

**DEMOGRAPHICS OF *ETMOPTERUS LUCIFER* (LUCIFER DOGFISH)**

BY

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## Abstract

This study provides the first comprehensive description of the demographics of lucifer dogfish (*Etmopterus lucifer*) from the Chatham Rise, New Zealand during January 2012. Lucifer dogfish is a non-QMS species commonly taken as bycatch in New Zealand deepwater trawl fisheries, where it has low commercial value and is usually discarded. Sexual maturity of females was determined by assessing the condition of the ovary and uterus, and the width of the uterus and oviducal gland. Male maturity was assessed by determining clasper and testes condition, inner clasper length, testes length, and testes weight. A sample of lucifer dogfish was aged by counting growth bands on the internal section of the dorsal fin spine ( $n = 97$ ), assuming annual deposition of bands. Intra- and inter-reader bias in age estimates was estimated, but count precision was high within ( $CV = 12.71\%$ ) and between reader age estimates ( $11.98\%$ ). A number of growth models were fitted to the length-at-age data, including the traditional and modified Von Bertalanffy growth formula (VBGF) and four cases of the Schnute growth model. Selection of the best growth model was based on the Akaike Information Criterion (AIC). The fourth case of the Schnute growth model best represented growth. Lucifer dogfish had an estimated age and length at maturity of 10.4 years and 34.0 cm respectively for males, and 13.0 years and 41.0 cm for females. The oldest observed fish were 17 and 14 years for males and females respectively. The total mortality estimates were in the range of 0.14 to 0.35  $\text{yr}^{-1}$ . Lucifer dogfish fed primarily upon mesopelagic fishes, with Hector's lanternfish (*Lampanyctodes hectoris*) identified as being the most common prey. Lucifer dogfish had late maturity relative to its longevity. Although sampling of the population was likely to be incomplete, and biases in age estimates may have occurred, these observed life history characteristics indicate that productivity will be low, and as a consequence, the precautionary approach should be applied, as the potential impact of commercial fishing on this species is high.

## Introduction

There has been a dramatic decline in many shark populations over recent decades due to increased levels of commercial fishing (Barker & Schluessel, 2005; Clua et al., 2011). These declines have been attributed to both targeted and incidental capture in fisheries (Cosandey-Godin & Morgan, 2011). Sharks are particularly vulnerable to overfishing because they exhibit life-history characteristics associated with a low reproductive potential and hence a low capacity to recover from exploitation, including slow growth, late maturation, and low fecundity (Francis & Mulligan, 1998; Verossimo et al., 2003; Irvine, 2004; Blackwell, 2010). In addition, for many shark species, their role as an apex predator means that their numbers may be relatively low as they are limited by the availability of resources (Camhi et al., 1998), further increasing their vulnerability to overfishing.

Sharks are targeted for a number of useable products including their meat, cartilage, fins, and liver (MPI, 2013a), and are considered to be an important commodity for communities in both developing and developed nations (Simpfendorfer et al., 2011). Traditionally, the economic value of sharks compared with other marine commercial species has been low (Coelho, 2007). While most shark meat is considered relatively unpalatable and of low export value (Barker & Schluessel, 2005; Harry et al., 2011), more recently, the growing global demand for shark fins for the Asian food market has exacerbated shark exploitation (Worm et al., 2013). Shark liver oil is also an important commodity as it has a wide range of industrial applications, including the pharmaceutical industry where it is used in cosmetics, sunscreen, and as an immune boosting health supplement (Bakes & Nichols, 1995; Wetherbee & Nichols, 2000).

Shark populations have declined due to targeted fishing, and also as a result of incidental capture which is often discarded as unwanted bycatch (Cosandey-Godin & Morgan, 2011; Vianna et al., 2012). Bycatch has been defined as “that part of the catch made up of the non-target species or species assemblages” (MPI, 2013a). Assessing the impacts of bycatch and discarding by commercial fisheries on sharks is

difficult, because catches are poorly reported, however it has been estimated that unreported bycatch may represent as much as 50 % of the total reported shark catch (Stevens et al. 2000). It is estimated that bycatch threatens up to 70 % of shark species (Gallagher et al., 2014). In New Zealand waters, sharks are taken both as bycatch and targeted species (MPI, 2014b), with whole weight catches averaging around 18,000 tonnes per year, having an export value in 2013 of NZ\$24.7 million (MPI, 2014b). As a result of the growth of target and bycatch fisheries, many shark populations worldwide have declined, with some species now considered to be at risk of extinction (Nadon et al., 2012).

Some shark species have experienced greater levels of overexploitation than others (Baum et al., 2003; NEFSC, 2006). In response to primarily fishing intensification, Baum et al. (2003) estimated population declines of between 40 - 89 % for various large oceanic and coastal shark species in the northwest Atlantic since the late-1980's. Female spiny dogfish (*Squalus acanthias*) were heavily targeted on the east coast of the USA in the late 20<sup>th</sup> Century, and over a 10 year period from 1988 to 1998, spawning stock biomass was estimated to decrease from 260,000 metric tonnes (mt) to 50,000 mt (NEFSC, 2006). The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species has assessed the extinction risk of 480 species of sharks from around the world. Of the 271 species that were not data deficient, 150 have been classified threatened or near threatened with extinction (Pew Environment Group, 2012).

It has been difficult to determine the status and resilience of many exploited shark populations to fishing pressure, due to the limited knowledge of their biology (Frisk et al., 2001). Significant information gaps on fecundity, age, mortality, and growth rates make effective management and conservation problematic (Frisk et al., 2001). Historically, due to the limited global market for shark meat and the lack of recorded information on the catches and landings of elasmobranchs, research and management of shark populations has been given low priority in comparison to other commercial species (Walker, 1998; Harry et al., 2011).

Scientists suspect that the decline of shark populations could also have significant ecological impacts on marine ecosystems (Stevens et al. 2000). Many sharks are apex predators, often being found at the top or near to the top of the food chain (Stevens et al. 2000). As well as directly consuming prey, they may indirectly influence prey distribution by changing prey feeding behavior (risk effects), as well as potentially bringing about trophic cascades when their numbers are depleted (Heithaus et al., 2007; Myers et al., 2007). Heithaus et al. (2007), in their study of green turtle (*Chelonia mydas*) grazing behavior, found that the presence of tiger sharks (*Galeocerdo cuvier*) in sea grass beds in Western Australia modified the spatio-temporal pattern of green turtle grazing. In summer when the tiger sharks were abundant, green turtles in good condition were found in areas where there was a reduced risk of shark predation, but lower food quality. In contrast, turtles in poor condition were found in areas where sharks were abundant and food quality was greater. However, when the sharks migrated away in winter, the turtles in good condition moved back into the areas with higher foraging quality (Heithaus et al., 2007). Myers et al. (2007) hypothesized that declines in shark populations may contribute to the release of mesopredator prey populations from predator control thereby inducing trophic cascades. Myers et al. (2007) examined the effects of the reduction of apex predators on lower trophic levels in coastal northwest Atlantic ecosystems. They postulated that a decline in predatory sharks coincided with an increase in the catch rates (abundance) of 12 prey species of small sharks, rays and skates.

There is, however, some debate among an increasing number of shark researchers surrounding the validity of shark depletion causing trophic cascades and risk effects on prey community structure due to the lack of empirical evidence supporting this hypothesis (Heithaus et al., 2008). Processes other than top-down effects could also be operating on prey populations sizes, such as changes in migration patterns, habitat expansions, and fishing pressure causing mortality or habitat modification (Ferretti et al., 2010).

The vast majority of the research is directed towards high profile species, such as the whale shark and the white shark, with bycatch species, such as lucifer dogfish, being largely ignored (Molina & Cooke, 2012).

In response to concerns about the continual shark decline and the widening public interest in shark conservation, the Food and Agricultural Organisation (FAO) introduced the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) in 1999. The framework's main goal was to "to ensure the conservation and management of sharks and their long term sustainable use" (MPI, 2013a). The IPOA states that all FAO members should adopt a corresponding National Plan of Action if their fisheries either target sharks, or regularly take sharks as incidental bycatch (MPI, 2013a). New Zealand responded with the introduction of the New Zealand National Plan of Action for Sharks 2008 (MPI, 2008; hereafter referred to as NPOA), which was then renewed in 2013 (MPI, 2013 a). The NPOA has a number of goals dealing specifically with the conservation and management of pelagic and deepwater sharks, including improved data collection of bycatch in the deepwater fisheries (MPI, 2013a). Francis and Lyon (2012), in their report commissioned by MPI to identify NPOA research gaps, recommended reducing the use of generic codes for species identification in order for fishers to accurately identify their catch, and also strengthening existing research and monitoring programmes. The collection of basic fisheries data, such as catch statistics, remains a priority for New Zealand shark management.

The key to the conservation and management of shark populations, and their long-term sustainable use, is for fisheries management to ensure that sharks are not overfished (Barriera, 2007). Some shark groups are considered to be particularly at risk from overfishing. Deepwater sharks are believed to be more vulnerable to exploitation than their pelagic and coastal counterparts, due to their assumed slower growth and reproduction rates (Clarke et al., 2002). It has been suggested that relatively low productivity occurs because the deep sea is a cold water and unproductive environment where food availability is low (Kyne & Simpendorfer, 2007).

The IUCN Shark Specialist Group defines deepwater chondrichthyans as “those species whose distribution is predominantly restricted to, or which spend the majority of their life-cycle at, depths below 200 m” (Camhi et al., 2009). Even though up to half of the extant species of shark occupy the deep sea, there is little research on their biology compared with inshore and pelagic species (Kyne & Simpfendorfer, 2007; Cotton et al., 2011). Over time, the continued depletion of coastal fish populations has meant that many deepwater fish stocks, with some less resilient species, are now targeted by fishing fleets (Klaer, 2001; García et al., 2008). Deep sea fisheries commonly use bottom trawling to harvest fish (Norse et al., 2012). In addition to the physical impact of trawling on the seabed, the effect on non-target fishes, including sharks, is also a major problem, as trawls generally have a broad selectivity resulting in high mortality (Jones, 1992; Norse et al., 2012; Uhlmann & Broadhurst, 2013).

