. squamosus* (see Sminkey & Musick 1996, Simpfendorfer 1999 and Brooks et al. 2007). We conducted a more traditional analysis to estimate the spawning potential ratio over a range of fishing mortalities using CASAL (Bull et al. 2008). All other analysis was conducted using the statistical software R (R Development Core Team 2008).

3. RESULTS AND DISCUSSION

3.1 Samples collected

Length and weight data have been collected intermittently from *C. squamosus* and *D. calcea* during trawl surveys since 1979, though reproductive stage data were not routinely collected until 1996. Fin spine samples were collected from 370 *C. squamosus* and 1202 *D. calcea* during 12 voyages since 2002, but most were the result of sampling for the present study beginning in 2007 (Table 1).

Length and weight data have been collected for the two species in New Zealand waters during a number of trawl surveys, though mainly around the South Island. *Deania calcea* were sampled around the North Island during the RV *Wanaka* surveys in the late 1980s (Figure 3), and also sporadically measured during a few other surveys in the 1980s, in small numbers (e.g., gal8603 n = 142, jco8405 n = 129, all other trips had fewer than 100 measured). Catches of *Centrophorus squamosus* were rare. Their spatial distributions were well mapped within the various trawl survey footprints, but little sampling has occurred in areas outside trawl survey footprints. Both species have large Australia-New Zealand region distributions, and occur on continental slopes in all non-polar regions of the oceans. Veríssimo et al. (2012) showed that *C. squamosus* were genetically panmictic, but that movement of individuals across the Indian Ocean was slow and likely to be different for each sex. Studies in other related species found no evidence of distinct structure over large areas, which is likely to be due to substantial large distance movement rates (Veríssimo et al. 2011, 2012).

The two areas where population data were collected for this study (Chatham Rise and the Sub-Antarctic area) have experienced different fishing effort histories and could harbour different components of the population for each of the two species. Therefore we maintained separate time series of length and age structure for these two regions for each species. However, summaries of biological data are presented as pooled data for each species to maximize sample size for parameter estimation.

Table 1: Number of fin spine samples collected from *Deania calcea* and *Centrophorus squamosus* from New Zealand bottom trawl surveys, tabulated by sex. East Coast deepwater voyages targeted orange roughy (*Hoplostethus atlanticus*) on bathymetric features, so were not used as population surveys.

		C. squamosus			*D. calcea*			
Region	Voyage	Female	Male	Total	Female	Male	Total	Total
Chatham Rise	tan0208	8	3	11	4	10	14	25
Sub-Antarctic	tan0219	2		2				2
Chatham Rise	tan0301	1	3	4				4
East Coast	tan0709	4	8	12	114	157	271	283
Sub-Antarctic	tan0714	21	11	32	44	97	141	173
Chatham Rise	tan0801	20	7	27	122	115	237	264
Sub-Antarctic	tan0813	41	40	81	49	54	103	184
Chatham Rise	tan0901	24	17	41	149	112	261	302
Sub-Antarctic	tan0911	44	39	83	61	57	118	201
Chatham Rise	tan1001	17	12	29	50	59	109	138
East Coast	tan1003	48	12	60	93	126	219	279
East Coast	tan1008	54	43	97	42	72	114	211
	Total	226	144	370	572	630	1 202	1 572

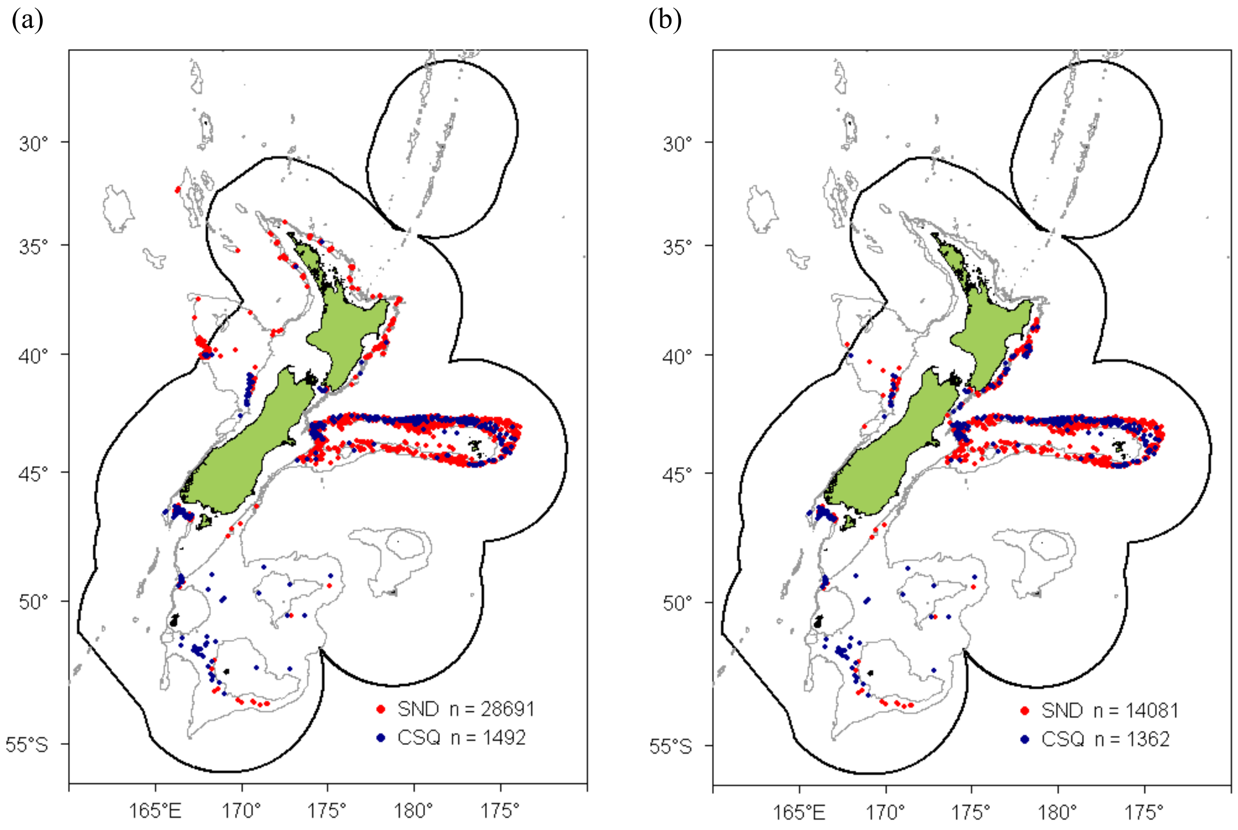

Figure 3: Locations of *Deania calcea* (red) and *Centrophorus squamosus* (blue) sampled for (a) total length and (b) for biological data (weight and reproductive stage) from research trawl surveys (1979–2010). Data source: MPI Trawl database

3.2 Scaled length distributions

Blackwell (2010) produced scaled length frequency distributions of catch for a number of deepwater shark species using trawl survey data. We updated the Chatham Rise survey series and the Sub-Antarctic survey series (where most of the survey data exist) for each species through to 2010. Both species are known to exist deeper than the survey strata (Froese & Pauly 2011). Some deepwater strata were not surveyed in every year, so were excluded for consistency; if different size fish inhabit different depths, a bias in length distributions could be caused by variations in depth zones surveyed in different years. We therefore re-analysed previous strata to provide a more consistent survey area for length frequency comparisons. The methodology of O'Driscoll et al. (2011) was used, where a station-level review of trawl survey data was conducted to provide the most appropriate dataset for time series analysis on the Chatham Rise. These same core strata were also used to estimate biomass trends (see Section 4).

The Chatham Rise survey shows a consistent length structure for male *D. calcea* spanning 35–90 cm with a mode near 83 cm (Figure 4). The 90th percentile length ($L_{90\%}$) showed no trend with time, and was typically 87–88 cm. There was no evidence for inter-annual length mode progression, as expected with an elasmobranch reproductive strategy because of the necessarily low juvenile mortality rates. The female length frequency distribution was broad and uni-modal, with no clear dominant peak, but a maximum abundance near 85 cm, and a size range from 35–115 cm (Figure 5). The $L_{90\%}$ was typically 103–104 cm and showed no consistent time trend.

The $L_{90\%}$ for male *D. calcea* in the Sub-Antarctic survey series was almost identical, with a mode near 85 cm and an $L_{90\%}$ of 89 cm. Females in the Sub-Antarctic tended to be somewhat larger, with fish commonly larger than 110 cm, and the distributions in this region often lacking fish smaller than 50 cm (Figure 6). However sample sizes were also small and therefore the overall shape and quantiles were poorly estimated. Accordingly, the $L_{90\%}$ was variable through time, typically ranging between 104 and 109 cm. The 2005 survey had the highest sample size (244 females), and was very similar to the typical Chatham Rise length frequency distribution.

The much lower frequency of occurrence for *C. squamosus* limited the usefulness of length distributions and only surveys sampling more than 50 individuals are presented for combined sexes. In the two Chatham Rise surveys, *C. squamosus* length ranged from 40–140 cm, with most fish more than 100 cm (Figure 7). A similar range was observed in the Sub-Antarctic series. Interestingly, there was a distinct size mode near 50 cm, a lack of individuals 60–100 cm, an adult male mode near 110 cm, and an adult female mode near 130 cm. No strong temporal trend in the $L_{90\%}$ was observed, although the quantiles were poorly estimated due to the low sample sizes and variable influence of the smaller size mode in the Sub-Antarctic survey.

Both *D. calcea* and *C. squamosus* are not typically observed shallower than 300 m and although they occur to the limit of current trawl survey depths (approximately 1200 m), they are less abundant at those depths. For *D. calcea*, small individuals may be found throughout the main depth range of 500–1100 m, but are mostly absent at depths shallower than 400 m and deeper than 1100 m (Figure 8a). No relationship of *C. squamosus* length was observed with depth, however, a scatterplot shows that while large and small fish are found at all depths, medium sized fish (60–100 cm) are under-represented, so much so that it suggests that they are not available to the survey gear (Figure 8b). This could be due to a more pelagic habitat, or a shift in geographic distribution. A similar observation was noted by Clarke et al. (2002a) in the North Atlantic, with their size distributions containing only large adult individuals of both sexes (more than 75 cm length). Yano & Tanaka (1988) reported that females of two related species were segregated by reproductive status and depth, but this phenomenon has not been observed in *D. calcea* or *C. squamosus*. Neither species shows any sex-specific depth distribution from trawl survey data.

Within the trawl survey data, significant effort occurs to approximately 1250 m, as shown by records for *D. calcea*, but *C. squamosus* abundance significantly declines deeper than 1100 m. Globally, *C. squamosus* has been found to 2400 m, and also pelagically in 1250 m over a 4000-m bottom depth (Compagno & Niem 1998), but size distributions of any pelagic *C. squamosus* remain unknown.

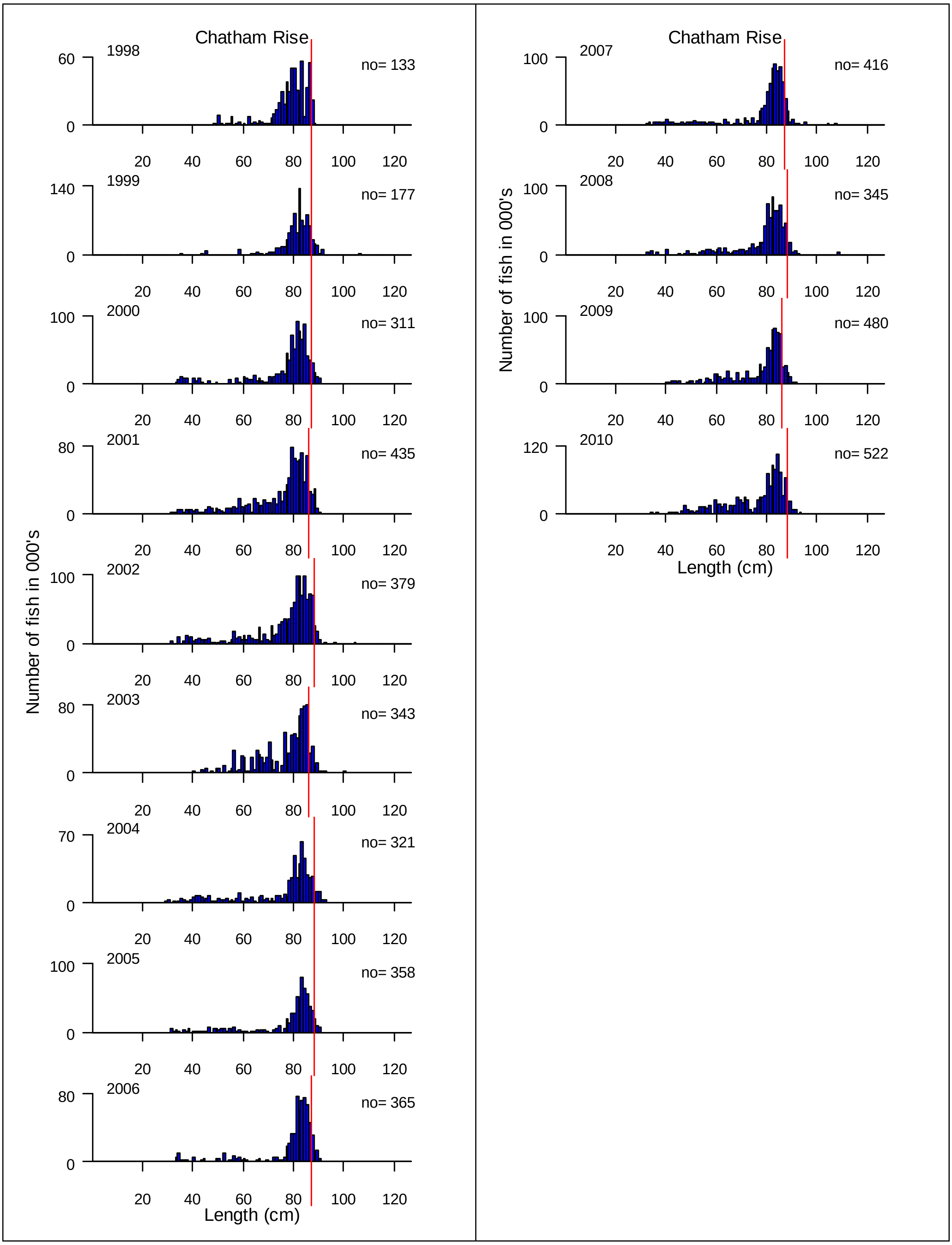

Figure 4: **Scaled length frequency distributions for male *Deania calcea* from trawl surveys of the Chatham Rise 1992–2010. Red vertical lines indicate the 90th percentile length ($L_{90\%}$) of the scaled male population in each year.**

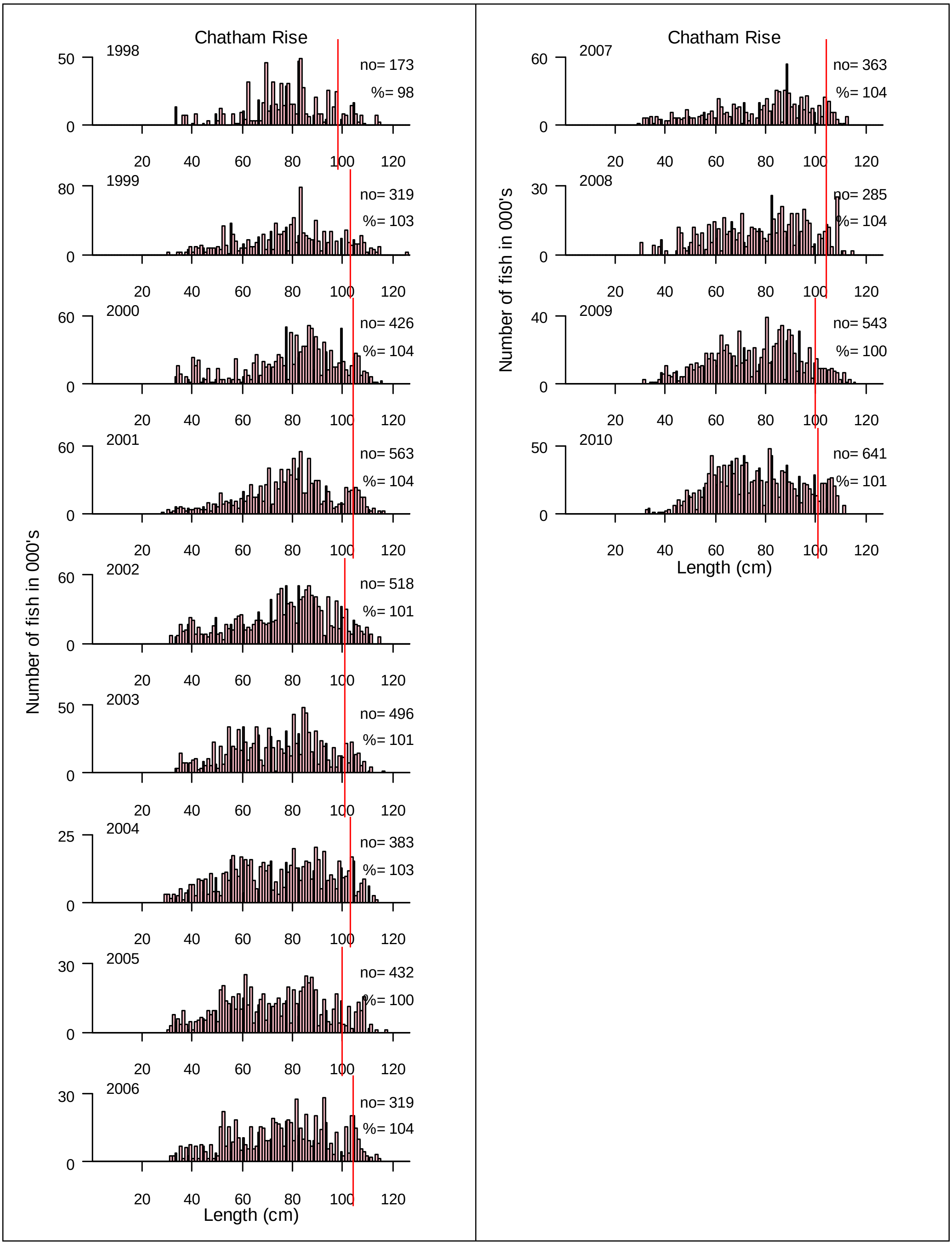

Figure 5: Scaled length frequency distributions for female *Deania calcea* from trawl surveys of the Chatham Rise 1992–2010. Red vertical lines indicate the 90th percentile length ($L_{90\%}$) of the scaled female population in each year.