Assessing the stock status of deepwater sharks caught as bycatch in trawl fisheries is extremely difficult, as they are often discarded, or when catches are reported they are specified under a generic code ‘other sharks and dogs’, because they are difficult to identify (Kyne & Simpfendorfer, 2007; Blackwell, 2010; Parker & Francis, 2012). In addition, there is a paucity of information on their life history characteristics compared with pelagic species, due to taxonomic uncertainty and the difficulties and relative sparsity in sampling at such depths (Chatzisprou & Megalofonou, 2005; Kyne & Simpfendorfer, 2007; Harry et al., 2011). Obtaining reliable data on the species composition of catches is also hampered by a low and unrepresentative scientific observer coverage in many commercial deepwater fisheries (MPI, 2013b).

Deepwater sharks in New Zealand represent a widely distributed, but poorly known resource (Blackwell & Stevenson, 2003). Blackwell (2010) reported that in general, little was known about their life history, abundance, and productivity. Concerns have been raised about the ability of deepwater sharks to sustain anything other than low levels of fishing mortality (Daley et al., 2002). In New Zealand, deepwater sharks are mainly taken as bycatch in middle depths and deepwater fisheries for hoki (*Macruronus novaezelandiae*), orange roughy (*Hoplostethus atlanticus*), and oreos

(Oresomatidae spp) (Blackwell, 2010). Usage of retained sharks in New Zealand is high with 70 % of all Quota Management System (QMS) species and 45 % of non-QMS species fully utilised or reported as fully utilised or released alive in the 2011/12 fishing year (MPI, 2014b).

If shark populations are to be managed responsibly an understanding of life history traits is essential in order to help accurately determine the status of the population, and thus ensure their long-term sustainability (Neves et al., 2009). The information that is lacking for many deepwater shark species includes age at maturity, longevity, fecundity, growth rate, and natural mortality. The estimation of these biological parameters is essential for understanding productivity of deepwater shark populations, as well as assessing a species relative exploitation risk (Irvine et al., 2006a; Goldman et al., 2012; Crespi-Abril et al., 2013).

Among the biological parameters, precise and accurate age estimates are considered to be one of the most influential variables, as age data are used to derive important parameters used in fisheries management, such as growth, age at maturity, fecundity at age, and mortality rate (Campana, 2001). A number of different structures have been used to age sharks, including vertebral centra, dorsal spines, and neural arches (Goldman et al., 2012). The age of sharks is determined by counting calcified growth bands on the various structures. Each growth band is usually assumed to represent one year's growth (Goldman, 2005), although in some species, bands are formed at different periodicities (Natanson & Cailliet, 1990).

Vertebral centra are the most commonly used structures to age sharks (Bubley et al., 2012). Shark vertebral centra, vary considerably in their degree of calcification and the clarity of the bands and rings, making them unsuitable for age determination in all species (Gennari & Scacco, 2007). Deepwater sharks generally have poor band definition, hypothesized to be caused by the lack of seasonality in the deep sea (Gennari & Scacco, 2007), in combination with low levels of calcium and food availability (Cailliet & Bedford, 1983). Other structures, primarily dorsal fin spines, have therefore been used to age deepwater sharks.

The use of dorsal fin spines as an alternative ageing structure has proven successful for some species of deepwater sharks, including Baxter's dogfish (*Etmopterus baxteri*; Irvine et al., 2006a ), golden dogfish (*Centroselachus crepidater*; Irvine et al., 2006b), birdbeak dogfish (*Deania calcea*; Irvine et al., 2012), and longsnout dogfish (*Deania quadrispinosa*; Irvine et al., 2012). Growth bands were observed on both the external surface, and inner sections of the dorsal fin spine, and were used in age and growth studies with varying success (Irvine et al., 2006b). Irvine (2004), found that external bands on spines were more accurate for age determination, as internal growth bands are thought to cease formation after a certain age. Irvine et al., (2006a) successfully aged golden dogfish using external dorsal fin spine banding. However, Irvine (2004), in her study of six species of deepwater sharks, found that of the 49 dorsal fin spines of a sample of Owston's dogfish (*Centroscymnus owstoni*), only 12 spines allowed confident age estimates using external banding, with internal bands being difficult to interpret, and so unable to be used to ascertain age. Given the above, there is an obvious difference in the reliability of interpreting age from external bands.

There are few reliable ageing studies of deepwater sharks and, in addition, few of these validate the age estimates (Clarke et al., 2002). Validation is defined by Francis et al. (2010) as "a determination of whether the age estimates are, on average, approximately correct". Validation of age estimates is considered to be more important in deepwater sharks as the reduced clarity of bands is thought to be a potentially significant source of underestimation of age (Gennari & Scacco, 2007) if age estimates are not validated (Francis et al., 2007; Hamady et al., 2014). Rigby et al. (2014) used a novel technique of Near Infrared Spectrometry (NIRS) in an attempt to validate the ages of the piked spurdog and the Philippine spurdog. They found a good correlation between the estimated ages of the dogfish dorsal fin spines and the NIRS spectra.

Age at maturity has been shown to be an important parameter influencing productivity, as species that mature at a younger age are better able to recover from overexploitation than those that mature later (Smith et al., 1998; Francis & Duffy,

2005; Parker & Francis, 2012). Sexual maturity of sharks can be examined both macroscopically and microscopically (Segura et al., 2013). Macroscopic determination of shark maturity is based on assessing the condition of the uteri and ovaries in females, and the claspers, testes, and sperm storage in males (ICES, 2010). Microscopic assessment commonly uses follicle development in females, and spermatocyst development in males (ICES, 2010). Hormone studies are also used to ascertain maturity of live animals (Awruch, 2007).

Lucifer dogfish (Figure 1) belongs to a genus characteristically referred to as the 'lantern sharks' (family Etmopteridae), as a number of species within the genus have small light-emitting organs on the sides of their body (Iwai, 1960). Etmopteridae is the most diverse family of squaloid sharks, encompassing ~ 12 % of current shark diversity, with greater than 50 described species (Kyne & Simpfendorfer, 2007; Claes et al., 2014). Bioluminescence is a key adaptation which has evolved in a number of deep-sea organisms in response to limited light availability (Straube et al., 2010). Named for its bioluminescence, lucifer dogfish is thought to utilize it for conspecific detection (Claes et al., 2014), but it may also be used to attract prey (Blackwell, 2010) or for counterillumination (Claes et al., 2010), enabling the shark to hide their silhouette in the water column and remain hidden from predator and prey below.



Figure 1: Photograph of lucifer dogfish from Chatham Rise, New Zealand.

Lucifer dogfish is commonly taken as bycatch in New Zealand deepwater trawl fisheries (Blackwell, 2010). It is found in temperate waters (40° N to 48° S) throughout the world's oceans but it is most frequently reported in the Western Pacific (Ebert et al., 2013). Lucifer dogfish is found at depths ranging between 150 and 1250 metres (Blackwell, 2010), but is found most frequently between 400 and 900 metres (Last & Stevens, 2009). The depths at which lucifer dogfish is commonly sampled however varies among studies (Baba et al., 1987; Bagley et al., 2013).

Bagley et al. (2013), in their sub-Antarctic survey, collected lucifer dogfish at depths greater than 800 metres, whereas Baba et al. (1987), in their study of shark diets of a number of species in Japan, found that lucifer dogfish had a relatively shallow distribution of between 200 and 300 metres. Lucifer dogfish has a widespread distribution around New Zealand, and is commonly found at depths between 400 and 900 metres (McMillian et al., 2011). Often described as a demersal species, lucifer dogfish has been reported in some midwater trawls. There is taxonomic confusion between lucifer dogfish and a number of other species of the family Etmopteridae, including Baxter's dogfish, smooth lantern shark (*Etmopterus pusillus*), and the slendertail lanternshark (*Etmopterus molleri*) (McMillian et al., 2011).

Lucifer dogfish is characterised by its small size (to 47 cm total length; Blackwell, 2010) and luminescent belly (Blackwell, 2010). Males are thought to mature between 29 and 42 cm and females at 34 cm or larger (Ebert et al., 2013). Lucifer dogfish feed on both mesopelagic and benthopelagic fishes and invertebrates such as myctophids, crustaceans and cephalopods (Dunn et al., 2013; Claes et al., 2014). While the reported bycatch of lucifer dogfish has increased in a number of commercial fisheries, for example those targeting squid (*Nototodarus sloanii*) and ling (*Genypterus blacodes*) (Anderson, 2013), it has been hypothesized that this species may also benefit from the increased level of commercial fishing of other species. Dunn et al. (2013) postulated that an increase in hoki capture may enhance lucifer dogfish population numbers due to reduced interspecific competition between the two species for food and resources, however this hypothesis has yet to be tested.

There is some information available on the abundance of lucifer dogfish in New Zealand waters. Estimated biomass trends from Sub-Antarctic trawl surveys carried out between 1991–1993 and 2000–2009 (Bagley et al., 2013), indicated that there was no change in the estimated biomass of lucifer dogfish. Doonan and Dunn (2011) in the trawl survey of the Mid-East Coast orange roughy management area, however, reported a significant increase in the biomass of lucifer dogfish between

1992-1994 and 2010. In contrast, O' Driscoll et al. (2011) observed no change in the biomass of lucifer dogfish in their trawl surveys of Chatham Rise from 1992 to 2010.

At present, lucifer dogfish is not managed under the Quota Management System as it is not a commercially valuable product (Boyd, 2011). It is identified under the IUCN red list as of 'Least Concern' (Ebert et al. 2013) because there is not enough evidence to suggest that declines have occurred, given lucifer dogfish's relatively wide depth and geographic range (Ebert & Schaaf-DaSilva, 2009). Like many deepwater shark species, there are very few studies on lucifer dogfish, so uncertainty remains about their biology and population dynamics as no data on growth rate, age at maturity, mortality, fecundity and other life history aspects exist. The unregulated catch and the limited knowledge of lucifer dogfish life history may mean that the populations are vulnerable to unnoticed localised depletion associated with the development of commercial harvesting of deepwater fisheries (MPI, 2014a).

The **objective** of this research was to increase the knowledge of the biology and demographics of lucifer dogfish, to help inform fisheries management and future evaluations of the population status and risk to this species from fishing.