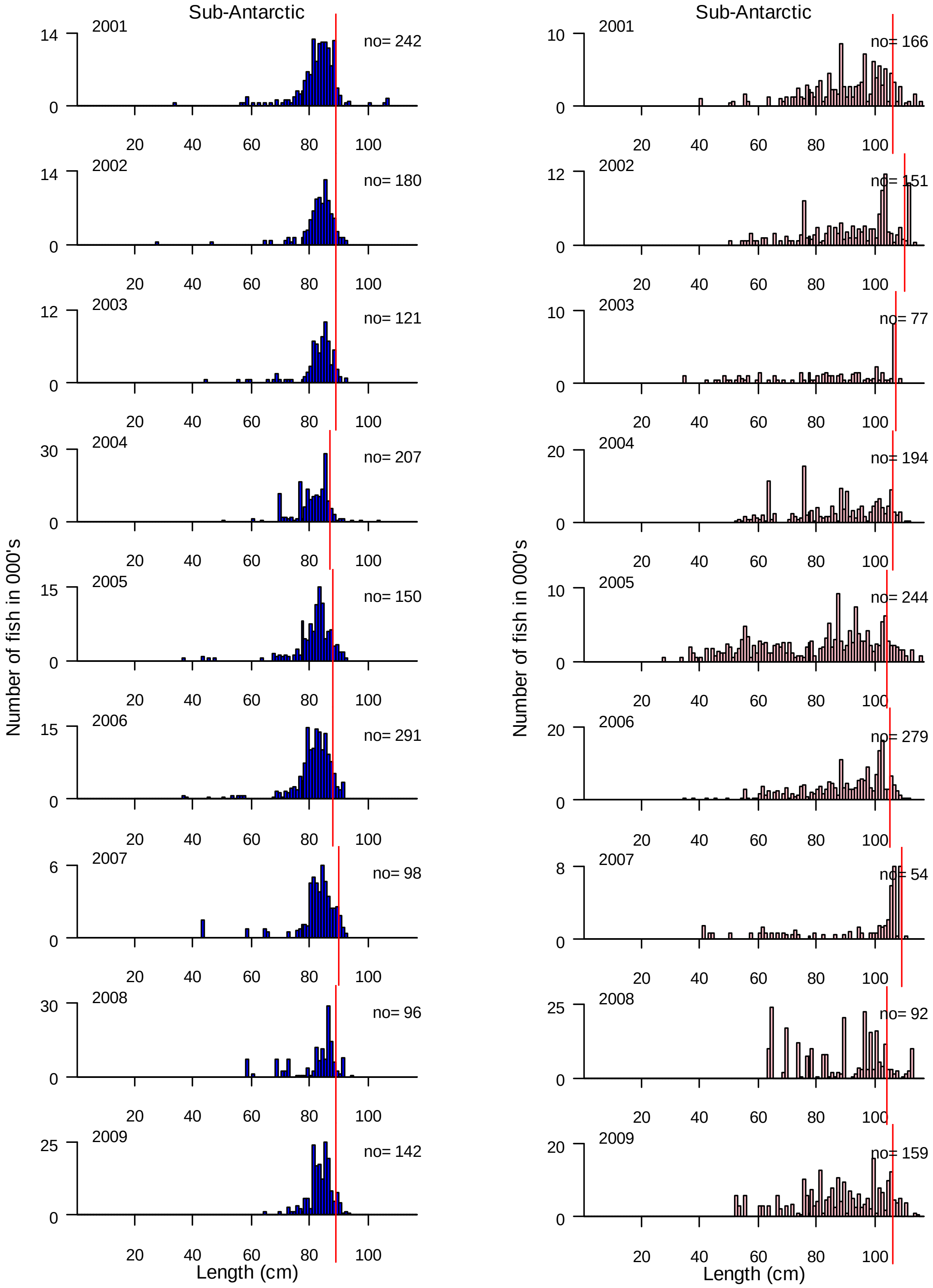

Figure 6: Scaled length distributions for male [left] and female [right] *Deania calcea* from trawl surveys of the Sub-Antarctic plateau from 2001–2009. Red vertical lines indicate the 90th percentile length ($L_{90\%}$) of the scaled population in each year for each sex.

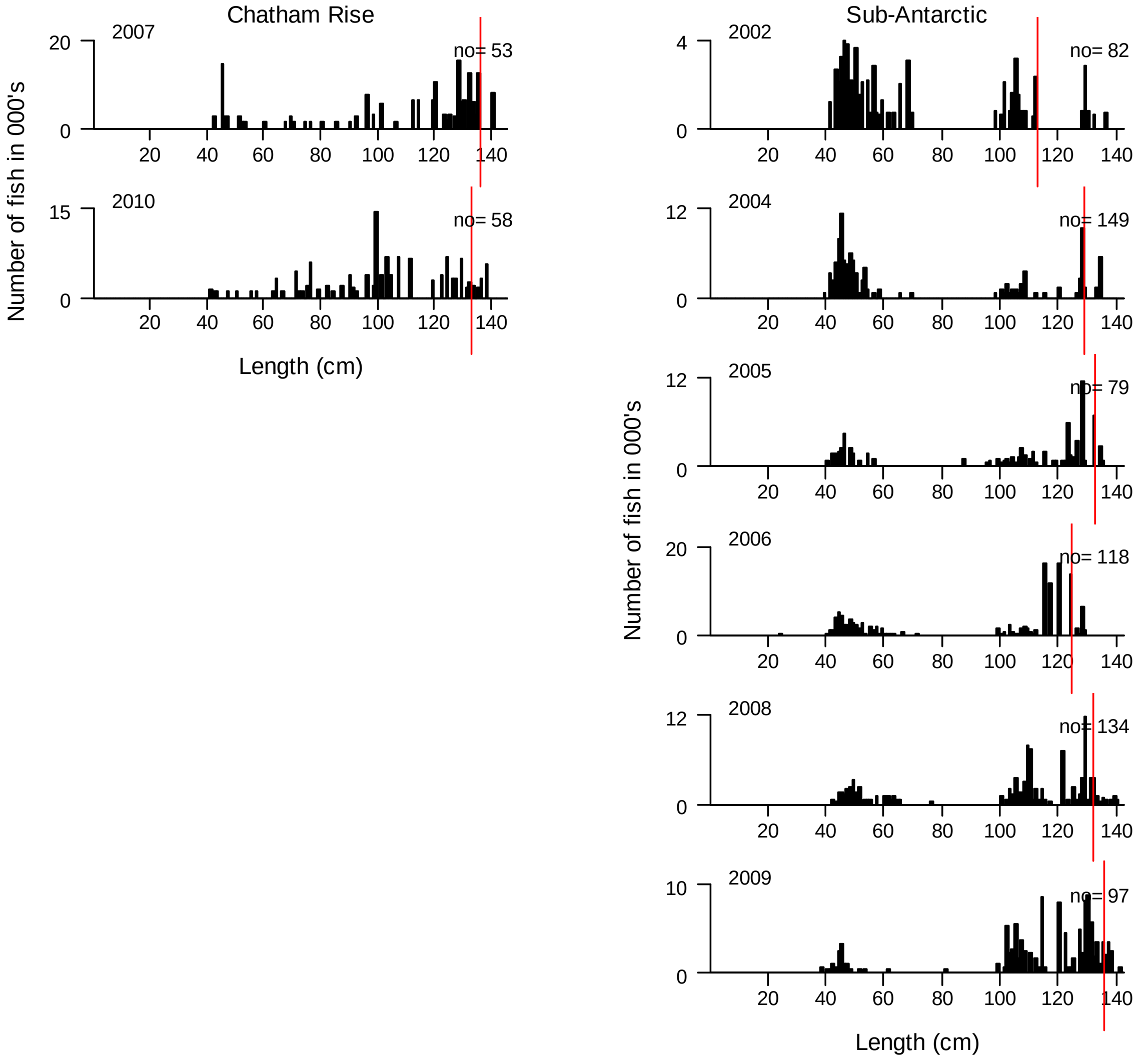

Figure 7: **Scaled length frequency distributions for *Centrophorus squamosus* from trawl surveys of the Chatham Rise and the Sub-Antarctic plateau for years when more than 50 individuals were measured. Red vertical lines indicate the 90th percentile length ($L_{90\%}$) of the scaled population in each year. Distributions were not split by sex due to low sample sizes.**

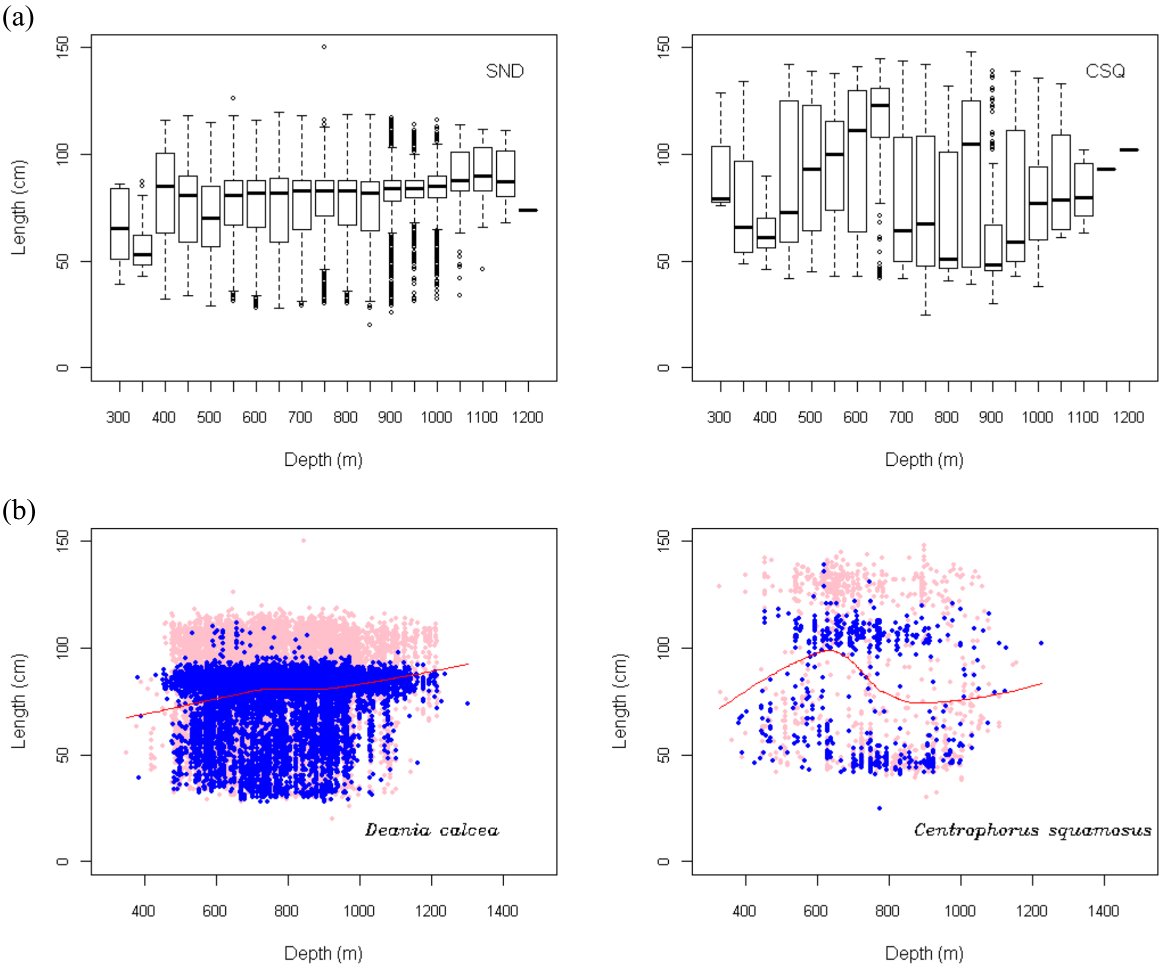

Figure 8: **(a) Boxplots of the length distributions of *Deania calcea* (SND) and *Centrophorus squamosus* (CSQ) in relation to depth in 50-m increments. Horizontal lines show the median, boxes the interquartile range, error bars the interquartile range, and circles show outliers. (b) Scatterplot of observed lengths versus bottom depth for *D. calcea* and *C. squamosus* from bottom trawl survey data. Pink dots are females, blue dots are males. Red line is a combined sexes LOWESS smoother.**

Sex ratios for the two species in the two surveyed areas were stable throughout the time series. On the Chatham Rise and in the Sub-Antarctic, the proportion of female *D. calcea* was close to 50% (56 % female for Chatham Rise, and 49% female for Sub-Antarctic). The proportion of female *C. squamosus* was typically higher (70% on the Chatham Rise and 60% in the Sub-Antarctic). Although this female bias may be real and due to the lack of juvenile samples and adult females attaining a larger size than males (see below), it may also be influenced by low sample sizes early in the time series. In other locations, differences in sex ratios of adult *C. squamosus* have been reported and explained due to gear and spatial selectivity (Clarke et al. 2001, Severino et al. 2009).

3.3 Length-weight relationships

Length versus weight plots show that for each species, males and females have a similar weight-length relationship when young, but that adult females attain a much larger size and are somewhat heavier than males of a similar length (Figure 9, Table 2). The fits tend to underestimate the steep increase in weight observed for some large individuals (mainly females) for each species, which may be due to the added weight of developing gonads or large livers in some individuals (but note that very few pregnant females with pups have been observed for either species).

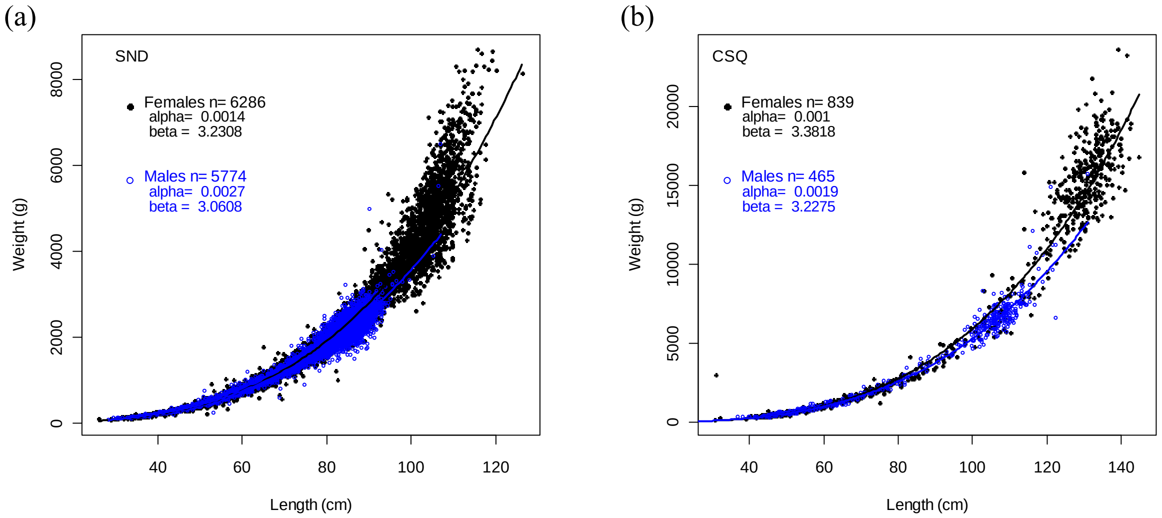

Figure 9: Length and weight relationship observations and sex-specific non-linear regression fits for males (open blue circles) and females (black dots) for a) *Deania calcea* and b) *Centrophorus squamosus* for trawl survey data (1998–2009).

Table 2: Parameter values for length–weight regressions for *Deania calcea* and *Centrophorus squamosus* sampled from research trawl surveys (1998–2010).

Species	*D. calcea*		*C. squamosus*	
Sex	Female	Male	Female	Male
Length range (cm)	26.2–126.5	28.5–107.1	30.8–144.9	25.0–131.2
Weight range (g)	75–8 700	70–6 500	160–23 600	70–15 700
α	0.0014	0.0027	0.0010	0.0019
β	3.231	3.061	3.382	3.228
N	6 286	5 774	839	465

3.4 Age determination

The Index of Average Percentage Error (IAPE) was 23.4 for *D. calcea* and 19.11 for *C. squamosus*. These values were slightly higher for *D. calcea* and lower for *C. squamosus* than reported by Francis & Ó Maolagáin (2004) (Figure 10). In both studies, Reader 2 tended to count more bands than Reader 1, though the disagreement, especially for *C. squamosus,* was lower in the present study than in Francis & Ó Maolagáin (2004).