The specific **objectives** of this research were to:

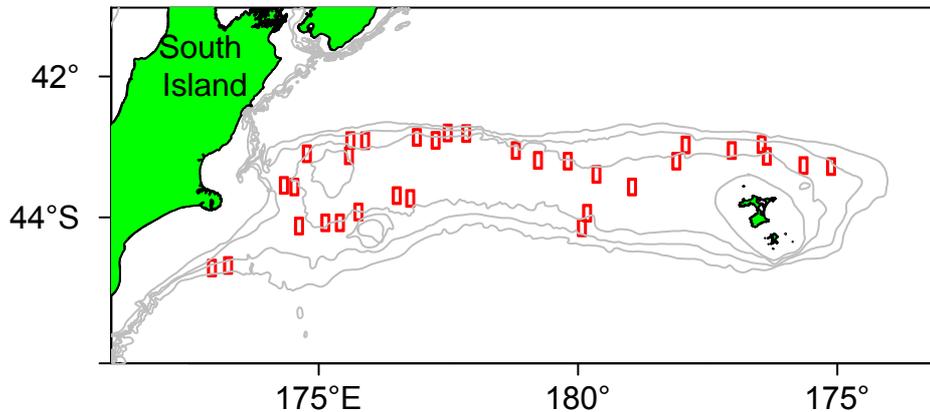
- To determine demographic parameters of lucifer dogfish (*Etmopterus lucifer*) where these parameters are unknown or deficient, suitable for inclusion in population models. These include length-weight relationships, growth (length-at-age), sex ratio, variability in length-at-age, maturity at age and length, fecundity, and other observations of biology and ecology.
- To fit standard and alternative models (where appropriate) for the demographic processes and determine which provides the best fit to the data.

## Methods

### Data collection

#### *Specimen collection*

A sample of 351 lucifer dogfish (*Etmopterus lucifer*) was collected from a bottom trawl survey conducted by the National Institute of Water and Atmospheric Research [NIWA], for the Ministry for Primary Industries [MPI], by RV *Tangaroa* on Chatham Rise (Figure 2), during January 2012. The survey followed a stratified random two-phase sampling design and completed 134 bottom trawl stations (Stevens et al., 2012). The main survey area of 200-800 m was divided into 27 strata. A full wing bottom trawl with a codend mesh of 60 mm, and a door spread averaging 125.9 m, was towed at each station for three nautical miles at 3.5 knots (Stevens et al., 2012). Lucifer dogfish were selected from the catch and all specimens from each tow bagged together, labelled, frozen at  $-20^{\circ}\text{C}$  and returned to the laboratory.



**Figure 2:** Map of the Chatham Rise showing the isobaths (200, 500, 750, 1000 m depths) and sites (31 sampling sites) where lucifer dogfish were caught and sampled during the 2012 Chatham Rise research survey (marked as red squares).

#### *General biology*

In the laboratory, the sharks were thawed. Individual total length (TL) and total weight measurements were made to the nearest 1 mm, and 0.1 g, respectively. TL was measured from the tip of the snout to the posterior tip of the straightened caudal fin (Ramos, 2007).

The relationship between total length and weight was described for each sex using the power relationship:

$$W = aL^b$$

where weight =  $W$ , total length =  $L$ ,  $a$  and  $b$  are constants, estimated using nonlinear least squares using the software R (R core team, 2012). Two outliers were removed from the analysis because it was clear that an error had been made in the recording of weight.

### *Stomach analyses*

Stomach fullness was evaluated subjectively using the volume occupied by the food contents and classified as empty, trace, half full, or full. Trace was identified according to the presence of well-digested material. Stomach contents were emptied into a petri dish, and recognisable prey items identified to the lowest taxon possible, with the assistance of NIWA scientists (Darren Stevens and Jeff Forman), and using reference guides. The contribution of different prey items to the diet of the lucifer dogfish sample was assessed using the frequency of occurrence (% F), which was  $\frac{n_{prey}}{n_{total}}$ , where  $n_{prey}$  is the number of stomachs containing each prey type, and  $n_{total}$  is the total number of stomachs.

### **Maturity**

Each shark was externally sexed by the presence or absence of claspers. Male sexual maturity was assessed macroscopically by determining if the claspers were calcified, and by examination of the testes, and vas deferens. In addition, inner clasper length (ICL), testes length, and testes weight were measured. All lengths were measured to the nearest mm and weights to the nearest 0.01 g. ICL was measured with electronic calipers from the anterior margin of the cloaca to the distal tip of the claspers. To classify sexual maturity, a three macroscopic stage scale was used (Table 1; adapted from ICES 2010; Parker & Francis, 2012). Male sharks were considered mature when they were at Stage 3.

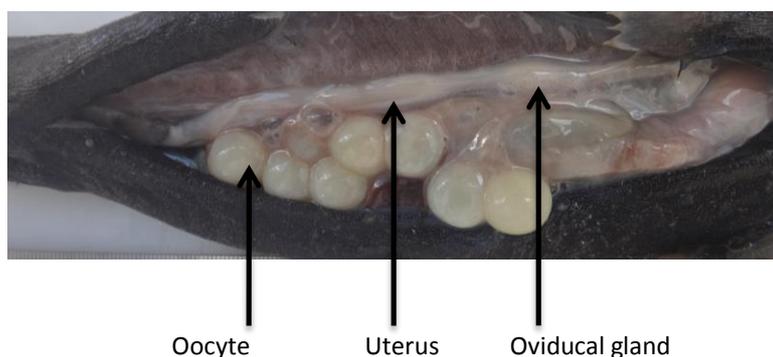
Table 1: Macroscopic maturity scale used to evaluate the sexual maturity of male lucifer dogfish (adapted from ICES, 2010; Parker & Francis, 2012).

Stage	Description
1	Claspers: non-calcified and non-rotatable Testes: threadlike and narrow Vas deferens: straight
2	Claspers: Tips partially calcified; non-rotatable Testes: wider and more developed Vas deferens: beginning to coil
3	Claspers: fully calcified and rigid; rotatable Testes: well developed and wide Vas deferens: fully coiled

The level of clasper calcification was measured by hand. Male sharks with rigid claspers that were easily rotated to reveal clasper spines were classified as mature. The vas deferens changes upon maturity from being straight (Stage 1) to becoming tightly coiled (Stage 3; Irvine, 2004).

Female maturity was assessed macroscopically by examining the uteri and the ovaries. The maximum uterus width, oviducal gland width, the number, and diameter of oocytes, and the presence of embryos were also recorded (Figure 3). If embryos were present, the embryos were sexed and total length, weight, and the number of pups in each uterus was recorded. The liver weight and maximum yolk diameter were also recorded. A six-stage macroscopic maturity scale (Table 2) was used (adapted from ICES (2010); Parker & Francis (2012)). Female sharks were considered mature when they were at Stage 3 or above. Stages 2 and 6 in females can be hard to distinguish (S. Irvine, personal communication, May 7, 2015), therefore the females identified as Stage 2, but with relatively large uteri widths (greater than 6 mm), were changed to maturity Stage 6. This assumed that the objective measurement of uterus width was a better indicator of the distinction

between maturity Stages 2 and 6 than the visual criteria given in the macroscopic stage key.



**Figure 3:** Location of the uterus, oocyte and oviducal gland on a Stage 3 female lucifer dogfish.

**Table 2:** Macroscopic maturity scale used to evaluate the sexual maturity of female lucifer dogfish (adapted from ICES, 2010; Parker & Francis, 2012).

	<b>Stage</b>	<b>Description</b>
<b>Immature</b>	1	Ovaries: oocytes absent. Uteri: threadlike and narrow. Oviducal gland: not visible.
<b>Maturing</b>	2	Ovaries: oocytes at different stages of development; none larger than 5 mm. Uteri: becoming wider. Oviducal gland: not clearly visible.
<b>Preovulatory</b>	3	Ovaries: large vitellogenic oocytes pale yellow in coloration. Uteri: wide. Oviducal gland: clearly visible and measureable.
<b>Early pregnancy</b>	4	Ovaries: flaccid Uteri: contain fertilised eggs; presence of candles (membranous envelope surrounding eggs); no embryos visible.
<b>Pregnant</b>	5	Ovaries: flaccid containing some remnants of absorbed oocyte (corpora lutea). Uteri: contain visible embryos at any different developmental stages.
<b>Post-partum</b>	6	Ovaries: flaccid, containing small follicles. Uteri: flaccid and vascularized, indicating recent birth.

### *Mean length at maturity*

The mean length at maturity was estimated for each sex by fitting logistic curves to the proportion of mature individuals ( $\lambda$ ) in 2 cm TL size classes. The logistic curve was specified following Bull et al., (2008) as:

$$\lambda = 1 / \left[ 1 + 19^{(L_{50} - \text{Length}) / (L_{t0.95})} \right]$$

where  $L_{50}$  is the length at which 50 % of the sharks were mature, and  $L_{t0.95}$  is difference between the lengths at 50 % and 95 % mature. The logistic curve was fitted using non-linear least squares in the software R (R core team, 2012).

### *Maturity data analysis*

For analyses of males the inner clasper length, testes length, and testes weight were standardised by the TL of the shark (i.e. ICL/TL, RT/ TL etc.). This was done because it was assumed the most important statistic was the relative, not absolute, magnitude of these measures. A Dunnett-Tukey-Kramer pairwise comparison test (DTK) was used to evaluate whether differences in measurements between the three macroscopic maturity stages were significant. The DTK was performed using the DTK (Lau, 2013) package in R (R core team, 2012). The DTK is similar to the Tukey HSD test but was used in this study because it includes an adjustment to account for unequal sample sizes. The differences were considered significant if the p value was less than 0.05.

A t-test was conducted to determine whether there was a significant difference in the ratio of left to right testes lengths, before and after the shark had reached a TL of 32 cm. A TL of 32 cm was selected, as a slight bias was observed in testes length of sharks less than 32 cm TL, due to the higher number of males with a greater left testes length than right. In sharks above 32 cm TL there were equal ratios between testes lengths.

For analyses of females, uteri and oviducal gland width were standardised by the TL of the shark. As with the males, a DTK (Lau, 2013) was used to test whether

differences in measurements between the six macroscopic maturity stages were significant. The differences were considered significant if the p value was less than 0.05.

#### *Using objective measures to assign maturity*

A number of relatively large females were classified as immature (Stage 1 or 2; see Results, Table 9). For example, one female was classified as Stage 2 despite being one of the largest females observed (TL of 44 cm). This observation suggested that the macroscopic maturity stage key (Table 2) could be inaccurate. An alternative definition of maturity was therefore used, where any female with a standardised (to TL) right uterus width above 0.01074 cm (the minimum width seen for a mature female) was considered mature. Estimates of length at maturity, and age at maturity (see methods below) were then made with this alternative classification.

#### *Sex Ratio*

The sex ratio at length was examined by plotting the number of females as a proportion of the total (% female) in 2 cm size classes.