A number of issues were encountered when attempting to determine ages from fin spines of *D. calcea* and *C. squamosus*, and in total they created a moderate level of uncertainty in the estimated ages. We detail these here to identify aspects for further study and to incorporate into a validation experiment.

- Spine erosion, particularly in older fish, results in loss of the tip of the spine. To choose the spine location to include all bands, we made two sections, typically 5 and 10 mm from the spine tip to be close to where the lumen of the spine ends. There is some variation in these distances due to processing effects. In addition, differences in spine section diameter and lumen diameter means that band width changes with distance from the spine tip, making band interpretation among individual spines difficult as band width is not always similar among preparations.

- The density of canaliculi (radially oriented tubules within the spine matrix) varies enormously both among individual spines, and with the distance from the spine tip. High densities of

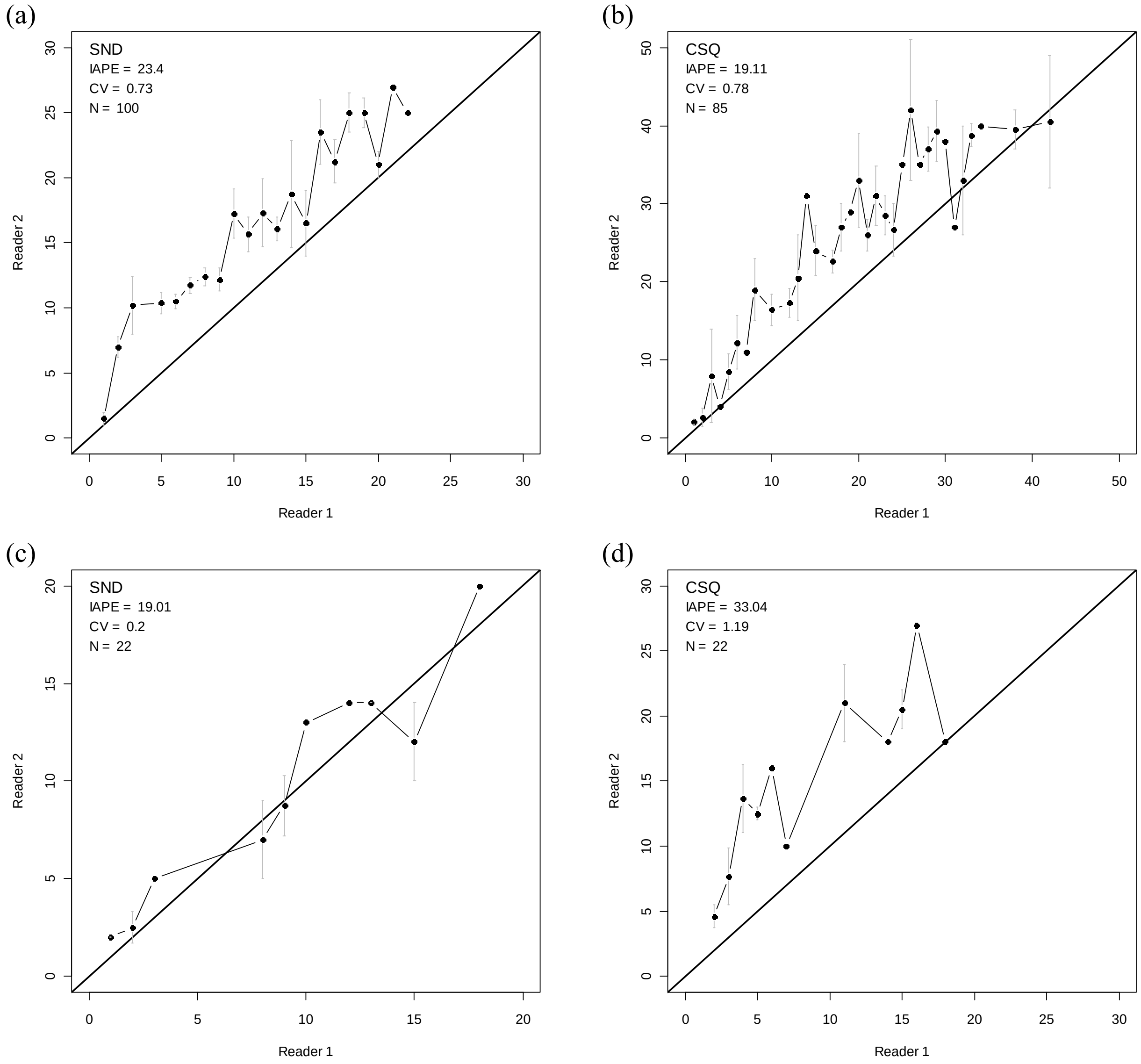

Figure 10: Age reader bias plots showing the mean (plus or minus one SE) age estimate of Reader 2 compared to Reader 1 for (a) and (c) *Deania calcea,* and (b) and (d) *Centrophorus squamosus*. Data (c) and (d) are from the initial aging study conducted by Francis and Ó Maolagáin (2004). Index of average percent error (IAPE), the overall c.v., and sample size are provided for each study. The diagonal line represents perfect agreement. Reader 1 and Reader 2 are the same people in each plot.

canaliculi make band identification and counting very difficult. Often, opposite sides of the spine section vary substantially in canaliculi density.

- Section thickness likely varies substantially, though this was not measured. The sections are cut with a single blade that is advanced a measured distance between the two cuts to create a cross section. This should produce a reasonably constant thickness apart from the effect of blade wobble. Nevertheless, spine sections varied a lot in their clarity, which may be related to uneven thickness, possibly due to the effects of grinding and polishing each section differently.

- Determining the starting point (trunk primordium) for counting was difficult. There is a distinct narrow line just inside the outer spine margin, and there is growth inside this in the smallest/youngest spines examined. This layer likely forms in utero, but may not occur in all species and was hypothesized to fade with age in *D. calcea* (Irvine 2004). A broad growth zone is also present in neonates. The first visible band beyond this is difficult to determine reliably. Because our lowest counts on the smallest sharks were one, we subtracted one from all counts of both readers to account for the 'birth band'.

- The finish point in the lumen is difficult to determine. Bands appear to continue down into the lumen and can be counted by increasing the focusing depth down into the lumen. It is possible that these bands represent growth bands that were not intersected by the section plane (because the plane was too far down the spine) and it appears sensible to add these lumenal bands to the counts. This was done by both readers in this study.

- Often, spine sections show a convergence of 2–4 bands between clock points of 1000 and 0200 (with 0000 defined as the anterior edge of the spine). These bands can be counted around the posterior half of the spine but not around the anterior half, which often has a wide bright zone with no obvious banding structure). These additional bands were included by only one reader (Reader 2), and may explain some of the IAPE in Figure 10.

- Band appearance (clarity, colour, and thickness) varies enormously from the outer bands towards the lumen, sometimes with abrupt transitions. The outermost zones could be counted as either a smaller number of broad, diffuse bands, or a larger number of narrow bands. Variation in how these were interpreted between readers could generate count differences.

- It was rarely possible to count a full set of bands along a single straight path. Usually multiple counting paths were required. As these paths are likely to be different between readers, variation in band counts can result.

3.4.1 *Age validation*

Obviously, addressing these issues will require an independent age validation experiment. However, recent attempts at validating age of *C. squamosus* in the USA using lead-radium dating have failed. The main cause appears to be variable uptake rates of lead into the spine matrix during growth (Allen Andrews, NOAA and Chip Cotton, VIMS, pers comm.). It is not clear why this would occur, or how to analyse data if each fish could have a different lead absorption profile through time.

Other possible age validation methods have been discussed in the literature, with the most promising being bomb radiocarbon (Campana et al. 2006). The method would parallel that shown for bluenose (*Hyperoglyphe antarctica*) by developing a deepwater bomb carbon decay curve (Horn et al. 2010). However, spine samples would need to be sourced from young sharks during 1965–1980. Our investigations indicated that few specimens exist in museums from this period in Australia or New Zealand, and destructive sampling of spines is problematic for these samples. Therefore, at this stage, no feasible method for conducting an independent age validation study for these two species exists.

3.4.1.1 International ager comparisons

Without a formal age validation method, the best approach to interpreting spine band count information is to examine the precision of various researchers conducting age and growth studies. There are very few researchers globally with experience with these species.

Although these two species are global in distribution, longevity estimates are different for different regions. We attempted to carry out interpretation comparisons to determine whether the ageing methods differ, or if population structures were biologically different. We identified several researchers working on longevity of these species in different regions and provided a reference spine section set of New Zealand region *D. calcea* and *C. squamosus*, along with a set of ageing protocols developed by NIWA agers (see Appendix II) to compare age interpretation methods. Each international ager volunteered to read 25 sections for each species following their normal procedure before shipping the set to another laboratory.

Agers that participated in the ageing protocol comparison were:

Malcolm Francis	NIWA
Caoimhghin Ó Maolagáin	NIWA
Sarah Irvine	CSIRO Marine and Atmospheric Research, Australia
Teresa Moura	Instituto de Investigação das Pescas e do Mar (IPIMAR), Portugal
Neide Lagarto (*C. squamosus* only)	Instituto de Investigação das Pescas e do Mar (IPIMAR), Portugal
Charles Cotton	Virginia Institute of Marine Science, USA

Comparisons showed that *D. calcea* spine sections were interpreted consistently, with fair agreement among readers on individual samples (Figure 11a, 12a). The overall c.v. was high (0.31), indicating that spine bands were difficult to interpret precisely, but that there was no strong bias by any readers. The resulting length-at-age plot by reader shows variable ages for a given fish length. This is common in deepwater species even with validated ages, and is likely to be a combination of poor structural readability and biological variation in length at age. Comparison of the New Zealand reference set data with published growth curves from other regions shows that large differences do not exist between New Zealand and Australian or North Atlantic *D. calcea*, and that the Australian reader (Sarah) was consistently interpreting *D. calcea* spine sections through time (yellow curve versus yellow dots). Note that male and female samples are combined here, as sample sizes were small and the objective was to investigate bias, not the actual growth functions.

Pairwise comparison plots showed little agreement or trend between readers for *C. squamosus* (Figure 11b). The most similar readers were those from the same laboratory. Ager agreement for *C. squamosus* was more variable and despite the overall c.v. being only slightly higher (0.36), the c.v. was much higher for older individuals (Figure 12b). The resulting length-at-age curves for each reader were similar as they were all anchored by small, young fish with high agreement. However the curves all diverge widely for older or larger individuals, mainly driven by outliers of each reader. Malcolm, Teresa, and Niede estimated ages greater than 40 years for some samples, almost 20 years older than estimates made by others on the same length fish. All agers reported using essentially the same protocol (*i.e.*, none reported differences between their method and the protocol provided by NIWA). Spine section interpretation could still be different, but that difference is not driven by a defined methodological choice. Clearly, there is an age signal in *C. squamosus* spine sections, but it is interpreted differently by agers using the same criteria and it is not yet known if the age signal is in fact linear with the age of the individual.

There appears to be no strong regional bias in interpretation of spine sections, and we now have no reason to doubt the nominal ages of up to 70 years described in the North Atlantic for *C. squamosus*. However, even with more extensive collections in New Zealand, ages greater than 42 are absent, suggesting that longevity may be dramatically different between the North Atlantic and New Zealand populations. Our recommendation is to utilize the range in ages estimated in any demographic analysis as a sensitivity analysis, but to exercise caution in interpreting longevity in this species.

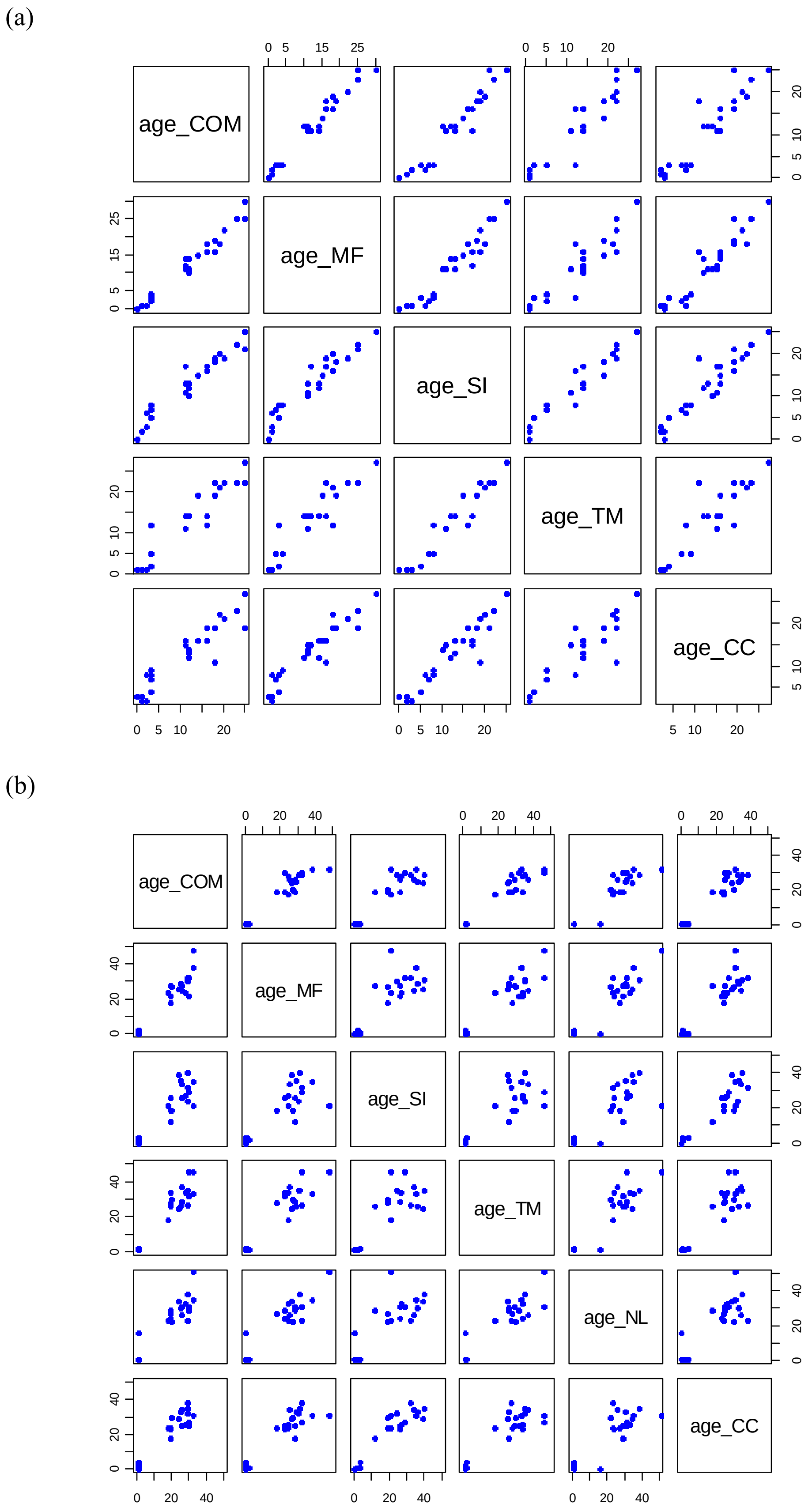

Figure 11: Pairwise comparison plots of the band counts determined by a group of international deepwater dogfish spine age readers for (a) *Deania calcea* and (b) *Centrophorus squamosus*.

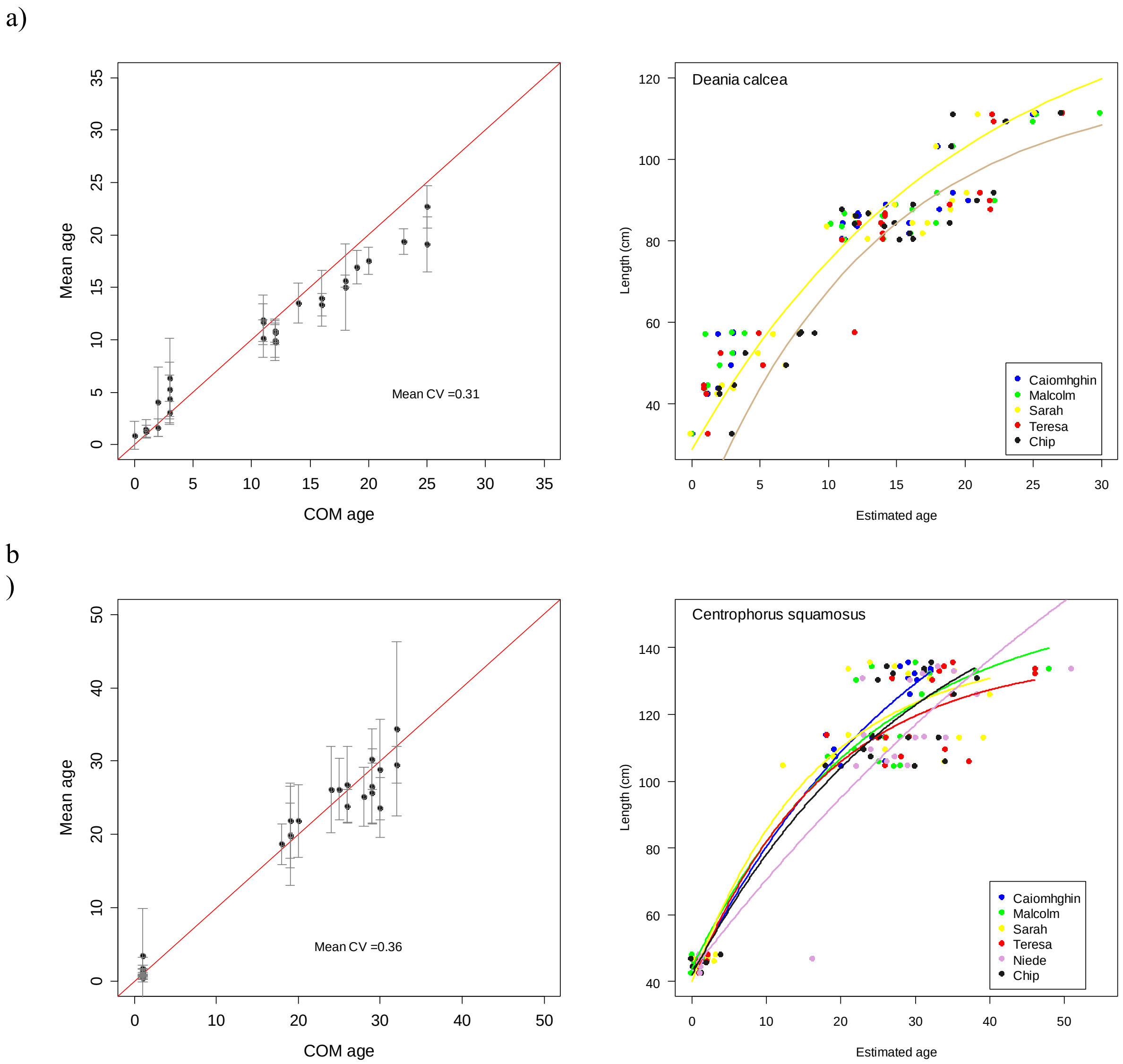

Figure 12. Mean age estimates by international experienced age readers of thin section spine preparations for a) *Deania calcea* and b) *Centrophorus squamosus* plotted for each sample (sorted by nominal age as determined by NIWA) or as individual length at age plots to detect bias among readers.