### **Age and growth**

#### *Spine preparation*

The second dorsal fin spine from each shark was removed. The second dorsal fin was selected as the first dorsal fin spine is often more damaged than the second (Irvine et al. 2006 b). Dissected spines were stored in a bag, labeled, and frozen for later examination. After defrosting, excess flesh and cartilage were removed from each spine using a scalpel. The spines were then immersed in hot water (following Irvine, 2004) for up to twenty minutes, depending on spine size (longer for larger spines). After submersion, any remaining flesh or cartilage was removed, and the spine length was measured from the base of the spine to the tip, using calipers (to the nearest mm). The spines were then refrozen. Heavily eroded or broken spines were noted, and were not used for the ageing study.

### *Growth band interpretation*

External growth bands could not be observed on the external surface of the cleaned lucifer dogfish spines. Two calcium affinity stains were therefore used to attempt to enhance the external bands: alizarin red (Irvine, 2004) and the Von Kossas technique (Cunning, 1974).

**Alizarin red:** Following Irvine (2004), a sample of test spines were soaked in a solution of saturated alizarin red in 1 % potassium hydroxide (KOH) for up to five days, with regular spine examination to determine whether the banding was enhanced. After two trials no visible banding patterns were observed.

**Van Kossa's technique:** Following Culling (1974), another sample of test spines were cleaned with distilled water and placed in a citrate buffer (9.09 ml of 0.2 M disodium hydrogen phosphate and 10.91 ml of 0.1 M citric acid) for twenty minutes. Spines were then removed from the buffer, washed, and flooded with 5 % silver nitrate and exposed to a 150 Watt light for ten minutes. After silver nitrate exposure the spines were washed in distilled water and then treated with 5 % sodium thiosulfate for two minutes. Spines were then counterstained with 0.5 % neutral red solution, and then dehydrated and mounted in DPX Mountant on a slide. Slides were observed under a dissecting microscope at 40x magnification to see if banding had been enhanced. After three trials no banding patterns were observed.

Following trials with staining the remaining spines were examined for internal bands. Spines were air dried for 24 hours then embedded in clear epoxy resin (diethylenetriamine and RENLAM M1 at 1:5) and left to set in a low temperature oven (35°C) overnight. Once set, the spines were sectioned using a lapidary saw at a thickness of 400 µm (±20 µm). Sections were mounted on a glass microscope slide using epoxy resin.

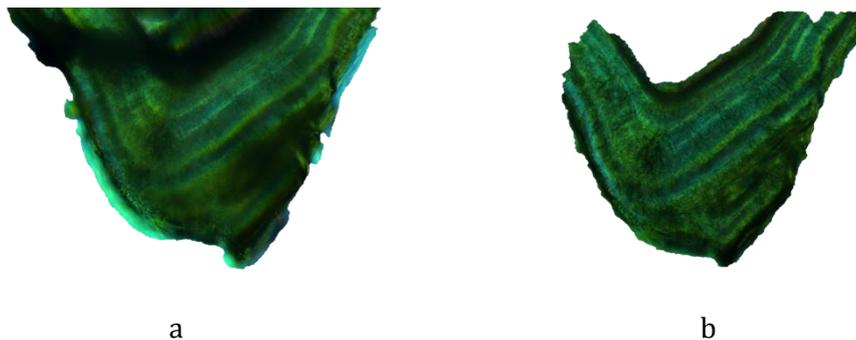
### *Optimum sectioning position*

A trial was carried out to determine the best position for sectioning. Five randomly chosen spines were sectioned using a lapidary saw at 2 mm increments from the

spine tip to the spine base. A section of the spine taken 6 mm from the spine tip gave the clearest banding pattern. Transverse sections of 109 dorsal fin spines from a selection of males, females, and pups, were therefore sectioned as close to 6 mm from the spine tip as possible.

#### *Section thickness*

Initial observation of sections under a stereo microscope (100x) with transmitted light revealed that the sections were too thick (Figure 4a), impairing band resolution. To improve resolution, the sections were ground down using wet and dry sand paper (Grit size: 150, 400, 1200, 4000) attached to a grinding wheel. Sections that were between 200  $\mu\text{m}$  and 300  $\mu\text{m}$  thickness were found to have the best growth zone clarity (Figure 4b).

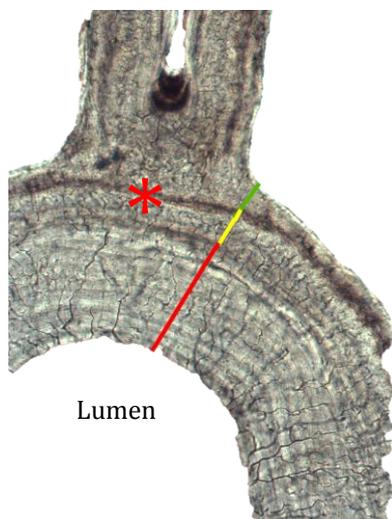


**Figure 4:** Transverse section photomicrograph (100x magnification) of the section of the second dorsal spine of a female lucifer dogfish (20.4 cm): a) section thickness greater than 500  $\mu\text{m}$  b) section thickness between 200 - 300  $\mu\text{m}$ . The image has been modified by interference contrast.

#### *Interpretation of internal growth bands*

Transverse sections of the spines were examined under a stereomicroscope using transmitted light at 100x magnification. Paraffin oil was used to mask the saw blade and sanding marks from section preparation. Interference contrast lighting was used to increase band clarity. Band spacing was clearest in the inner dentine layer, and following Irvine et al (2006b), only bands in this layer were counted. Each internal growth band, consisting of one dark (opaque) band and one light (translucent) band, was assumed to represent an anullus, and although zone counts were not validated as true ages, throughout this report zone counts are referred to as 'age'.

Initially, the section was observed under low magnification (40x) in order to locate the trunk primordium (Figure 5). Once this was located, the magnification was increased to 100x. Bands were then counted from the trunk primordium inwards towards the central lumen (Figure 5). Bands were not counted in other sections due to the reasoning provided in Clarke and Irvine (2006). An extra band was counted if the distance between the last visible band and the pulp cavity was as large as previous bands, thereby assuming that the most recent growth check was not yet visible at the outer edge, and the shark had nevertheless experienced one year's growth. No eroded dorsal spines were aged in this project.



**Figure 5:** Transverse section photomicrograph (100x magnification) of the second dorsal fin spine of a 38.1 cm male lucifer dogfish taken at ~ 6 mm from the spine tip. The red line indicates the internal dentine layer where counting took place, yellow and green lines are the location of the middle and outer dentine layers. The red asterix illustrates the location of the trunk primordium.

Band clarity was subjectively evaluated using the readability scale outlined by Irvine (2004) ranging from very clear (1) to unreadable (5) (Table 3). Two readers, without knowledge of the animal's length or sex, counted the internal growth bands for a subsample of 88 dorsal-fin spines. In preliminary age estimates, a reader bias was identified. To resolve this, the readers reviewed and agreed their interpretation and all sections were then re-read. For final age estimates, age bias plots were used to evaluate the differences in intra-reader and inter-reader biases.

A chi-squared test was used to determine if significant differences existed between the two readers' age estimates. A contingency table was generated in a spreadsheet, which compared the number of observations above and below the 1:1 agreement line for reader 1 and reader 2 (Hoenig et al., 1995).

**Table 3:** Definition of dorsal fin spine growth readability measurements for lucifer dogfish (scale from Irvine, 2004).

Readability Score	Definition
1	Section has unambiguous bands with excellent readability
2	Section has clear bands
3	Section has readable bands $\pm$ 1-2 years
4	Section has bands that are subject to multiple interpretations
5	Section is unreadable

#### *Age at maturity*

Age at maturity was estimated for each sex by fitting logistic curves to the proportion of mature individuals in each age class ( $\lambda$ ), using a logistic curve following Bull et al. (2008) with the equation:

$$\lambda = 1 / [1 + 19^{(A_{50} - \text{Age}) / (A_{t0.95})}]$$

where  $A_{50}$  corresponds to the age at which 50 % of the sample sharks are mature; and  $A_{t0.95}$  corresponds to the difference in years between the ages at 50 % and 95 % mature. The logistic curve was fitted using weighted non-linear least squares (**nls**) in the software R (R core team, 2012) where the weight was the sample size of each age.

#### *Length-at-age (growth)*

A number of mathematical models have been used to describe fish growth (Pardo et al., 2013). The most commonly used model to fit length-at-age data is the Von Bertalanffy growth function [VBGF] (Von Bertalanffy, 1938). The VBGF appeals to fishery biologists because it is very widely used, and so allows for easy comparison

between populations (Musik & Bonfil, 2005). Two forms of the VBGF (the “traditional”, and “modified” version of the VBGF) were fitted to the growth data as recommended by Cailiet et al. (2006). The Traditional VBGF is expressed as:

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

where  $L_t$  is the length at age  $t$  years,  $L_\infty$  is the asymptotic or maximum average length,  $k$  is the growth coefficient, and  $t_0$  is the age at length 0.

The modified version of the VBGF is mathematically equivalent to the traditional VBGF, but expressed as:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where  $L_0$  is the size at birth, and other parameters have the same meaning. The starting values for parameter estimation used for the modified model were the same as the traditional VBGF, with  $L_0$  estimated from the following formula:

$$L_0 = L_\infty (1 - e^{kt_0})$$

An alternative to the VBGF was proposed by Schnute (1981). The Schnute growth model has similar features to the VBGF, but it is more flexible and versatile (Welch & Mcfarlane, 1990; Wise, 2005). By changing the Schnute growth model parameters ( $y_1, y_2, \gamma$  and  $\kappa$ ) and the structure of the formula, Schnute’s growth model can take the form of a number of popular fisheries models, including the VBGF and the Gompertz model (Schnute, 1981).