3.5 Growth

Assuming that spine bands are generated annually, and that the bands were interpreted correctly, we used Reader 1's spine band counts to estimate age for each species and fit von Bertalanffy growth curves (von Bertalanffy 1938) to the data for each species by sex (Figure 13, Table 3). Although somewhat variable, the curve fits for both species were generally sensible and showed differences by sex. If band counts were not related to age, these growth functions would not be sensible. However, there are some marked differences between these curve fits and previously published data from other regions. Clarke et al. (2002a, b) estimated maximum ages near 35 years for *D. calcea* and 70 years for *C. squamosus* in the North Atlantic. Our maximum age estimates, based on much larger sample sizes, are about 30% lower. It is possible that longevity is lower in New Zealand populations of these species, because no methodological differences in age interpretation are apparent (see 3.4.1.1).

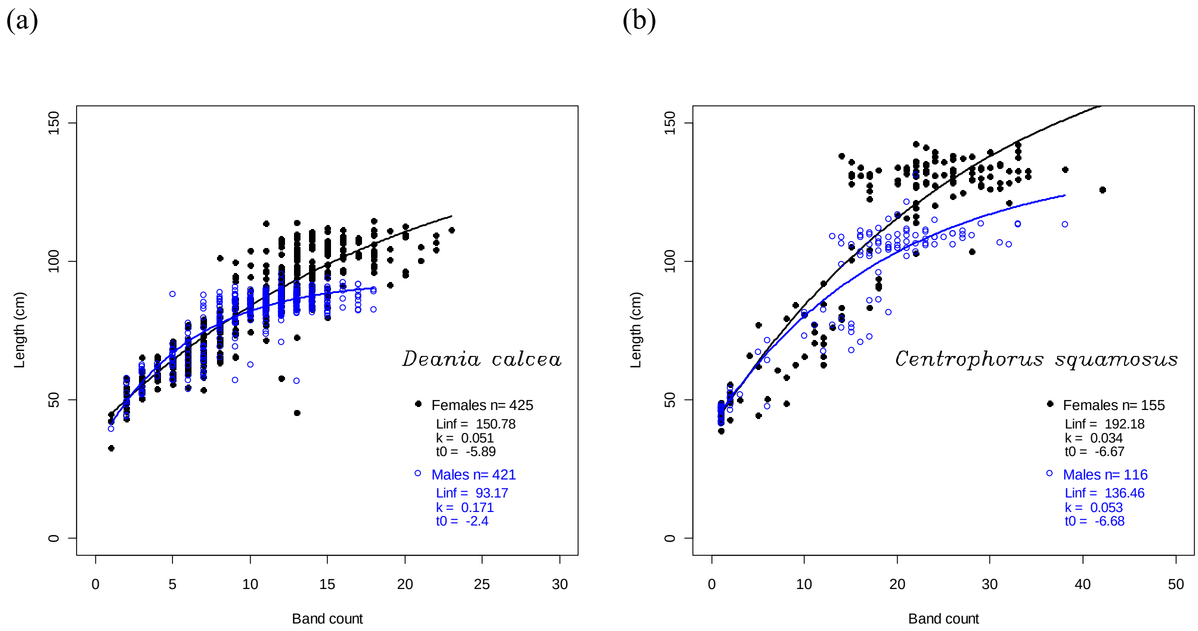

Figure 13: Spine band count versus length and sex-specific non-linear regression fits for (a) *Deania calcea* and (b) *Centrophorus squamosus*. Males (open blue circles) and females (black dots).

Table 3: Parameter estimates for von Bertalanffy growth equations for *Deania calcea* and *Centrophorus squamosus* samples from research trawl surveys.

Species	*D. calcea*		*C. squamosus*	
Sex	Female	Male	Female	Male
Length range (cm)	32.8–114.5	39.7–95.3	39.0–142.3	41.6–131.2
Maximum age observed	23	18	42	38
L_{inf}	150.78	93.17	192.18	136.46
k	0.051	0.171	0.034	0.053
t_0	-5.89	-2.40	-6.67	-6.68
N	425	421	155	116

For *D. calcea*, growth functions were different for each sex, with male growth slowing earlier than for females (Figure 13a). The fitted relationship for females does not come to an asymptote as the data do, and there appears to be a discontinuity in length and age near age 8. Asymptotic length (L_{inf}) for females is much larger than for males because of this poor fit (151 cm versus 93 cm) (Table 3). The relationship for males fits the data well and asymptotes by about age 15. There were few observations to anchor the relation for 0+ individuals, but the values of 35–45 cm are reasonable for average birth length. In fact several neonates were sampled specifically for this study. The male and female curves diverged at age 10, and females appeared to live longer than males in addition to growing faster post-maturity.

The growth curves for *D. calcea* males and females are different from the fits of Clarke et al. (2002b) in both length at birth and in maximum age (Figure 14). The relationship generated by Irvine (2004) for *D. calcea* in Australia was intermediate. Both male and female growth curves from Clarke et al. estimate a much lower birth length than the present study. The small fish used by Clarke et al. were from Machado & Figueiredo (2000), were aged by a different lab, did not contain fish younger than two years, and fish with 2–3 bands were only 20–40 cm in length. Irvine's (2004) fit had a larger birth length of 35 cm, which matches the observed lengths in New Zealand of 33–45 cm. The L_{inf} for males from Clarke et al. is similar to the present study at 93 cm, but the New Zealand female L_{inf} is poorly estimated at 151 cm. This poor fit is due to the discontinuity near age 8 and outliers of small fish aged between 7 and 13 years (see Figure 13). Additional work to confirm length at birth in Atlantic and in

New Zealand waters, as well as developing a consistent ageing protocol among labs working on deepwater shark life history, is necessary.

For *C. squamosus*, growth curve fits are poor due to a number of factors (See Figure 13b). Overall sample size was low, especially given a longevity of more than 40 years. There were also few fish sampled between 2 and 15 years old to inform the curve (i.e. a lack of juvenile samples). In addition, the data for fish less than 15 years old appeared disjunct from data for fish older than 15 years (even more so than for *D. calcea*). This created steeper curves and a lack of asymptote for either sex, underestimating the age of old fish and overestimating the age of juveniles (5–15 years). It is possible that the juveniles sampled were not representative of the population (e.g., most juveniles are not available to the sampling gear and only slow growing individuals are available to be caught). Most of the medium-sized fish were sampled from Chatham Rise surveys, with the very small and very large fish sampled during Sub-Antarctic surveys (See Figure 7), so it is also possible that Chatham Rise fish grow more slowly than Sub-Antarctic individuals. However, juveniles on the Chatham Rise are still rare and regional differences in growth rates are not consistent with the presumed large migratory movements.

Clarke et al. (2002a) were not able to fit growth curves to *C. squamosus* data because of the lack of juvenile fish. An assumed length at birth of 33 cm (fixing t_0) did not produce useable fits. Our data suggest birth lengths of 30–45 cm, which is similar to the range reported by others in the Atlantic (Bañón et al. 2006, Figueiredo et al. 2008, Severino et al. 2009).

The two main issues to resolve regarding *C. squamosus* aging are the lack of juvenile samples, and the discontinuity in size (or age) between fish less than 15 years of age and those greater than 15 years. It is possible that small individuals with certain growth characteristics are being interpreted as older than they actually are, which would shift their ages to the right and create the discontinuity observed in both males and females.

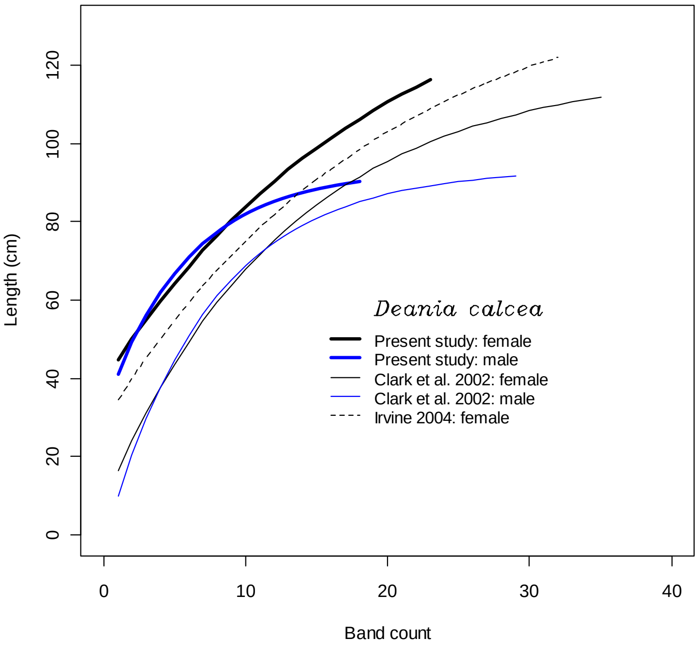

Figure 14: Comparison of von Bertalanffy curve fits for male and female *Deania calcea* from the present study, Clark et al. (2002b), and females only (using internal band count data) from Irvine (2004).

3.6 Age Composition

The scaled age distributions for *D. calcea* on the Chatham Rise were very consistent through time, relatively flat, and showed a peak abundance at age 12, although individuals were present in significant proportions at all ages including as neonates (Figure 15). This indicates that availability to the survey gear may be lower for juvenile *D. calcea*, as catchability for those in the path of the trawl should be relatively high given their size, shape, and presumed swimming abilities. Young *D. calcea* may spend significant proportions of their time off the bottom or be distributed off the Chatham Rise.

In the Sub-Antarctic survey series, a relatively flat adult age distribution was observed, but younger fish were less prevalent (Figure 16). Lower relative abundance of individuals younger than 12 years, and the near absence of neonates compared with the Chatham Rise, suggest that parturition may occur further north than the Sub-Antarctic plateau.

C. squamosus was not observed often on the Chatham Rise survey, and only the 2007 and 2010 surveys sampled more than 50 individuals (Figure 17). The age distributions were not well estimated with mean weighted coefficients of variation (MWCVs) of 86%, but suggest a flat, wide age distribution with an abundance peak at age 1, an absence of juveniles until approximately age 10, an adult mode near 20 years, and a long flat tail to a maximum age near 40 years. This same pattern was observed in the Sub-Antarctic series, but also with high MWCVs. The dominant peak of 1-year old fish suggests that pupping can occur on both the Chatham Rise and the Sub-Antarctic plateau, but that individuals subsequently become more pelagic or otherwise leave the survey areas for approximately a decade.

3.7 Natural mortality estimates

Using maximum observed ages, natural mortality was estimated using Hoenig’s (1983) method as 0.200 for *D. calcea* ($A_{max} = 23$ years) and 0.110 for *C. squamosus* ($A_{max} = 42$ years). Because these populations have been exploited since the 1970s, natural mortality estimates using catch curve analysis are not directly applicable. Hoenig’s method uses only the observed maximum age (assuming that is the 99th percentile of age). However, an estimate of total mortality using catch curve analysis can be compared with the estimate using Hoenig’s (1983) method to check feasibility and to potentially estimate fishing mortality experienced by the population (SeaFIC 2007).

The maximum abundance at age for *D. calcea* was at age 12 in both survey series in almost every year (Figures 15, 16). Estimates of total mortality using the Chapman-Robson estimator (Robson & Chapman 1961, Dunn et al. 2002), with an estimated full recruitment to the fishery at age 12 indicate total mortality levels (Z) of 0.41 – 0.46 for the Chatham Rise and 0.32 – 0.41 for the Sub-Antarctic surveys (Figure 18a). The annual distributions are not independent, but combined they give an indication of the level of total mortality experienced. The total mortality is 15 – 25% higher than the estimated natural mortality rate, and is an indicator of the fishing mortality experienced by the stocks.

Age at full recruitment is confounded for *C. squamosus* because of the apparent unavailability of individuals from approximately 2 – 10 years of age (Figure 17). Therefore age at full recruitment was estimated to be 15 years (approximately 100 cm) to estimate total mortality of adults for *C. squamosus*, while the most abundant age class (age 1) was used as an alternative for sensitivity. An age at full recruitment of 1 resulted in unrealistic Z estimates of 0.05 – 0.11; less than the estimate of natural mortality. Using an age at full recruitment of 15 generated Z estimates between 0.10 – 0.14, similar to the natural mortality estimate of 0.11, and suggesting a low fishing mortality rate for both stocks (Figure 18b).

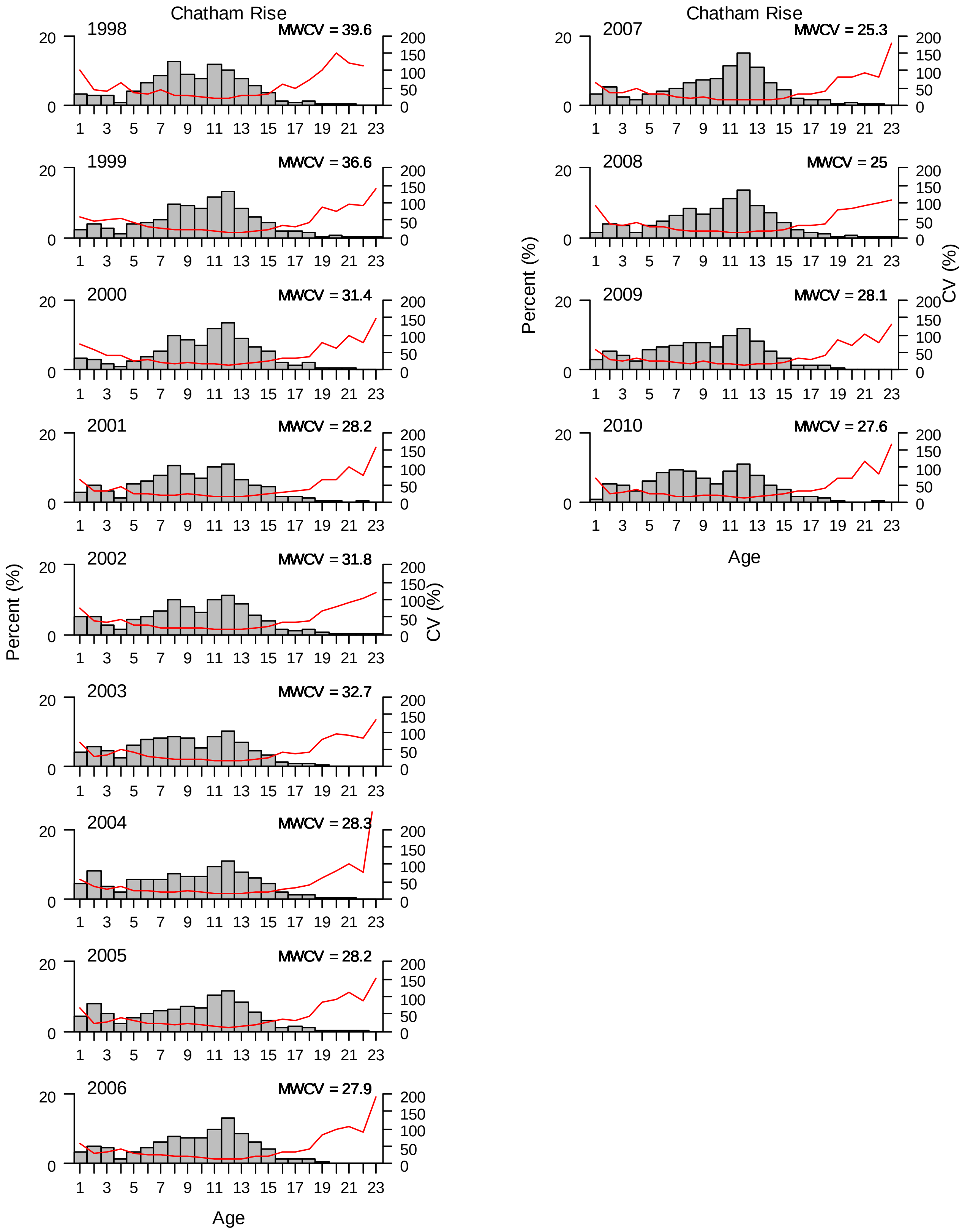

Figure 15: **Scaled age frequency distributions for *Deania calcea* from the Chatham Rise survey series 1998–2010. Note: Length data were not collected prior to 1998. Red lines indicate age-specific coefficient of variation, and mean weighted coefficient of variation is given for each year as MWCV.**

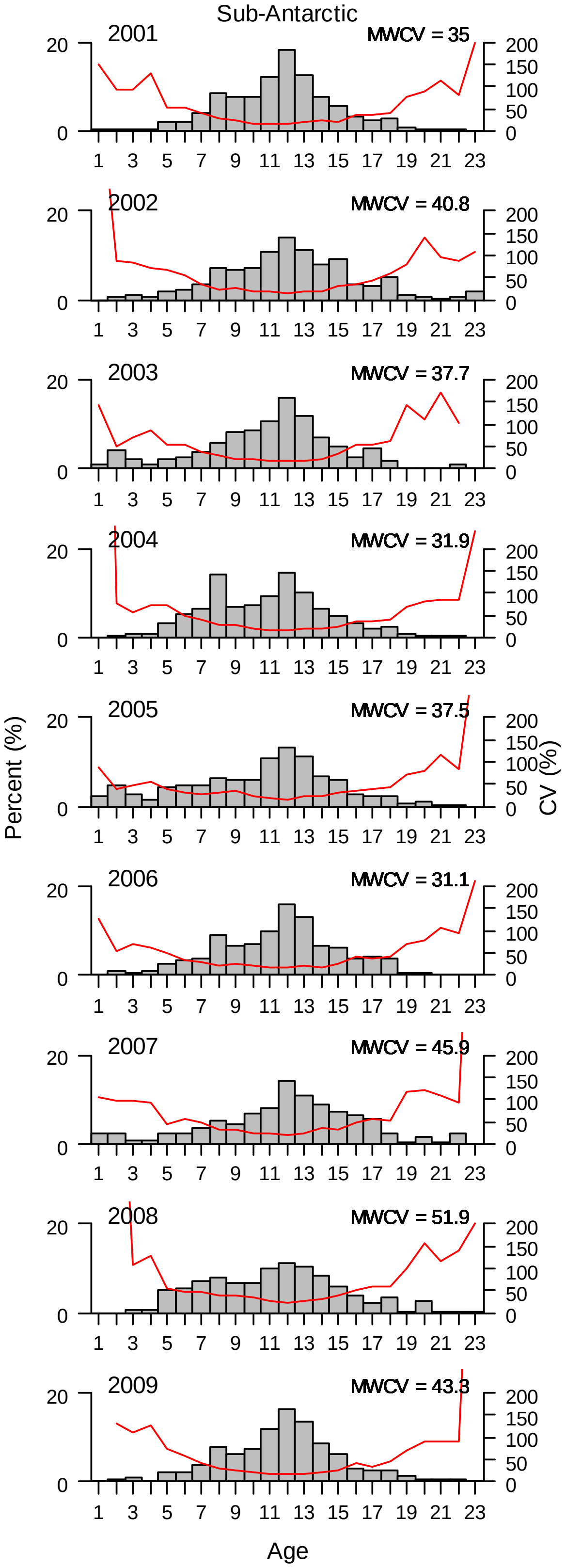

Figure 16: Scaled age frequency distributions for *Deania calcea* from the Sub-Antarctic survey series 2002–2009. Red lines indicate age-specific coefficient of variation, and mean weighted coefficient of variation is given for each year as MWCV.

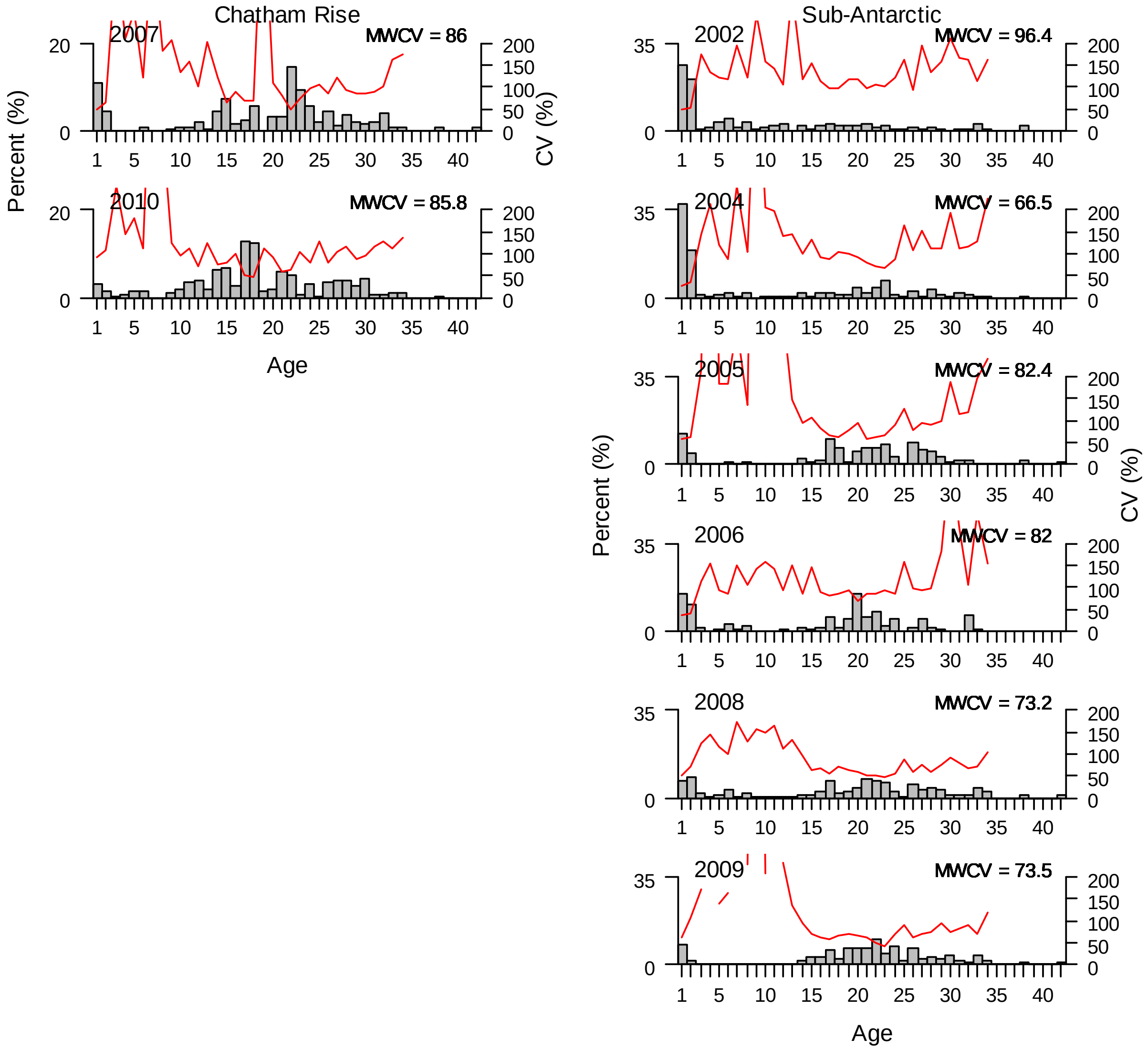

Figure 17: (a) Scaled age frequency distributions for *Centrophorus squamosus* from the (a) Chatham Rise survey series and (b) Sub-Antarctic survey series. Distributions are presented only if more than 50 individuals were sampled. Red lines indicate age-specific coefficient of variation, and mean weighted coefficient of variation is given for each year as MWCV.

The estimates for *C. squamosus* total mortality are suspect for a number of reasons. First, sample sizes were low, so the proportions at each age were not well estimated. There could be an ageing methodology error that tends to create flat, older age distributions, and the Chapman-Robson estimator can be sensitive to large year classes as they move through the age distribution (though no evidence of this was observed). Most likely, the reason for the flat age distribution is that full recruitment to the fishery does not occur at a particular age, due mainly to the spatial distribution of these males and females as they grow. Samples indicate that juveniles are relatively rare until age 10 – 15, but older fish may still not be fully available to the survey gear until much later, or at random, resulting in a flattened and unrealistic age structure from survey samples.

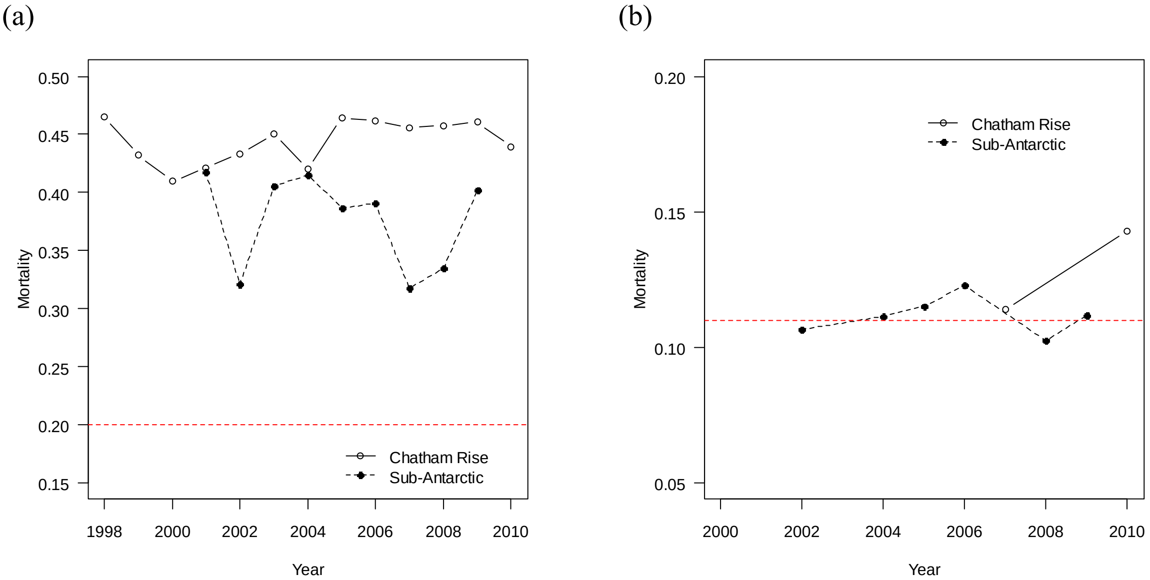

Figure 18: Estimates of total mortality (Z) estimates for each survey for (a) *D. calcea* (full selection at age 12) and (b) *C. squamosus* (full selection at age 15) using the Chapman-Robson (Robson & Chapman 1961) estimator. The red dashed horizontal line shows the estimated level of natural mortality based on the Hoenig (1983) method.

3.8 Reproduction

3.8.1 *Staging*

Maturity stages were collected from each species using new staging criteria developed by Francis and Lyon (unpublished data, Appendix I). These are an improvement over the previous "Wanaka" staging criteria (Clark & King 1989) by providing specific squalid characteristics for both males and females that separate immature, maturing, and gravid individuals in a simplified notation system. We note that the change in gonad staging method must be addressed during analysis as database extracts with "Wanaka" stages need to be translated to the new stages set out in Appendix I.

3.8.2 *Timing of reproduction*

The developmental stages of *D. calcea* gonads have been recorded during trawl surveys in December, January, March, April, and June. Mature fish of both sexes have been observed in each of these months, but gravid and post-partum females were rare and observed only in March and April (Figure 19a, b). However, this is based on observing only four females with pups after sampling 1703 females. Mature males did not show a seasonal trend in maturity status, indicating that they may be able to deliver reproductive products during mating throughout the year and that migration to mating areas does not occur (Clark & King 1989, Irvine 2004).

Developmental stages of *C. squamosus* were also recorded during these same surveys, and showed mature fish of both sexes throughout the year (Figure 19c, d). Only three females with pups have been observed out of 287 females sampled, and no indication of seasonality can be inferred.

Gestation periods have not been determined for either of these species. Gestation in *Squalus acanthias* has been estimated at 24 months (Hanchet 1988), and long gestation periods are hypothesized for other deepwater squalid sharks (Hamlett 1999, Irvine 2004). It is not clear why, if gestation is two years in duration, that observations of females with pups are so rare (Girad & De Buit 1999, Clarke et al. 2002a,b, Irvine 2004, Figueiredo et al. 2008). For the North Atlantic population, there has been a suggestion that pregnant females migrate away from areas where fishery sampling occurs, but it is not known to where. Severino et al. (2009) reported a high proportion of females with embryos off

Madeira suggesting a parturition area there. In New Zealand, young of the year are often sampled in fishery surveys, indicating that parturition in this region does not occur far away. An alternative hypothesis is that pregnant females become pelagic or move deeper and are therefore not available to bottom trawl gear. The lack of a distinct annual reproductive period, the large energy requirement to produce large yolky eggs, and the potential for a long resting period between pregnancies makes the number of reproductive events and their duration difficult to determine. Further, Clark & King (1989) suggested that because the frequency of reproductively maturing adult-sized females is so low throughout the year (approximately 25% of observations, Figure 19), *D. calcea* may have a resting period between pregnancies of four years.

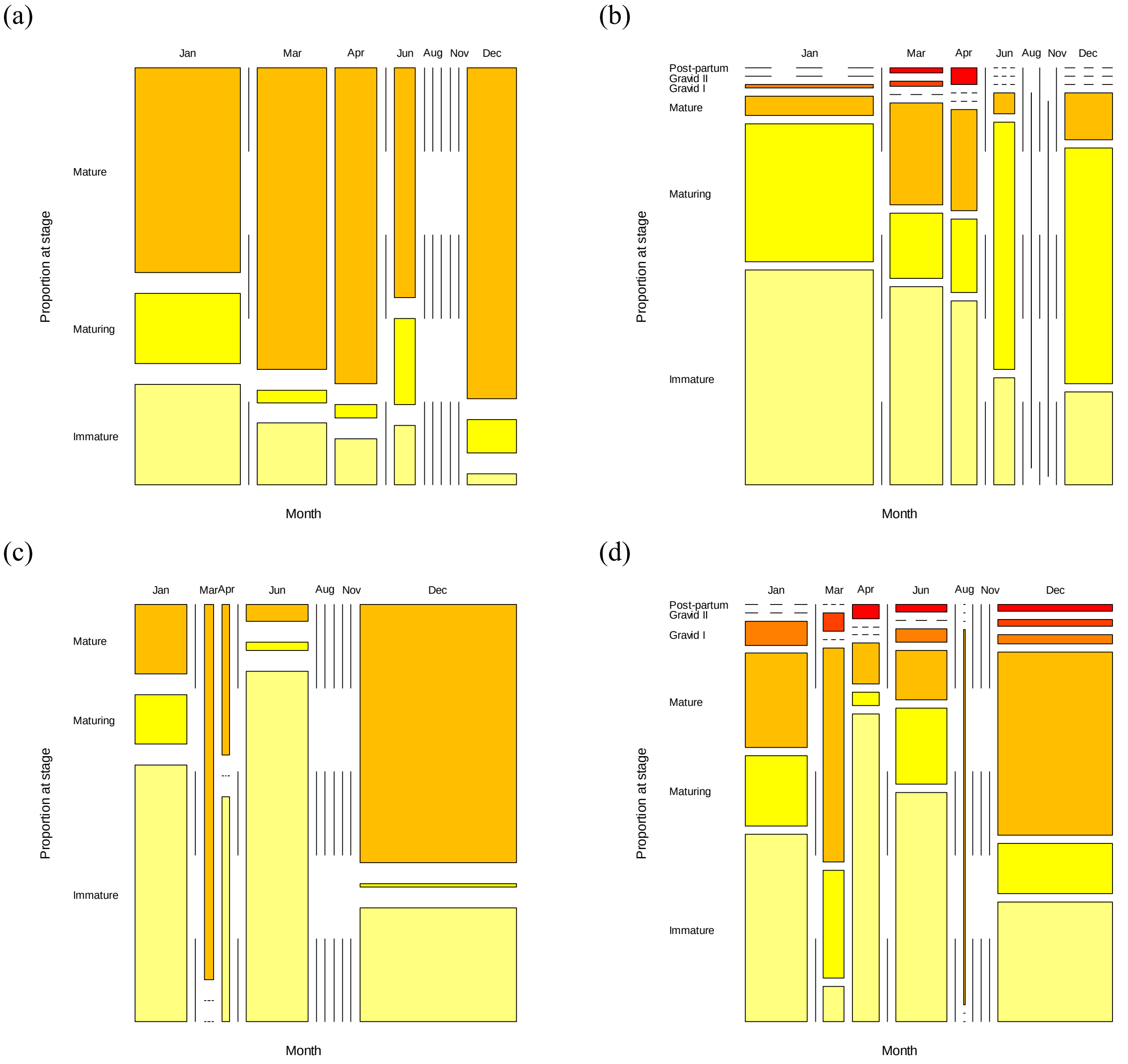

Figure 19: **Proportion of observed *Deania calcea* (a) males and (b) females, and *Centrophorus squamosus* (c) males and (d) females in each reproductive stage (see Appendix I for criteria) for each month sampled. No samples were available for February, May, or July–November. The width of each bar is proportional to the sample size in that month.**

3.8.3 *Length at maturity*

Length-at-maturity ogives for *D. calcea* fitted observations well and suggested an $L_{50\%}$ of 106 cm for females, and a much smaller $L_{50\%}$ of 78 cm for males (Figure 20a, Table 4). The main length mode observed in the trawl surveys was 80–90 cm, with an even sex ratio. Therefore, most of the males caught would be sexually mature (greater than 78 cm), but most of the females encountered would not yet be mature (less than 106 cm). Both ogives were steep, indicating a strong relationship with length and that resting adults were identifiable and not erroneously considered as maturing (i.e. immature status). These values compare well with those reported for *D. calcea* in the North Atlantic (85 cm male and 105 cm female, Clarke et al. 2002b) and in Australia (74 cm male and 95 cm female, Irvine 2004).