The Schnute growth model (**Case 1**) is expressed as:

$$Y(t) = \left\{ y_1^\gamma + (y_2^\gamma - y_1^\gamma) \frac{1 - \exp[-\kappa(t - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}^{1/\gamma}$$

where  $Y(t)$  is the change in length over time (i.e. growth),  $\tau_1$  is the youngest age,  $\tau_2$  is the oldest age,  $y_1$  is the average total length at the youngest age,  $y_2$  is the average total length at the oldest age,  $\kappa$  and  $\gamma$  are model parameters (Quinn & Deriso, 1999). In Case 1, it is assumed that  $\kappa \neq 0$  and  $\gamma \neq 0$ . Depending on the values of  $\kappa$  and  $\gamma$ , the Schnute growth model general equation has three possible variations. These are:

**Case 2** where  $\kappa \neq 0$  and  $\gamma = 0$ :

$$Y(t) = y_1 \exp \left\{ \ln \left( \frac{y_2}{y_1} \right) \frac{1 - \exp[-\kappa(t - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}$$

**Case 3** where  $\kappa = 0$  and  $\gamma \neq 0$ :

$$Y(t) = \left[ y_1^\gamma + (y_2^\gamma - y_1^\gamma) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{\frac{1}{\gamma}}$$

**Case 4** where  $\kappa = 0$  and  $\gamma = 0$ :

$$Y(t) = y_1 \exp \left[ \ln \left( \frac{y_2}{y_1} \right) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]$$

Case 2 and 3 of the Schnute growth model are three-parameter models that are each nested or simplified models of Case 1, and Case 4 is a two-parameter model that is nested within Case 2 and 3. Up to eight models are nested within the Schnute growth model (Andrade, 2004). For example, in Case 3 if  $\kappa > 0$ , and  $\gamma = -1$  then the Schnute growth model resembles the logistic growth model (Quinn & Deriso, 1999).

#### *Model fitting procedure*

A lognormal error distribution for the length-at-age data was assumed, because histograms (Figure A1) of length-at-age were skewed. The Schnute growth model and VBGF parameters were estimated using maximum likelihood, which involved minimising the negative log likelihood of the residuals using the optim function in R.

The negative log likelihood at age  $t$  is given by:

$$L_t = \log(\sigma_V) + \frac{1}{2} \log(2\pi) + \frac{d_t^2}{2\sigma_V^2}$$

where  $d_t$  is the difference between the observed length-at-age and the model predicted length-at-age, and the variance is  $\sigma_V$  (Hilborn and Mangel, 1997).

Bounds on the estimated values of the parameters were included in the optimization procedure to assist the optimization (minimization) algorithm.

Each of the growth models were fitted only to length-at-age estimates where both readers estimated the shark's age. The models were then weighted according to the proximity of reader 1's age estimates to reader 2. The procedure was as follows:

If there was no difference between reader 1 and reader 2's age estimates, then the estimate was given a weighting of 1 (female  $n = 24$ , male  $n = 10$ ). If there was one to three years difference between reader 1 and reader 2's age estimates, then the age estimate was given a weighting of 0.5 (female  $n = 19$ , male  $n = 22$ ), and lastly, if the difference in age estimates was greater than three years then the estimate was given a weighting of 0 (female  $n = 2$ , male  $n = 0$ ), and the estimate was excluded.

#### *Growth model selection*

A variety of model selection techniques have been used to assess model performance and identify which model fits the data best (Panhwar et al., 2010). One of the most commonly used statistics is the Akaike's Information Criterion (AIC; Akaike 1973), which balances goodness of fit (the likelihood) against model complexity. The model with the lowest AIC value is considered to be the best fit to the data (Haddon 2011).

The AIC for each model was calculated as:

$$AIC = -2L_i + 2K_i$$

where  $L_i$  is the negative log likelihood and  $K_i$  is the number of parameters in the model.

### *Ageing precision*

The coefficient of variation is the most commonly used statistic to describe precision of age estimates (Campana et al., 1995). The coefficient of variation is expressed as:

$$CV = \frac{1}{N} \sum_{j=1}^N \sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R - 1}} \frac{1}{X_j}$$

where  $N$  is the number of dogfish aged,  $R$  is the number of times the sample of dorsal fin spines has been read,  $X_{ij}$  is the  $j$ th age estimate of the  $i$ th fish and,  $X_j$  is the average age calculated for the  $j$ th fish. A coefficient of variation of less than 10 % for length-at-age data is considered to provide precise age estimates (ICES, 2013a). The CV was used to compare within-reader and between-reader precision of age estimates using the `agePrecision` function in the R package, FSA (Ogle, 2007).

The coefficient of variation for length-at-age was also estimated using the formula:

$$CV_L = SD/mean_L \cdot 100,$$

where  $SD$  is the standard deviation and  $mean_L$  is the average length at each age.

### **Mortality**

Two models were used to estimate instantaneous total mortality rate; the Hoenig's (1983) model, and the Chapman Robson (1960) estimator.

Hoenig's regression model is expressed as:

$$\ln(Z) = 1.46 - 1.01[\log_e(t_{max})]$$

where  $Z$  is the total mortality rate,  $t_{max}$  is the maximum age reached by the lucifer dogfish sample and  $\ln$  is the natural logarithm.

The Chapman Robson (1960) estimator is expressed as:

$$Z = \ln_e \frac{1+a-1/n}{a}$$

where  $a$  is the mean age above the recruitment age,  $n$  is the sample size, and  $Z$  is the total mortality rate. These methods estimate mortality rate from longevity. Where there is no fishing, the mortality rate is  $M$  (natural mortality), otherwise (as here) it is total mortality.

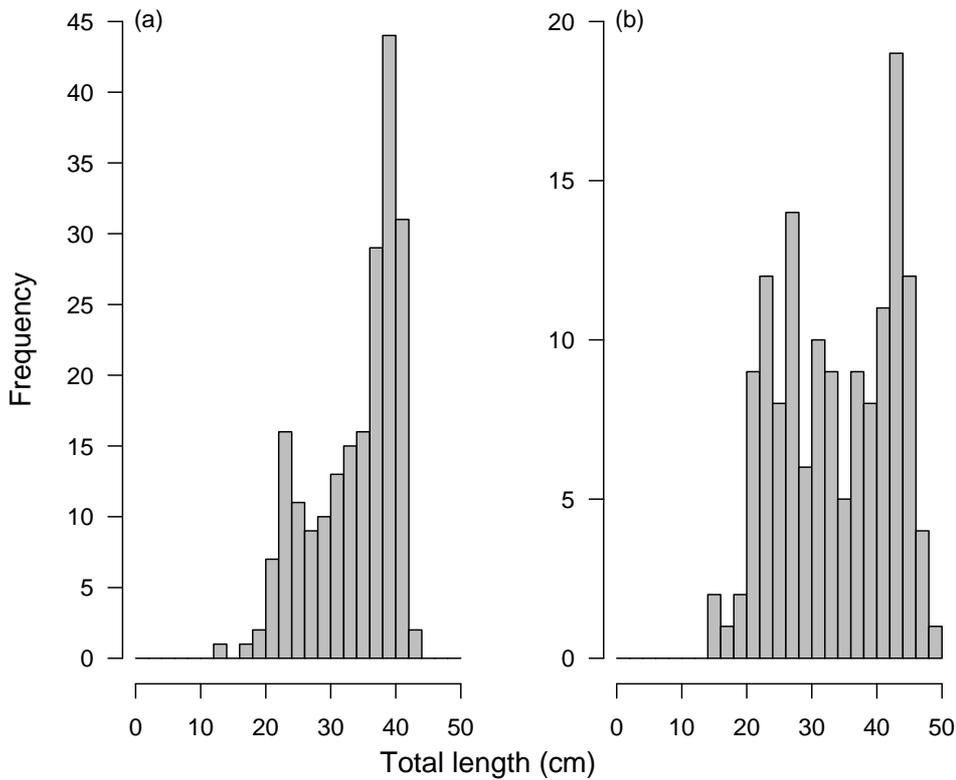
### **Confidence intervals**

The specified objective of this research was to provide parameter estimates for population (stock assessment) models. These models require only point estimates of parameters (Bull et al. 2008). As a result confidence intervals were not estimated here. Confidence intervals can be estimated by most procedures in R, from the inverse Hessian matrix, or from likelihood profiles (Bolker, 2008). In this study, likelihood profiles were calculated, to investigate problems in parameter estimation.

## Results

### Size composition

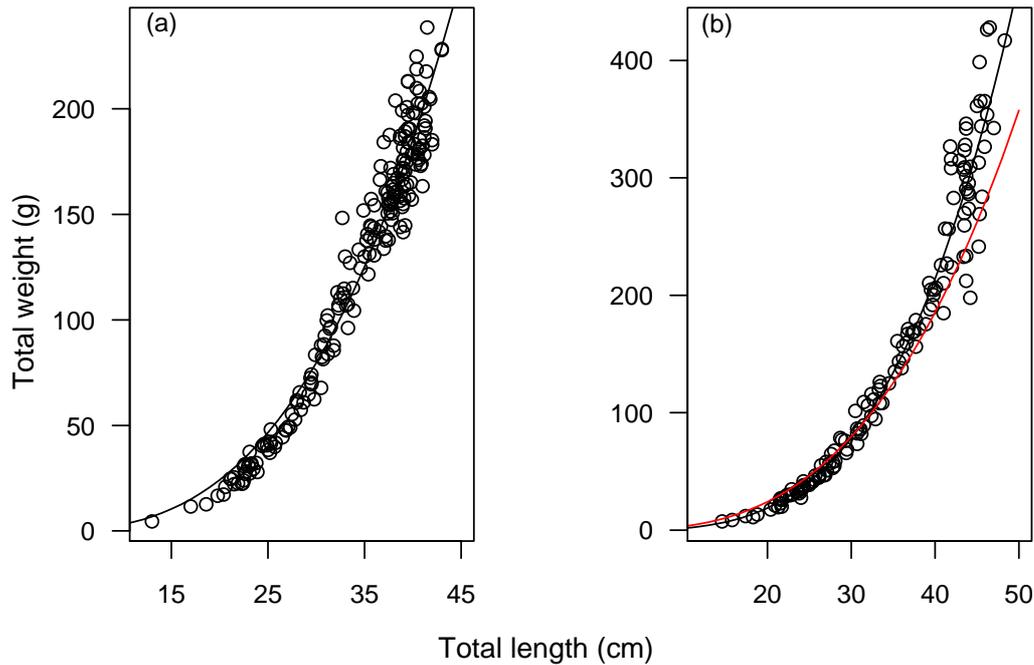
The total length of lucifer dogfish ranged from 13.0 to 43.0 cm in males, and 14.6 to 48.3 cm in females (Figure 6). This species was sexually dimorphic with females growing to a larger size than the males (Figure 6). Twelve embryos were measured from two litters, and they ranged in length from 11.1 to 13.0 cm TL.



**Figure 6:** Total length-frequency distribution for a) male (n = 207) and b) female (n = 142) lucifer dogfish excluding pups collected during the 2012 NIWA Chatham Rise survey.