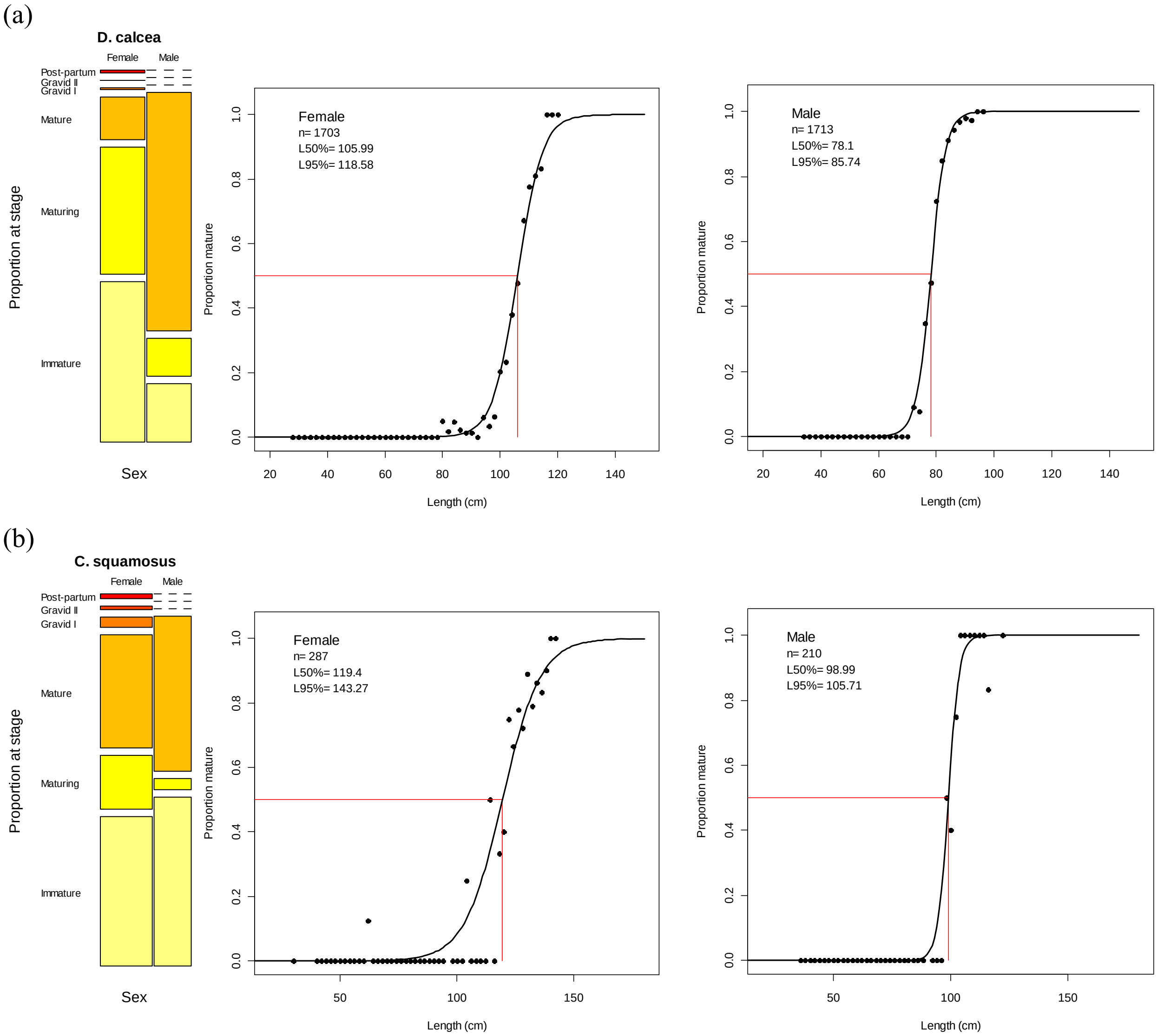

Figure 20: Overall proportion of observations at each gonad development stage by sex and length-at-maturity ogives for female and male (a) *Deania calcea* and (b) *Centrophorus squamosus*. Red lines indicate the $L_{50\%}$.

Length-at-maturity ogives for *C. squamosus* were a poorer fit to the data, especially for females, but suggested an $L_{50\%}$ of 119 cm for females and 99 cm for males (Figure 20b, Table 4). This is likely to be due to smaller sample sizes in each length bin to estimate the proportion robustly. These values are similar to those reported in the North Atlantic (101–102 cm male and 125–128 cm female, Clarke et al. 2002a, Bañón et al. 2006).

3.8.4 *Age at maturity*

Sample sizes to fit age at maturity directly were lower than those for length, and resulted in poorer fits to the observations. The effect of including “maturing” fish as mature is shown in Figure 21 as blue ogives, which are shifted left and steeper for each relation. The degree of left shift suggests that maturity is based more on size than age, and that the adolescent period may be fairly long.

The estimated age at 50% maturity ($A_{50\%}$) for *D. calcea* was very different between females (20.4 years) and males (8.7 years) (Table 4). However, the data for the female ogive were extremely variable with mature fish found as young as 9 years old and the first observation of 100% mature at age 22, with a maximum observed age of 23 years (Figure 21a,b). This is likely to indicate a poor ability to age this species and long reproductive rest periods, but interestingly, the variability is more pronounced in females than in males. Translated empirically from length, the $A_{50\%}$ should be approximately 16 years for females.

Similar problems with variable proportions mature were observed with *C. squamosus*, especially females, although the variability in proportion mature spanned a much large range of ages. Increasing sample size by reducing the number of age bins improved the fit somewhat (not shown), but large variation was still present.

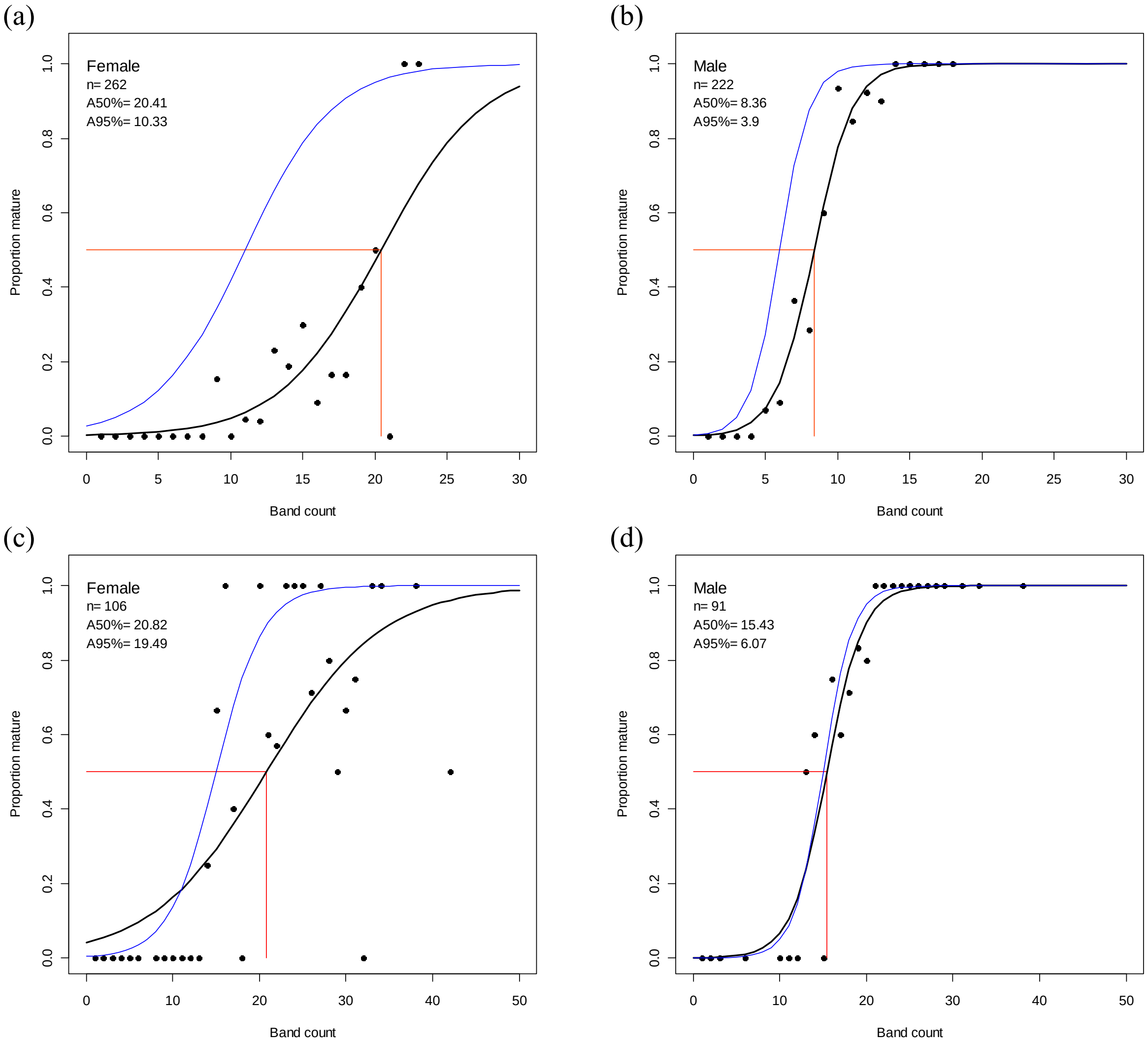

Figure 21: Age-at-maturity ogives for *Deania calcea* (a) females and (b) males, and *Centrophorus squamosus* (c) females and (d) males. Red lines indicate the A_{50}. Blue ogives indicate curves fit to data including maturing fish (stage 2) as mature.

Table 4: Parameter estimates for length- and age-at-maturity ogives for *Deania calcea* and *Centrophorus squamosus* sampled during research trawl surveys on the Chatham Rise and the Sub-Antarctic plateau.

Species	*D. calcea*		*C. squamosus*	
Sex	Female	Male	Female	Male
Length				
α	-24.78	-30.10	-14.73	-43.31
β	0.24	0.39	0.12	0.42
$L_{50\%}$	105.99	78.10	119.4	98.99
95% CI of $L_{50\%}$	105.13–106.91	77.44–78.67	114.77–122.75	94.87–100.96
N	1703	1713	287	210
Age				
α	-5.82	-6.32	-3.15	-7.48
β	0.59	0.76	0.15	0.48
$A_{50\%}$	20.41	8.36	20.82	15.43
95% CI of $A_{50\%}$	18.32–24.54	7.70–8.91	17.46–24.26	13.15–16.89
N	262	222	106	91

4. DEMOGRAPHICS

One of the inputs required for demographic analysis is litter size (number of female offspring per event), which is not available for either species from our samples. Litter size in *D. calcea* has been reported, from small sample sizes, as 8–14 (Clarke et al. 2002b, Irvine 2004), and a related species, *Deania profundorum*, as 6–11 (Sousa et al. 2009). Fecundity in *C. squamosus* has not been determined, but 7–11 developing ova have been observed in maturing females, with no obvious relation with maternal size (Girard & De Buit 1999, Clarke et al. 2001). The sex ratio of *D. calcea* embryos is approximately 1:1, but data are not available for *C. squamosus*. Other deepwater sharks have been shown to have sex ratios at birth that deviate from 1:1. However, the observed sex ratio of *C. squamosus* samples less than 80 cm in length (i.e. before sex-specific differences in growth rate are expressed) is 52% female, so we assumed a 1:1 sex ratio at birth for this species also. We assumed 6 females per litter for *D. calcea* and 5 females per litter for *C. squamosus* as inputs into demographic analysis.

The frequency of reproduction is difficult to estimate. Although large numbers of observations of each species exists, pregnant females were rare in the catch, and were only observed three times for *C. squamosus* in New Zealand samples (one noted with two pups, E. Jones, NIWA, unpublished data.). This lack of observations has led to speculation that pregnant adults inhabit depths too deep to fish or other unfishable habitats (as they are also not observed with longline gear). The alternative is that adult females undergo a resting period lasting three or four years (Clark & King 1989). Because gestation is likely to last up to two years, we conducted a sensitivity test using two years and four years between reproduction events (Rep_{freq}).

Natural mortality was estimated following Hoenig (1983) (See Section 3.7). Potential fishing mortality (F) was added to natural mortality and the fishing mortality associated with $r = 0$ was calculated (F_c) for different life history parameter values. Because of the lack of an independent method of age validation and the uncertainty associated with the aging method used, these estimates should be treated with caution. However, sensitivities to the maximum age were included in our estimates to assess robustness of the parameters.

Initial calculations for *D. calcea* showed that estimates of A_{Max}, fitted age at maturity of 20 years, with reproduction events every two years thereafter would not generate a positive value for r (Table 5). This was also true with a maximum age of 30 years with a reduced spawning frequency even with a more realistic $A_{50\%}$ of 16 years. When positive values of r were obtained, they were low, with a lifetime reproductive output (R_0) barely exceeding replacement value of one female offspring. The fishing mortality that would decrease *r* to 0 (F_c) is the equivalent of *r* when fishing mortality is zero, and therefore also low in these scenarios, well below the corresponding estimate of natural mortality. Generation times were typically 20–25 years.

Table 5: Table of life history parameters calculated from life history growth and reproduction parameters. Maximum ages for sensitivity from Clarke et al. (2002a,b). M was estimated for each scenario following Hoenig (1983). SPR and $SPR_{MER/S0}$ were calculated for the Ricker curve from Brooks et al. (2007). Calculations assumed that all age classes are selected by the fishery.

Species	A_{Max}	Rep_{freq}	$A_{50\%}$	*M*	*r*	R_0	G	SPR_{MER}	$SPR_{MER/S0}$
D. calcea	23	2	16	0.200	-0.050	0.38	18.93	3.60	1.02
	30	2	16	0.153	0.014	1.34	20.98	2.20	0.76
	30	4	16	0.153	-0.019	0.67	20.98	3.12	0.93
	35	2	16	0.132	0.039	2.36	22.25	1.80	0.68
	35	4	16	0.132	0.007	1.18	22.25	2.54	0.83
	35	2	20	0.132	0.010	1.22	25.47	2.43	0.80
C. squamosus	42	2	21	0.110	0.023	1.92	28.12	2.18	0.76
	42	4	21	0.110	-0.002	0.96	28.12	3.08	0.93
	70	2	21	0.066	0.070	8.84	34.57	1.31	0.57
	70	2	30	0.066	0.038	4.72	42.46	1.80	0.68

The SPR_{MER} as a proportion of the estimated initial biomass (survey estimate in 1991) was estimated to be high for *D. calcea*, 68–83% for scenarios with a positive *r*. This proportion (as a target) can be compared with the status from the relative biomass trends from standardised trawl surveys such as the Chatham Rise and Sub-Antarctic survey series (Figure 22). In each case, relative biomass indices for *D. calcea* showed a flat or modest increasing trend in the most current years relative to the initial years of the survey (Figure 22a,b). Therefore the metric of SPR_{MER}/S_0 would be greater than 1, indicating that either the initial value of S_0 was from an already impacted population, the population was not at equilibrium, the assumptions or parameter values of the demographic analysis were not accurate, or some combination of the above.

Productivity parameters were also low for *C. squamosus*, with values of *r* between -0.002 and 0.07. The level of fishing mortality that would depress *r* to 0 was also typically lower than estimates of *M* (except for the most productive life history scenario). Sample sizes for *C. squamosus* in either survey were typically too small and variable to generate precise biomass estimates. The Chatham Rise series was especially variable, but indicated a flat to modestly increasing trend over the period (Figure 22c). Estimates are somewhat more precise for the Sub-Antarctic survey, and relative to the estimates from the early 1990s, biomass appears have increased steadily since 2000 (Figure 22d). In each survey, the current biomass is close to or above the earliest biomass estimate for the series, suggesting as for *D. calcea*, that population status is likely to be stable or increasing.

The spawning potential ratio at maximum sustainable yield (SPR_{MSY}) is similar to SPR_{MER} as a metric for target stock status, though they reference slightly different points on the stock-recruit relation and are calculated using different estimators of stock productivity. SPR analysis shows the relationship between lifetime reproductive output and fishing mortality for a population with given productivity characteristics. Using CASAL (Bull et al. 2008), the %SPR was estimated as a function of various levels of fishing mortality (Figure 23).

For very low productivity stocks, F should be less than the rate that would result in a spawning biomass per recruit of 50% of a virgin population, resulting in a target biomass of greater than 45% B_0 (Ministry of Fisheries2008a). These results indicate that the current fishing mortality rate on *D. calcea* (15 – 25%, See Figure 18) would result in a SPR between 21% and 35% depending on the region, which is above the target level of fishing mortality (Table 6, Figure 23a). The target F to maintain the stocks at %SPR is approximately 0.09. The target fishing mortality rate for *C. squamosus* is even less, at 0.06, but this should be treated with caution because of the uncertainty in estimating M, Z, and %SPR (Table 6, Figure 23b). The $\%SPR_{MER}$ provides even more conservative estimates of target biomass ranging from 68 – 83% of B_0 for *D. calcea* and 57 – 76% for *C. squamosus*.

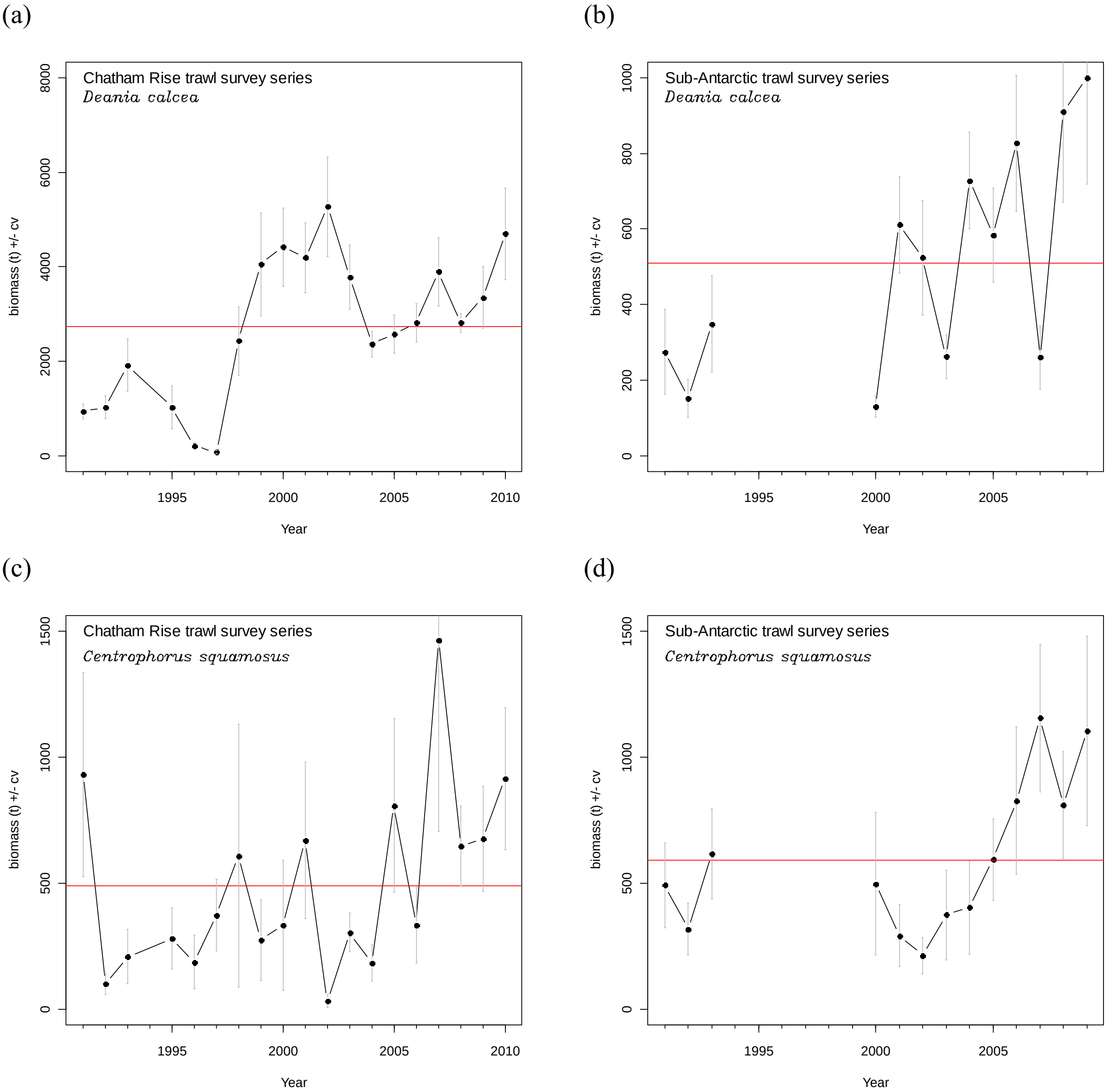

Figure 22: Relative biomass estimates for (a) *Deania calcea* from the Chatham Rise bottom trawl survey series (1992–2010) and (b) the Sub-Antarctic trawl survey series (1991–2009), and (c) *Centrophorus squamosus* from the Chatham Rise bottom trawl survey series (1992–2010) and (d) the Sub-Antarctic trawl survey series (1991–2009). Biomass estimates for core strata with 95% confidence intervals. Red horizontal lines shows the mean biomass during the series.

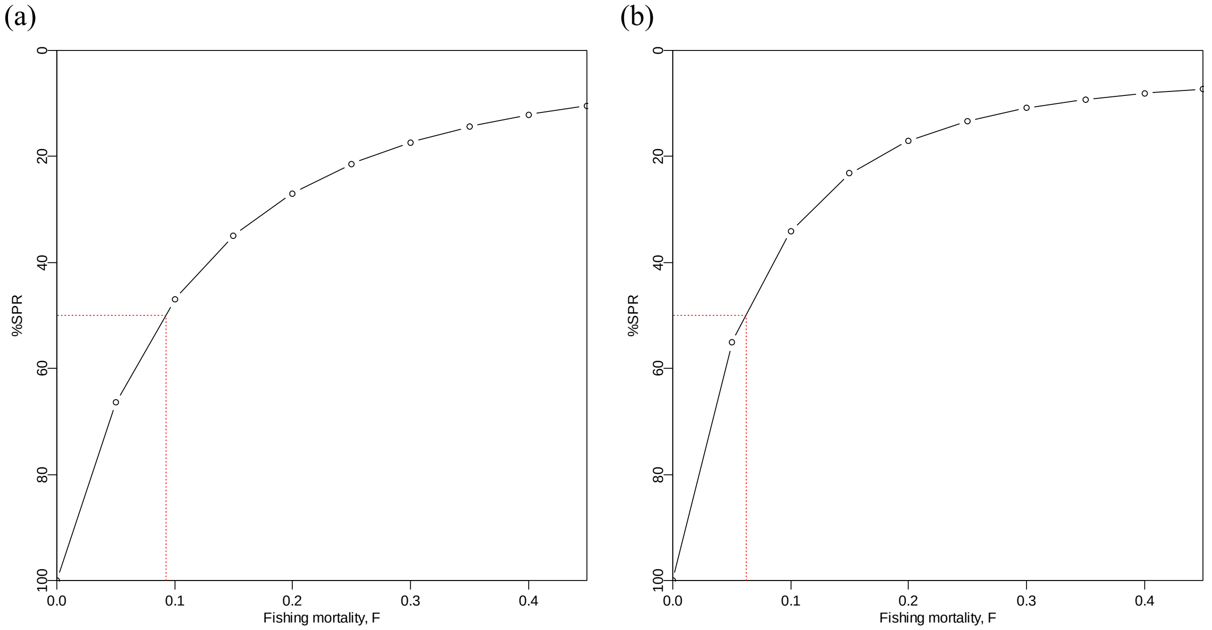

Figure 23: Percent spawning biomass per recruit in relation to fishing mortality for (a) *D. calcea* and (b) *C. squamosus*. Horizontal and vertical lines indicate the estimated fishing mortality at SPR$_{50\%}$

Table 6: Estimated fishing mortality (*F*) from Figure 18, the associated percent spawning biomass per recruit, target F approximating SPR$_{50\%}$, and the target %SPR$_{MER}$ for *Deania calcea* and *Centrophorus squamosus* from the Chatham Rise and the Sub-Antarctic regions.

Species	Region	Mean Z	Mean F	%SPR	Target %SPR	Target F	Target %SPR$_{MER}$
D. calcea	Chatham Rise	0.44	0.24	23	50	0.092	68–83
	Sub-Antarctic	0.38	0.18	30	50	0.092	68–83
C. squamosus	Chatham Rise	0.13	0.02	82	50	0.062	57–76
	Sub-Antarctic	0.11	0.00	100	50	0.062	57–76

5. THE POTENTIAL TO MONITOR STOCK STATUS

Assessing stock status for *D. calcea* and *C. squamosus* will be limited to very coarse methods for several reasons. First, available commercial landings and discard data are generally not useful (especially historically) as catches of these species were recorded as aggregate species codes of “deepwater dogfish” or “other sharks and dogfish”. Even as recently as 2005–2006, of the 1900 t recorded mortality for all deepwater sharks, 900 t was recorded using aggregated species codes, 600 t as seal shark, and 300 t as SND (*D. calcea*). Thus annual catch estimates of *D. calcea* or *C. squamosus* are not possible (Blackwell 2010).

Data from the Observer Programme are also inadequate to monitor historical trends in mortality because they too often used aggregate species codes, and the historical proportion of observed trips and spatial representation of observations varied significantly and would influence the levels of bycatch encountered. Significant levels of truly random deployment of observers on vessels operating in fisheries targeting hoki, oreo, and orange roughy could be useful in developing future time series of estimated total catch for these and other species of deepwater sharks if species-level identification is employed.

Bottom trawl survey data from the summer Chatham Rise hoki surveys and the summer Sub-Antarctic hoki surveys have recorded species-level data since the early 1990’s. However, we note that some errors in species identification may have occurred in the 1992 Sub-Antarctic survey (*D. calcea* mistakenly identified as *D. quadrispinosusm* (DEQ)), and small *C. squamosus* may have been aggregated as "other sharks and dogfish" in 1991. The trawl survey trends must be treated with caution as they do not monitor the entire depth range of these species, and therefore only index population biomass if the proportion of the stock within the surveyed strata remains constant through time. Biomass estimates are also limited by low sample sizes, especially for *C. squamosus*, but provide some coarse indication of biomass trend.

The demographic analysis above provides some indication of productivity, and population resilience for these two species by synthesizing life history data and making simplifying assumptions about stock structure, reproduction, and fishing impacts. It also provides a population status indicator similar to SPR_{MSY}, which could be used to evaluate current abundance. The sensitivities of this method regarding stock status at the beginning of the time series (S_0), and necessary life history parameters relating to age and reproductive frequency, constrain the utility of this method with the data available.

Earlier surveys do exist for both the Chatham Rise and Sub-Antarctic, though they are not strictly comparable because of differences in survey depths, areas, and gear and performance (Hurst & Schofield 1991). In addition, they only provide minimal length composition data for *D. calcea*. With the small sample sizes, no comparable distributions of length or weight are possible.

6. CONCLUSIONS

Demographic analyses are useful to quantify and scale the potential vulnerability of a species to impacts of fishing mortality and to project the speed of population recovery. However, they are sensitive to input parameters that are difficult to quantify, such as M (Cortès 2002, Carlson et. al. 2003, Braccini et al. 2006). We chose several possible values of maximum age and reproductive frequency to demonstrate the range of productivity values that resulted. The conclusion from sensitivity tests in this study is that regardless of the potential plausible values of A_{max} or reproduction frequency, values of r are low, and these species show low productivity. Further use of metrics such as SPR_{MER} still require an index of abundance and assumptions of population equilibrium for an unfished stock.

The flat or increasing biomass trends resulting from the Chatham Rise and Sub-Antarctic surveys are encouraging, especially given the unknown impacts of deepwater fisheries prior to 1992, and the scale of estimated annual mortality since then (see Blackwell 2010). The apparent conflict between low values for r, flat or increasing biomass trends, and stable age structures could be the result of several factors, such as:

a. The estimate of productivity is low because life history parameters are incorrect (e.g., age is too high, M is not constant, reproduction is more frequent),

b. A reduction in deepwater fishing mortality has allowed a slow recovery from pre-1990 impacts, or

c. Much of the population is not susceptible to fishing creating a cryptic spawning biomass (e.g., a portion of the population is pelagic).

Each of these effects could be significant and they are not mutually exclusive. Age has not yet been independently validated, so maximum age is based on interpretation of growth. The large orange roughy fisheries occurred during the 1980's (Ministry of Fisheries Science Group 2009), before the first biomass estimates were available and before any significant length data were collected for these species. Finally, the lack of medium size *C. squamosus* and the lack of pregnant females indicate that we do not yet know their reproductive life history or potential distribution or migratory behaviours.

Spawning biomass per recruit analysis and SPR_{MER} analysis both suggest that an F of less than 0.09 would result in a stable population at greater than 45% B_0. Current estimates of F from catch curve analysis for *D. calcea* indicate an F of 0.15 – 0.25 depending on region, although the estimate of M is very uncertain. Although the estimated value of F is higher than the target F, the population biomass trends for both species appear to be stable with the fishing pressure experienced for the past decade or more.

There are two feasible opportunities for monitoring stock status via maximum constant yield (MCY) at present; 1) monitor total mortality through the Observer Programme with a focus on species identification, and 2) utilize the biomass indices from the RV *Tangaroa* surveys of the Chatham Rise and Sub-Antarctic, perhaps with some expansion of deep-water stations to better incorporate the depth distribution of these species. Although *D. calcea* may be monitored in this way, *C. squamosus* and other deepwater shark catches are not consistent enough for precise estimates. This creates a problem in that some of these species may be less productive than *D. calcea*, and may respond differently to fishing mortality.

7. RECOMMENDATIONS TO IMPROVE STOCK MONITORING

Our recommendations fall into two categories. Those addressing stock monitoring needs (1–4) and those addressing research needs required to improve assessment of stock status of deepwater sharks (5–9).

1. Improve commercial fishing vessels identification and reporting of deepwater shark catch at the species level.

2. Design observer coverage to provide species-level identification of deepwater shark bycatch from all areas where fishing occurs deeper than 300 m to estimate mortality for the entire region. We have little information on the distribution of these species outside of surveyed areas.

3. Collect data on length, weight, and reproductive status for all species of deepwater sharks through the Observer Programme to increase sample sizes for less abundant species, especially over wider areas than sampled by trawl surveys (e.g. East Coast North Island, West Coast North Island).

4. Add deepwater survey strata to Chatham Rise and Sub-Antarctic surveys to increase sample sizes for *C. squamosus* (and other less abundant species), index a larger proportion of the population, and increase the precision of survey biomass estimates.

5. Develop a new method to validate spine ages. New Zealand collects comparatively large sample sizes of these species during trawl surveys. Collaboration with researchers developing new age validation techniques could provide the best information for New Zealand fishery managers while generating robust scientific progress in age validation methods.

6. Conduct research to establish the locations of parturition and utilise samples from those areas to determine gestation period and reproductive frequency in deepwater shark species, as productivity estimates are sensitive to values for these parameters. These locations would also be ideal areas to conduct tagging studies.

7. Conduct deepwater tagging experiments to determine the proportion of time different age classes spend in the pelagic environment, and potentially document the spatial movement patterns of individuals of reproductive age, especially pregnant females.

8. ACKNOWLEDGEMENTS

Caoimhghin Ó Maolagáin prepared the spine sections, developed ageing protocols for each species and provided nominal ages for all samples used in this analysis. We thank him for his diligence, insights into section interpretation, and suggestions made to improve the age determination process for deepwater sharks. We also thank the international age readers (Sarah Irvine, Teresa Moura, Neide Lagarto, and Charles Cotton) for their time and expertise in ageing the reference sets. Dan Fu generously provided R assistance, and also generated custom data extracts and scaling for length and age distribution analysis, as well as assisting with demographic analysis. Malcolm Clark provided historical reproductive stage data from the 1985–1986 *Wanaka* surveys of the North Island. This project was originally developed and led by Michael Manning, and we appreciate the thought and detail he gave it. Colin Simpfendorfer (James Cook University, Tasmania) generously provided the R code to calculate life history parameters in the demographic analysis. We thank the Ministry of Fisheries Aquatic Environment Working Group for helpful discussion and comments. This project was funded by the New Zealand Ministry of Fisheries as project ENV2008-04. We would like to thank Emma Jones for reviewing this report internally, and Mary Livingston for her thoughtful review and comments.

9. REFERENCES

Au, D.W.; Smith, S.E. (1997). A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Canadian Journal of Fisheries and Aquatic Sciences 54*: 415–420.

Bañón, R.; Piñeiro, C.; Casas, M. (2006). Biological aspects of deep-water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* in Galician waters (north-western Spain). *Journal of the Marine Biological Association of the United Kingdom 86*: 843–846.

Blackwell, R.G. (2010). Distribution and abundance of deepwater sharks in New Zealand waters, 2000–01 to 2005–06. *New Zealand Aquatic Environment and Biodiversity Report* No. 57. 51p.

Blackwell, R.G.; Stevenson, M.L. (2003). Review of the distribution and abundance of deepwater sharks in New Zealand waters. *New Zealand Fisheries Assessment Report* 2003/40. 48 p.

Braccini, J.M.; Gillanders, B.M.; Walker, T.I (2006). Hierarchical approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in southeastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences 63*:2456–2466.

Brooks, E.N.; J.E. Powers. (2007). Generalized compensation in stock-recruit functions: properties and implications for management. *ICES Journal of Marine Science 64*: 413–424.

Brooks, E. N., Powers, J. E., and Corte´s, E. (2010). Analytical reference points for age-structured models: application to data-poor fisheries. – ICES Journal of Marine Science, 67: 165–175.

Bull, B.; Dunn, A. (2002). Catch-at-age user manual v1.06.2002/09/12. NIWA Internal Report 114. 23 p. (Unpublished report held by NIWA library, Wellington.)

Bull, B.; Francis, R.I.C.C.; Dunn, A.; McKenzie, A.; Gilbert, D.J.; Smith, M.H.; Bian, R. (2008). CASAL (C++ algorithmic stock assessment laboratory): CASAL user manual v2.20-2008/02/14. *NIWA Technical Report 130*. 276 p.

Campana, S.E.; Annand, M.C.; McMillan, J.I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society 124*: 131–138.

Campana, S.E.; Jones, C.; McFarlane, G.A.; Myklevoll, S. (2006). Bomb dating and age validation using the spines of spiny dogfish (*Squalus acanthias*). *Environmental Biology of Fishes* 77:327–336.

Carlson, J.K.; Cortes, E.; Bethea, D.M. (2003). Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. *Fisheries Bulletin 101*:281–292.