### Length-weight relationships

As juveniles, the length-weight relationships were similar for both male and female lucifer dogfish (Figure 7; Table 4), however as the sharks grew the females attained a larger weight at length than males. The model fit over-estimated the weight of smaller male sharks, as these were poorly represented in the sample (the model fit was dominated by larger males).



**Figure 7:** Length-weight relationships and non-linear regression fits of the  $W = aL^b$  model for lucifer dogfish (a) males and (b) females, excluding pups, collected in the 2012 NIWA Chatham Rise survey. Fitted model for males is superimposed in red on panel b.

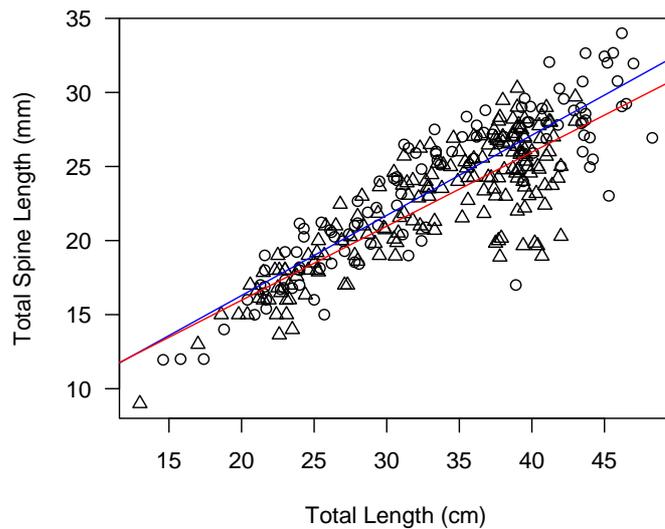
**Table 4:** Parameter values for length-weight regressions for lucifer dogfish sampled in the 2012 Chatham Rise survey. ( $n$  = sample size;  $a, b$  are constants)

Sex	Female	Male
Length range (cm)	14.6-45.3	13.0-43.0
Weight range (g)	7.5-428.1	4.5-238.6
$a$	0.00052	0.0036
$b$	3.50	2.90
$n$	142	207

## Age

The largest male spine was 30.3 mm (39.0 cm TL individual) and the largest female spine was 34.0 mm (46.2 cm TL individual). There was a cluster of samples around 37-42 cm TL, which had a comparatively small total spine length (TSL) in relation to their TL (Figure 8). These were most likely broken or eroded spines. The relationship between the total length and the total spine length was approximately linear (Figure 8).

The relationship between male total length and total spine length was  $TSL = 0.500TL + 5.981$  ( $r^2 = 0.69$ ,  $n = 181$ ), and corresponding females;  $TSL = 0.594TL + 5.321$  ( $r^2 = 0.80$ ,  $n = 115$ ). After approximately 20 cm TL, there was an even spread of spine lengths above and below the straight lines. Fish smaller than 20 cm tended to have relatively short spines and therefore the model would slightly over-estimate the TSL in smaller fish.

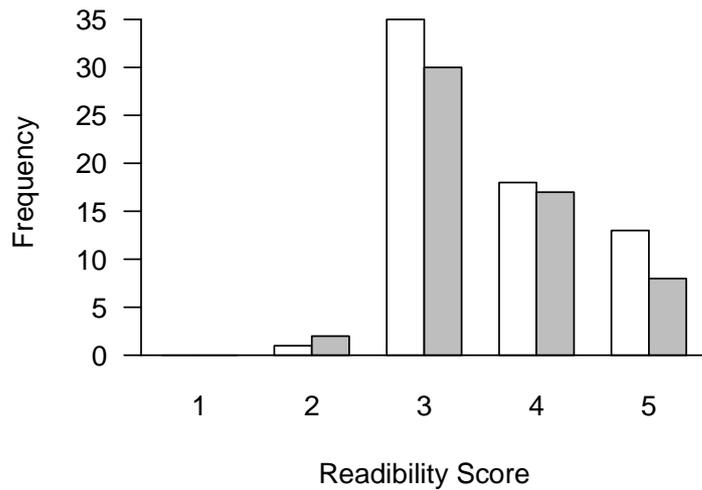


**Figure 8:** The relationship between total length (TL) and total spine length (TSL) for a sample of lucifer dogfish males ( $\Delta$ ) and females (O), excluding pups, from the 2012 Chatham Rise survey; Blue line = females, Red line = males.

### *Internal growth bands*

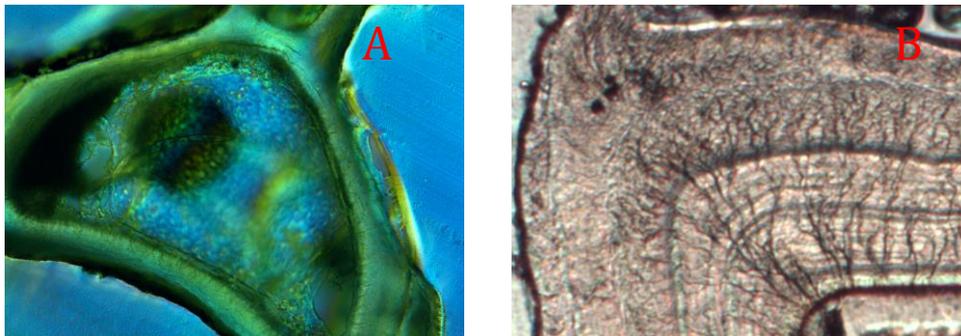
Of the 125 lucifer dogfish dorsal fin transverse sections prepared for age determination, 77 sections (32 males and 45 females) had readable banding patterns ( $\leq 4$  readability score).

Spine sections were often difficult to read. Of those spines with a banding pattern, 52 % of the male spines and 67 % of the female spines had a readability score of three (Figure 9). The remainder of the sections could be aged with multiple interpretations, were clear, or unreadable. None of the spines were considered to have excellent readability (Figure 9). Of the sharks aged, the lengths of the male sharks ranged from 13.0 to 43.0 cm, and the females between 14.6 and 48.3 cm TL.



**Figure 9:** Frequency distribution of the readability scores for internal bands in the second dorsal fin spine of lucifer dogfish collected on the 2012 Chatham Rise survey (excluding pups). Females (white columns, n = 67); and males (shaded columns, n = 57). Score definitions: 1 = excellent readability, 2 = clear readable bands, 3 = readable  $\pm$  1-2 bands, 4 = subject to multiple interpretations, and 5 = bands are unreadable.

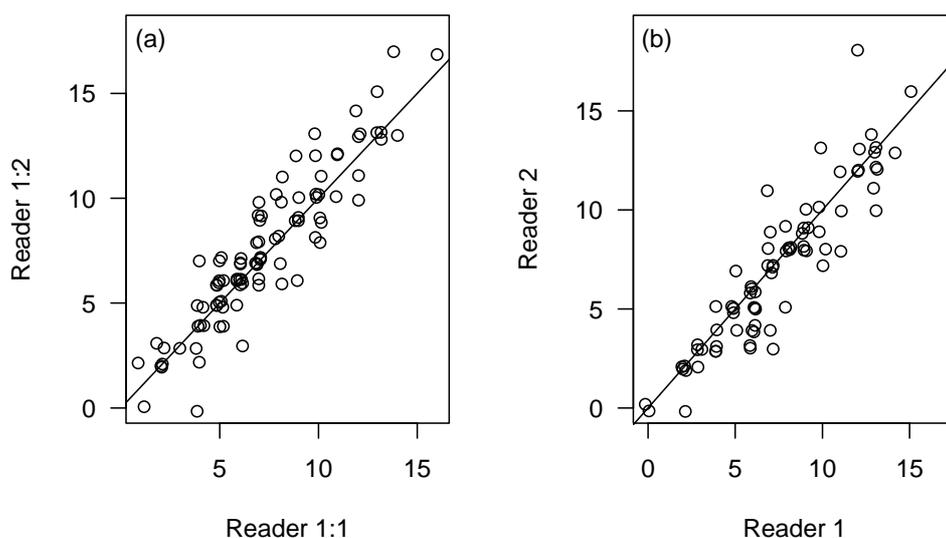
Pups and smaller sharks (TL = < 16 cm) had no visible growth bands (Figure 10A). The greatest number of bands observed was 17 (37.6 cm TL; Figure 10B) in the males, and 14 in the females (39.5 cm TL).



**Figure 10:** A) Transverse section of a lucifer dogfish pup dorsal fin spine, B) Transverse section of a lucifer dogfish dorsal fin spine (estimated age, 17 years).

### *Ageing precision and bias*

There was evidence of a within-reader bias, and in the second trial reader 1's age estimates were slightly higher than in the first trial (Figure 11 a). The between-reader plot showed some bias, (Figure 11 b) with reader 1, in the second trial, reading the sections slightly older than reader 2. However there was no significant difference in the symmetry of zone count estimates between readers 1 and 2 ( $\chi^2 = 24$ ,  $p = 0.055$ ; Table 5).

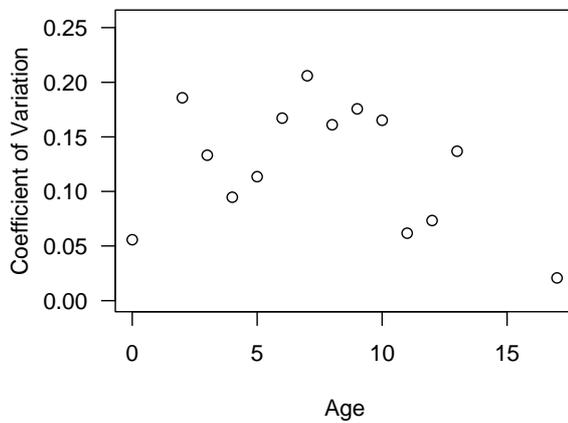


**Figure 11:** Zone count reader bias plots comparing: (a) within-reader zone count estimates ( $n = 82$ ) and (b) between-reader zone count estimates ( $n = 70$ ) using the second dorsal spines of lucifer dogfish (excluding pups) collected on the 2012 Chatham Rise survey. The solid line represents 1: 1 agreement.

In the within-reader trials, 37 % of reader 1's estimates were identical over the two trials, and 90 % were aged within 1-2 years of the first trial (Figure 11 a). Reader 2 aged 44 % of the sections the same as reader 1, and 86 % were aged within 1-2 years of reader 1's estimates (Figure 11 b). The age estimates of reader one and reader two were more consistent for zone counts greater than 7 (Table 5). The mean CV of length at ages was 0.12, with no clear trend in the CV's over ages (Figure 12). The mean CV for the precision of age estimates was 12.71 % for the within-reader test of precision, and 11.98 % for the between-reader test.

**Table 5:** Contingency table showing the comparison between the ages estimated by reader one versus the ages estimated for reader two for a small subsample of 70 lucifer dogfish dorsal fin spines. Bold numbers on the shaded diagonal are where the two readers agree.

		Reader 1 age estimates																		
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Reader 2 age estimates	0	<b>2</b>																		
	1																			
	2	1																		
	3		1																	
	4			2																
	5				1															
	6				1	2	2													
	7				1	1														
	8						1													
	9							1												
	10								1											
	11									1										
	12										1									
	13											1								
	14												1							
	15													1						



**Figure 12:** The coefficient of variation of age estimates calculated across the lucifer dogfish sample ages.

## Reproduction and maturity

### Males

Out of 207 males, 75 were classified as immature (Stage 1), 21 were maturing (Stage 2) and 111 were considered mature (Stage 3), (Table 6; Figure 13).



**Figure 13:** Reproductive tracts of lucifer dogfish classified as macroscopic maturity stages A) Immature (Stage 1) female, B) Mature (Stage 3) female, C) Maturing (Stage 2) male and D) Mature (Stage 3) male.

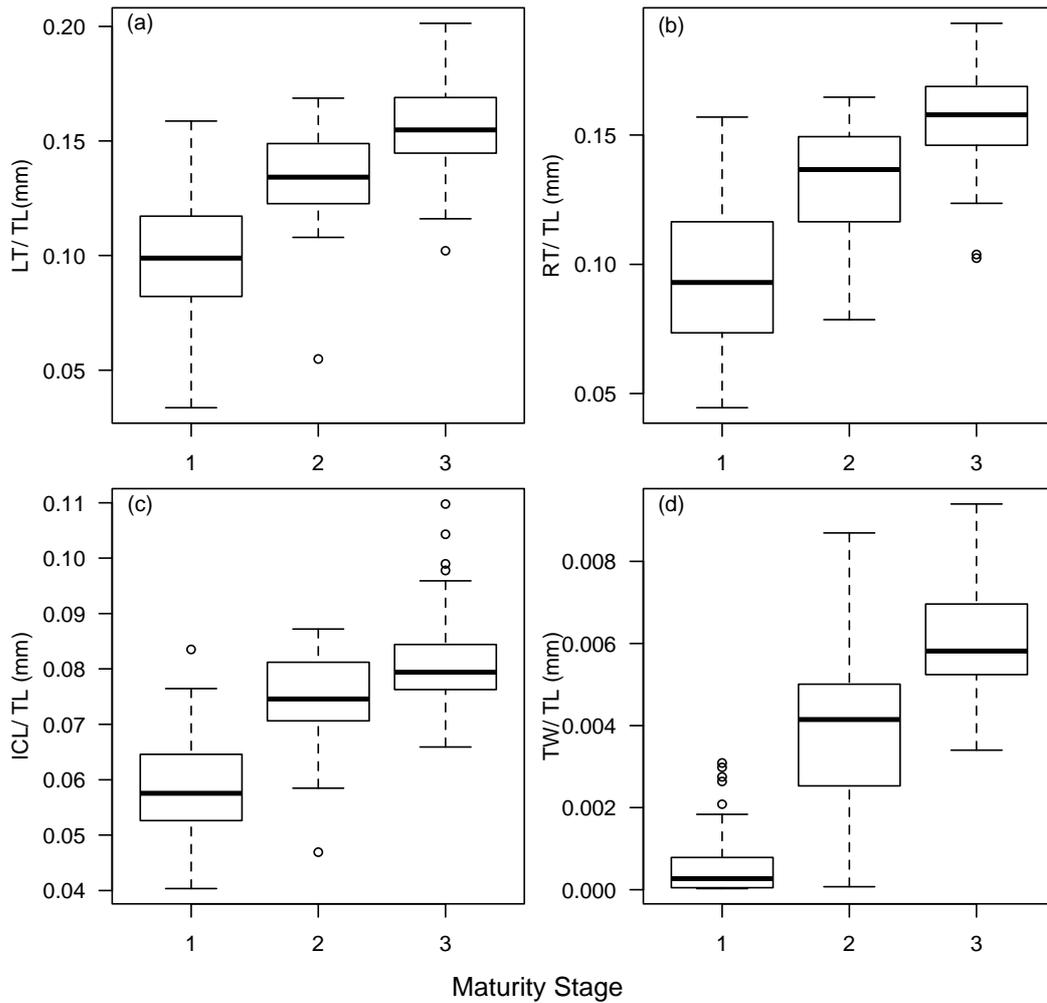
**Table 6:** Characteristics of a male sample of lucifer dogfish in each of the three maturation stages (Maturity stages categorised in Table 1) (n = sample size). Total length measured in cm, Left and right testes length, and Inner clasper length measured in mm, and total weight measured in g.

	Macroscopic maturity stage		
	1	2	3
	<b>Mean (range; n)</b>	<b>Mean (range; n)</b>	<b>Mean (range; n)</b>
<b>Total length</b>	25.8(13.0-35.4; 75)	33.8(27.8-40.4; 21)	39.1(35.0-43.0; 111)
<b>Total weight</b>	44.4(4.5-151.9; 75)	124.5 (52.8-224.8: 21)	172(130.0-238.6; 111)
<b>Left testes length</b>	25.9(9.1-51.7; 69)	45.8(15.3-60.1; 20)	61.4 (41.6-78.6; 111)
<b>Right testes length</b>	23.3(9.7-50.5; 68)	46.6 (21.9-61.3; 20)	61 (35.8-77.7; 111)
<b>Testes weight</b>	0.07(0.01-1.01; 70)	1.4(0.02-3.2; 20)	2.2 (1.2-3.7; 111)
<b>Inner clasper length</b>	14.6 (7.4-27.3; 75)	26.6(13.0-31.0; 21)	31.2 (24.9-41.3; 111)

There was a significant increase in testes length and weight as maturity progressed (Stage 1 versus 2: p value,  $\leq 0.05$  Stage 2 versus 3: p value,  $\leq 0.05$ , Stage 1 versus 3: p value,  $\leq 0.05$ ; Figure 14 a, b, d). The vas deferens developed, as described in the macroscopic key, from a straight tube in immature individuals to a coiled tube in mature males.

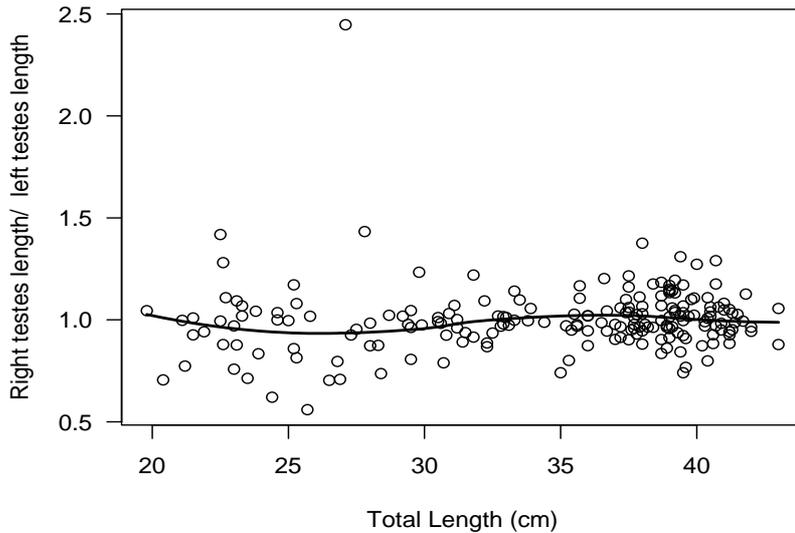
The inner clasper length (ICL) also increased significantly with macroscopic maturity stage (Stage 1 versus 2: p value  $\leq 0.05$ ; Stage 2 versus 3: p value  $\leq 0.05$ ; Stage 1 versus 3: p value  $\leq 0.05$ ; Figure 14c). The claspers became progressively more calcified as the males matured. The smallest calcified clasper was 24.9 mm ICL, which was a male at 37.2 cm TL (Table 6).

All of the objective measurements showed an increase with macroscopic maturity stage (Figure 14), providing support for the macroscopic key. An abrupt increase in all of the objective measures coincided with the onset of maturity (i.e. progression from Stage 2 to Stage 3). However the largest change was between Stages 1 and 2, indicating that these stages were most easily distinguished (Figure 14).



**Figure 14:** Relationship between male macroscopic maturity stage and (a) left testes length (LT), (b) right testes length (RT), (c) inner clasper length (ICL) and (d) testes weight (TW) for a sample of lucifer dogfish males from the 2012 Chatham Rise survey. All statistics are standardised to the percentage of total length (TL) of the shark. Sharks were classified as mature at Stage 3.

Sharks smaller than about 32 cm TL had a slightly larger left testicle, however as the sharks became larger the ratio became closer to a 1:1 (Figure 15). A t-test showed no significant difference between the ratios of testes length before and after 32 cm TL ( $t = 0.9369$ ,  $p \text{ value} = 0.3519$ ). The outlier at (TL = 27.1, RT/LT ratio = 2.45) is a shark, which had a large left testicle (22.7 mm) and a very small right testicle (9.1 mm). When this outlier was removed, a significant difference ( $t = -2.3556$ ,  $p = 0.021$ ) was observed between the ratio of testes length before and after the shark reached a TL of 32 cm.



**Figure 15:** Lucifer dogfish: relationship between the ratio of right testes length to left testes length and the total length of the shark. This relationship is fitted with a LOESS (moving average) smoother (bold line) to illustrate the trend.

#### *Females*

Out of 149 females, 69 were immature (Stage 1), 39 were maturing (Stage 2) and the remaining 41 females were considered mature (Stages 3, 4, 5, and 6; Table 7; Figure 13).

**Table 7:** Characteristics of a female sample of lucifer dogfish females in each of the six maturity stages (Maturity stages categorised in Table 2) (n = sample size). Total length measured in cm, left and right uterus width, and oviducal gland width measured in mm, weight in g.