Clark, M.R.; King, K.J. (1989). Deepwater fish resources off the North Island, New Zealand: results of a trawl survey, May 1985 to June 1986. New Zealand Fisheries Technical Report. Ministry of Agriculture and Fisheries, Wellington (New Zealand). 55 p.

Clarke, M.W.; Connolly, P.L.; Bracken, J.J. (2001). Aspects of reproduction of the deep water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. *Journal of the Marine Biological Association of the United Kingdom 81*: 1019–1029.

Clarke, M.W.; Connolly, P.L.; Bracken, J.J. (2002a). Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trought and Porcupine Bank. *Journal of Fish Biology 60*: 501–514.

Clarke, M.W.; Connolly, P.L.; Bracken, J.J. (2002b). Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* west and north of Ireland. *Fisheries Research 56*: 139–153.

Clarke, M.W.; Irvine, S.B. (2006). Terminology for the ageing of chondrichythan fish using dorsal-fin spines. *Environmental Biology of Fishes 77*: 273–277.

Compagno, L.J.V.; Niem, V.H. (1998). Squalidae. Dogfish sharks. pp. 1213–1232. *In:* K.E. Carpenter and V.H. Niem (eds.) FAO Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. FAO, Rome.

Cortes, E. (2002). Incorporating uncertainty into demographic modelling: Application to shark populations and their conservation. *Conservation Biology 16(4)*: 1048–1062.

Dunn, A.; Francis, R.I.C.C.; Doonan, I.J. (2002). Comparison of the Chapman Robson and regression estimators of Z from catch-curve data when non sampling stochastic error is present. *Fisheries Research 59(1–2)*: 149–159.

Figueiredo, I.; Moura, T.; Neves, A.; Gordo, L.S. (2008). Reproductive strategy of leafscale gulper shark *Centrophorus squamosus* and the Portuguese dogfish Centroscymnus coelolepis on the Portugese continental slope. *Journal of Fish Biology 73*: 206–225.

Francis, M.P.; Duffy, C. (2005). Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fishery Bulletin 103*: 489–500.

Francis, M.P.; Ó Maolagáin, C. (2004). Feasibility of ageing shovelnose dogfish (*Deania calcea*), leafscale gulper shark (*Centrophorus squamosus*), and seal shark (*Dalatias licha*). Final Research Report for Ministry of Fisheries Research Project ENV2001/05 Specific Objective 2. 31 p. (Unpublished report held by the Ministry for Primary Industries, Wellington.)

Froese, R. and D. Pauly. Editors. 2011.FishBase. World Wide Web electronic publication. www.fishbase.org, version

Girard, M.; Du Buit, M.H. (1999). Reproductive biology of two deep-water sharks from the British Isles, *Centroscymnus coelolepi*s and *Centrophorus squamosus*. *Journal of the Marine Biological Association of the U.K. 79*, 923–931.

Graham, K.J.; Andrew, N.L.; Hodgson, K.E. (2001). Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research 52*: 549–561.

Hamlett, W.C. (1999). Female reproductive system. pp 398–443 *In:* W.C. Hamlett & T.J. Koob (eds.). *Sharks, skates and rays; the biology of elasmobranch fishes*. John Hopkins University Press, USA.

Hanchet, S. (1988). Reproductive biology of *Squalus acanthias* from the east coast, South Island New Zealand. *New Zealand Journal of Marine and Freshwater Research 55*: 537–549.

Hoenig, J.M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin 81*: 898–903.

Holden, M.J.; Meadows, P.S. (1962). The structure of the spine of spur dogfish (*Squalus acanthias* L.) and its use for age determination. *Journal of the Marine Biological Association of the United Kingdom 42*: 179–197.

Horn, P.L.; Neil, H.L.; Paul, L.J.; Marriott, P. (2010). Age validation and growth of bluenose *Hyperoglyphe antarctica* using the bomb chronometer method of radiocarbon ageing. *Journal of Fish Biology 77*: 1552–1563.

Hurst, R.J.; Schofield, K.A. (1991). Preliminary biomass estimates of hoki and other main species from trawl surveys of Southland/Sub-Antarctic, Jul–Aug and Nov–Dec 1990. *New Zealand Fisheries Assessment Research Document* 91/15. (Unpublished report held by NIWA library, Wellington). 25 p.

Irvine, S.B. (2004). Age, growth and reproduction of deepwater dogfishes from southeastern Australia. Deakin University, Ph.D. dissertation. 309 p.

Irvine, S.B.; Stevens, J.D.; Laurenson, L.J.B. (2006). Comparing external and internal dorsal-spine bands to interpret the age and growth of the giant lantern shark, *Etmopterus baxteri* (Squaliformes: Etmopteridae). *Environmental Biology of Fishes 77*: 253–264.

Jones, E.G.; Beare, D.; Dobby, H.; Trinkler, N.; Burns, F.; Peach, K.; and Blasdale, T. (2005). The potential impact of commercial fishing activity on the ecology of deepwater chondrichthyans from the west of Scotland. ICES 2005/Theme Session N, ICES CM 2005/N:16. 19 p.

Ketchen, K.S. (1975). Age and growth of dogfish *Squalus acanthias* in British Columbia waters. *Journal of the Fisheries Research Board of Canada 32*: 43–59.

Krebs, C.J. (1985). Ecology: the experimental analysis of distribution and abundance, 3rd ed. Harper and Row, New York.

Machado, P.B.; Figueiredo, I. (2000). A technique for ageing the birdbeak dogfish (*Deania calcea* Lowe, 1839) from dorsal spines. *Fisheries Research* 45:93–98.

Ministry of Fisheries (2008a). Operational guidelines for New Zealand's harvest strategy standard. October 2008. 66p.

Ministry of Fisheries (2008b). New Zealand national plan of action for the conservation and management of sharks. Ministry of Fisheries, Wellington. 90 p.

Ministry of Fisheries, Science Group (Comps.) (2009). Report from Fishery Assessment Plenary, May 2009: stock assessments and yield estimates. 209 p.(Unpublished report held in NIWA Greta Point library, Wellington.)

Musick, J.A.; Harbin, M.M.; Berkeley, S.A.; Burgess, G.H.; Eklund, A.M.; Findley, L.; Gilmore, R.G.; Golden, J.T.; Ha, D.S.; Huntsman, G.R.; McGovern, J.C.; Parker, S.J.; Poss, S.G.; Sala, E.; Schmidt, T.W.; Sedberry, G.R.; Weeks, H.; Wright, S.G. (2001) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries 25*: 6–30.

O'Driscoll, R.L.; MacGibbon, D.; Fu, D.; Lyon, W.; Stevens, D.W. (2011). A review of hoki and middle depth trawl surveys of the Chatham Rise, January 1992–2010. *New Zealand Fisheries Assessment Report* 2011/47. 814 p.

R Development Core Team (2008). R: A language and environment for statistical computing. Version R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Robson, D.S.; Chapman, D.G. (1961). Catch curves and mortality rates. *Transactions of the American Fisheries Society 90*: 181–189.

Seafood Industry Council (SeaFIC) (2007). Silver warehou: SWA 1 Adaptive Management Programme Full-term Review Report. AMPWG-2007/22. Unpublished report held by the Ministry for Primary Industries, Wellington.

Severino, R.B.; Afonso-Dias, I.; Delgado, J.; Afonso-Dias, M. (2009). Aspects of the biology of the leaf-scale gulper shark *Centrophorus squamosus* (Bonnaterre, 1788) off Madeira archipelago. *Arquipélago: Life and Marine Sciences 26*: 57–61.

Simpfendorfer, C.A. (1999). Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia. *Fishery Bulletin 97*: 978–986.

Simpfendorfer, C.A. (2004). Demographic Models: Life Tables, Matrix Models and Rebound Potential. Pp. 187–204 *In:* Musick, J.A. and Bonfil, R. (eds) Elasmobranch Fisheries Management Techniques. APEC 203-FS-03.2, Asia-Pacific Economic Cooperation, Singapore.

Simpfendorfer, C.A; Kyne, P.M. (2009). Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. *Environmental Conservation 36*: 97–103.

Sminkey, T.R.; Musick, J.A. (1996). Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fishery Bulletin 94*: 341–347.

Soldat, V.T. (1982). Age and size of spiny dogfish, *Squalus acanthias*, in the Northwest Atlantic. *NAFO Scientific Council studies 3*: 47–52.

Sousa, R.; Ferreira, S.; Chada, T.; Delgado, J.; Carvalho, D. (2009). First approach to the biology of the deep-water shark *Deania profundorum* (Chondrichthyes: Centrophoridae). *Marine Biodoversity Records 2(e44)*:1–6.

Tanaka, S. (1990). The structure of the dorsal spine of the deep sea squaloid shark *Centrophorus acus* and its utility for age determination. *Nippon Suisan Gakkaishi 56*: 903–909.

Veríssimo, A; McDowell, J.R.; Graves, J.E. (2011). Population structure of a deep-water squaloid shark, the Portuguese dogfish (*Centroscymnus coelolepis*). *ICES Journal of Marine Science, 68*(3), 555–563. doi:10.1093/icesjms/fsr003

Veríssimo, A; McDowell, J.R.; Graves, J.E. (2012). Genetic population structure and connectivity in a commercially exploited and wide-ranging deepwater shark, the leafscale gulper (*Centrophorus squamosus*). *Marine and Freshwater Research*, 2012, 63, 505–512. http://dx.doi.org/10.1071/MF11237

von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology 10*: 181–213.

Yano, K.; Tanaka, S. (1988). Size at maturity, reproductive cycle, fecundity, and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coelolepis* in Suruga Bay, Japan. *Nippon Suisan Gakkaishi, 54*: 167–174.

Appendix I: Criteria used to determine reproductive stage for sharks including *Deania calcea* and *Centrophorus squamosus*. Note that these criteria may not be appropriate for all species of sharks depending on their life history. For the purposes of estimating maturity ogives, stages 1 and 2 were considered immature for each sex. Stages from the "Wanaka" system are given in parentheses.

Stage	Name	Males	Females
1	Immature	Claspers shorter than pelvic fins, soft and uncalcified, unable or difficult to splay open (11)	Ovaries small and undeveloped. Oocytes not visible, or small (pin-head sized) and translucent whitish (11)
2	Maturing	Claspers longer than pelvic fins, soft and uncalcified, unable or difficult to splay open or rotate forwards (12,21)	Some oocytes enlarged, up to about pea-sized or larger, and white to cream. (21,(27,37,47=resting))
3	Mature	Claspers longer than pelvic fins, hard and calcified, able to splay open and rotate forwards to expose clasper spine (22,23,24)	Some oocytes large (greater than pea-sized) and yolky (bright yellow) (31,41)
4	Gravid I	*Not applicable*	Uteri contain eggs or egg cases but no embryos are visible (22,32,42)
5	Gravid II	*Not applicable*	Uteri contain visible embryos. (23,33,43,24,34,44,25,35,45) *Not applicable to egg laying sharks and skates.*
6	Post-partum	*Not applicable*	Uteri flaccid and vascularised indicating recent birth (26,36,46)

Appendix II. Ageing protocol developed by NIWA spine age readers and provided as documentation in the comparison of age determination by international are readers.

Ageing protocol for dorsal fin spines of shovelnose dogfish (*Deania calcea*, SND)

National Institute of Water and Atmospheric Research Ltd
Private Bag 14901, Wellington, New Zealand

Contact: Steve Parker s.parker@niwa.co.nz
+64 03 545 7882

Spine sections

- Thick transverse sections (ca. 300 µm) were cut through the second dorsal fin spine approximately 10 mm from the tip of an unworn spine and mounted in epoxy resin on a glass slide with a glass cover slip. Additional sections taken ca. 5 mm from the tip are useful in some cases, particularly for worn spines.
- The reference set contains sections from 50 sharks. Each shark has sections taken at ca 5 mm and ca10 mm from the tip: the former are labelled with a number that ends in "-1" (e.g. SND-36-3-1) and the latter with a number that ends in "-2" (e.g. SND-36-3-2). Within each slide, the sections are numbered 1-6 in a clockwise fashion starting at the lower right (opposite side from label) corner. The section to be aged on each slide is marked with a black circle on the cover slip. The 10 mm sections (-2) are usually the best.
- Slide SND-78 has three circled sections from different sharks to include, labelled 2, 3 and 4.
- The reference set contains one very clear (and very unusual!) section (SND-OLD-130) which provides a good starting point for identifying important structures prior to counting other sections.
- The reference set contains a section from one very small (33 cm TL) shark (36-3) that was new-born (0+) based on the presence of a strong mode at 30-35 cm in length-frequency distributions. This section appears to have three dark and two light bands, but measurement of the antero-lateral spine thickness gives a value of about 107 µm, which indicates that the discontinuity zone had not yet formed. The banding pattern in this shark is outside the discontinuity and should not be counted. Spine thickness should be used as an indication of whether the discontinuity zone has formed.

Section viewing

- Sections should be viewed at a magnification of 100x under transmitted white light (bright field illumination).
- Sections can be viewed from either side (sometimes viewing through the back of the glass slide clarifies the bands).
- Band clarity is sometimes enhanced by viewing with Differential Interference Contrast.
- Focussing depth may be adjusted continuously while counting across the section as the best band clarity is not always at the same depth in different parts of the section.

Starting point for counting band pairs

- Counts should begin at the “discontinuity” zone between the middle and inner dentine layers of the spine (see Figure II.1). This is a distinct, bright-white (in transmitted light) zone. In young fish, the zone is usually very clear and present around the entire section. The zone fades with age, and in older fish it may be restricted to the anterior two-thirds of the section, or even disappear altogether.
- 0+ (young-of-the-year) fish do not have this discontinuity zone, but presumed 1+ fish do have it. The bright zone and its succeeding dark zone are therefore defined as the first band pair.
- In older fish that lack a visible discontinuity zone, the starting position can be determined by measuring from the outer margin of the section in the antero-lateral sector of the section. Discontinuities in this region are centred about 140-180 µm from the outer margin.
- In juvenile sharks, there may be visible band pairs outside the discontinuity. These pre-birth bands appear to merge and become fainter with increasing age, and should not be counted. In very small fish, the bright bands in this region may be confused with the discontinuity. If the spine thickness in the antero-lateral sector is markedly less than 140 µm, a discontinuity zone has probably not been deposited. In that case, the shark should be scored as 0+.

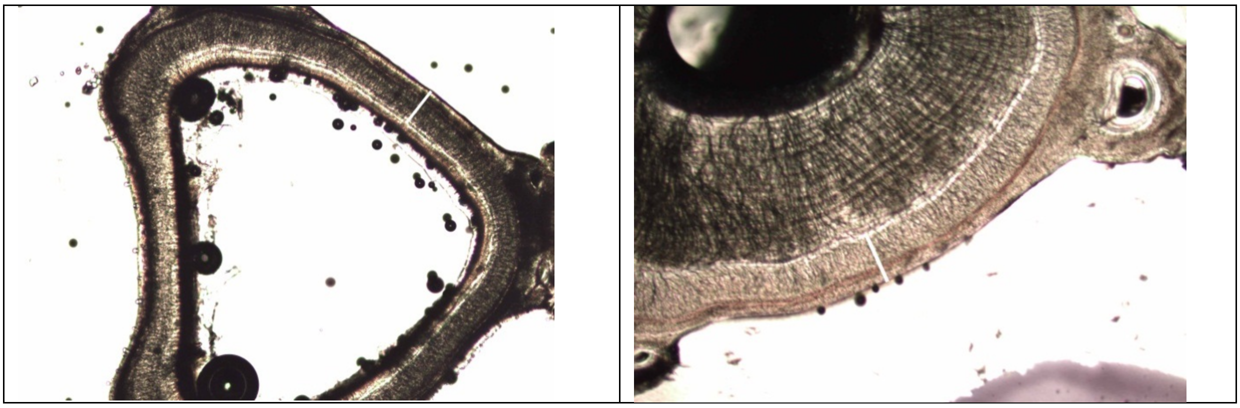

Figure II.1: Thick sections of *Deania calcea* dorsal fin spines of (left) 42.5 cm TL female (SND 78-3) and (right) 82 cm TL male (SND-OLD-130). White bars indicate locations for the measurement between the outer edge of the spine and the bright white discontinuity mark.

Counting bands

- Start counting at the discontinuity zone (count as band pair 1) and proceed towards the lumen.
- Count complete band pairs; i.e. pairs of light and dark bands. The number of band pairs is equal to the number of dark bands beyond the discontinuity zone. Some readers may find it easier to count light bands. However this will lead to a partial band pair being counted at the lumenal margin when the marginal composition is light. If so, the band pair count should be reduced by one. In practice, the composition of the lumenal margin may be difficult to determine and a simple correction for this difference may not be possible. Therefore, for consistency, dark bands should be counted to provide band pair estimates.
- It is often not possible to count a single transect across the whole section because of variations in band clarity, so look for and plan a counting path before starting your count. Move between counting paths by finding a distinct band and following it around the section until the new counting path is reached.

- Bands are frequently indistinct and hard to count in the region just inside the discontinuity. It helps to “get your eye in” by counting some relatively clear sections first, before progressing to difficult ones.
- The decision about whether to count narrow, closely-spaced bands as individual bands, or as split bands which should be grouped, may be difficult. In these cases, try following the bands around the section to see if they merge or separate. Be aware that narrow band spacing may indicate split bands, or it may indicate periods of slow growth. The decision about what to count in these situations is somewhat subjective.

Stopping point for band counts

- When reading the region just inside the lumenal margin, ensure that the margin is in sharp focus.

Age adjustments

- The timing of band deposition and parturition are not known, so no adjustments are currently made for date of birth and date of capture. Please indicate if band counts are adjusted for these factors.