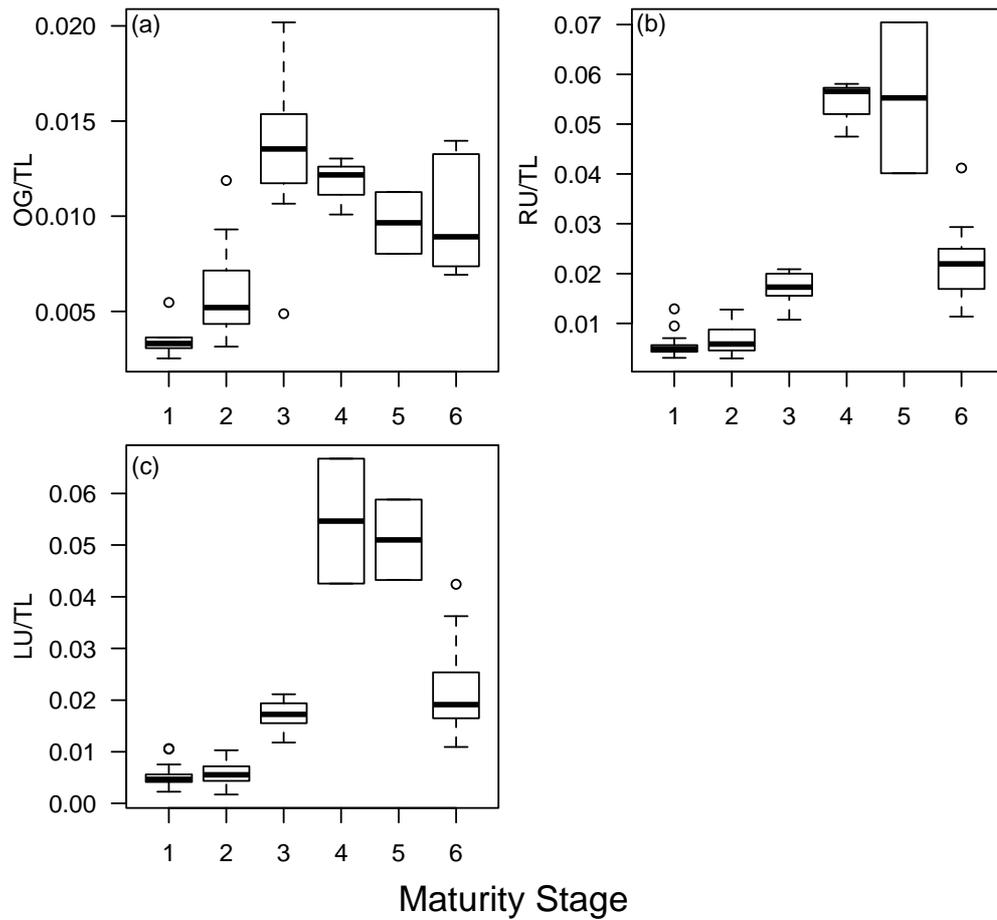
	Macroscopic maturity stage		
	1	2	3
	Mean (range; n)	Mean (range; n)	Mean (range; n)
<b>Total length</b>	26.1(14.6-40.7; 69)	36.75(27.4-43.7; 33)	44.0(41.8-48.3; 23)
<b>Total weight</b>	45.7(7.5-225.6; 69)	163.92(56.8-290.4; 39)	328.1(282.8-428.1; 23)
<b>Left uterus width</b>	1.3(0.5-2.9; 66)	2.26(0.57-4.23; 33)	7.7(5.1-9.6; 23)
<b>Right uterus width</b>	1.3(0.5-2.9; 62)	2.43(1.06-4.41; 33)	7.7(4.5-9.3; 23)
<b>Oviducal gland width</b>	1.2(0.8-1.6; 7)	2.3(0.57-4.23; 33)	6.0(2.2-9.1; 23)

**Table 7:** [cont] Characteristics of a female sample of lucifer dogfish females in each of the six maturity stages (Maturity stages categorised in Table 2) (n=sample size). Total length measured in cm, left and right uterus width, and oviducal gland width measured in mm, weight in g.

	Macroscopic maturity stage		
	4	5	6
	Mean(range; n)	Mean(range; n)	Mean(range; n)
<b>Total Length</b>	45.2(43.5-46.2; 3)	44.7 (43.7-45.6; 2)	43.4(39.4-45.3; 12)
<b>Total weight</b>	313.0 (259.5-353.8; 3)	248.1(212.3-283.9; 2)	250.6 (188.1-307; 12)
<b>Left uterus width</b>	25.3 (22.0-25.6; 3)	22.9(18.9-26.8; 2)	9.5(5-18.5; 12)
<b>Right uterus width</b>	24.9 (19.7-30.2; 2)	24.8(17.5-32.1; 2)	9.6(5.2-18.0; 12)
<b>Oviducal gland width</b>	5.5 (4.7-5.7; 3)	4.3(3.5-5.1; 2)	4.3(2.84-6.1; 10)

Post-hoc analyses with Dunnet-Tukey-Kramer HSD tests on the different maturity stages indicated that there was no significant difference in the oviducal gland width between all the different macroscopic maturity stages ( $p$  value  $\geq 0.05$ ) except for Stages 1 and 3, 1 and 4, 2 and 3, 1 and 6, and 3 and 6 ( $p$  value  $\leq 0.05$ ). The oviducal gland was difficult to identify in immature individuals (Stage 1 and Stage 2). The gland's width was greatest when the female was maturing (Stage 3), and then declined substantially to Stage 6 (Figure 16a)

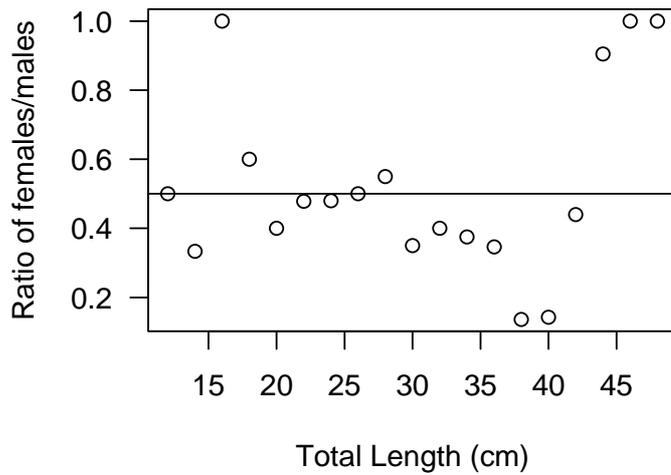
Post-hoc analyses with Dunnet-Tukey-Kramer HSD tests on the different macroscopic maturity stages indicated that both right and left uterus width increased significantly between successive maturity stages ( $p$  value  $\leq 0.05$ ) except between Stages 1 and 2, and Stages 4 and 5 (Figure 16 b, c). Stage 3 females had a mean ovarian fecundity of seven. Sharks that were pregnant had similar uteri widths to sharks in the candle formation stage (Stage 4). Stage 6 females had a similar uteri width to Stage 3 females, suggesting a cyclical reproductive pattern. Two pregnant females were collected in the 2012 survey (43.7 cm TL and 45.6 cm TL individuals). Each had a litter size of seven pups. The pup size ranged between 11.1 cm and 13 cm TL.



**Figure 16:** Relationship between female macroscopic maturity stage and (a) oviducal gland width (OG), (b) right uterus width (RU), (c) left uterus width (LU) for a sample of lucifer dogfish females from the 2012 Chatham Rise survey. All statistics are standardised to the percentage of total length (TL) of the shark. Sharks were classified as mature at Stage 3.

### *Sex ratio*

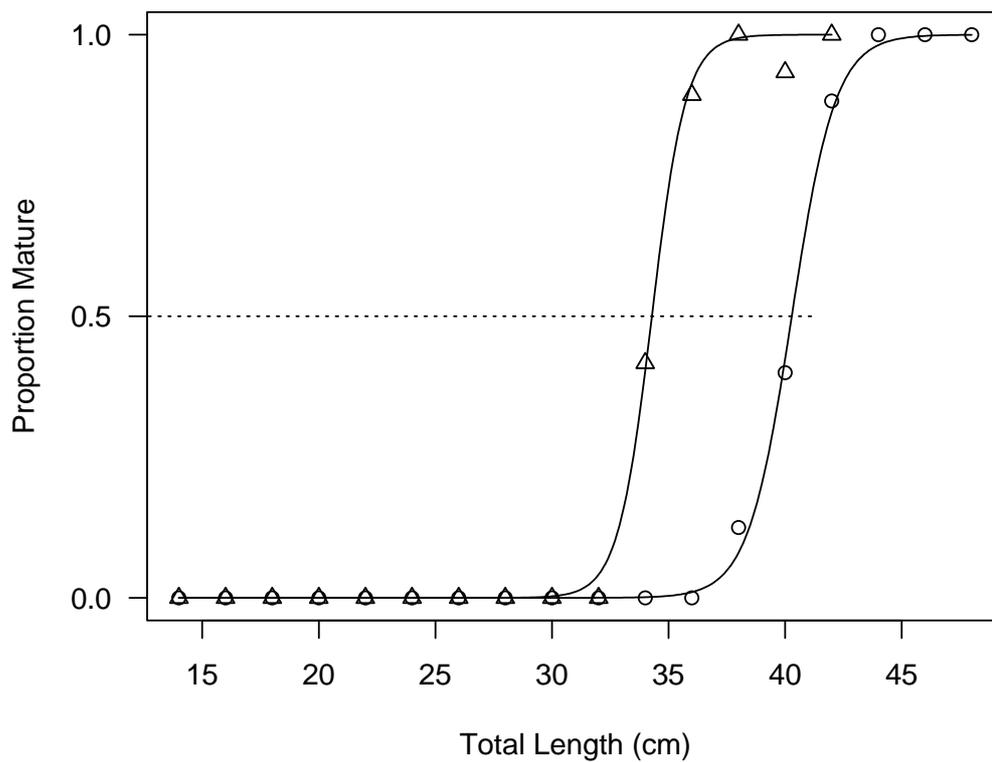
The sex ratio of embryos was 1:1. The overall sex ratio was significantly different from the expected proportion of 1:1, with a predominance of males ( $\chi^2 = 12.17$ ,  $p \leq 0.05$ ; Figure 17). The sex ratio became more male biased in sharks between 30 and 42 cm TL; and female biased in length classes above 42 cm TL ( $\chi^2 = 89.04$ ,  $p \leq 0.05$ ).



**Figure 17:** Sex ratio of lucifer dogfish from Chatham Rise 2012 Chatham Rise trawl surveys, in 2 cm total length size classes. The straight line represents the 1:1 ratio.

*Length at maturity*

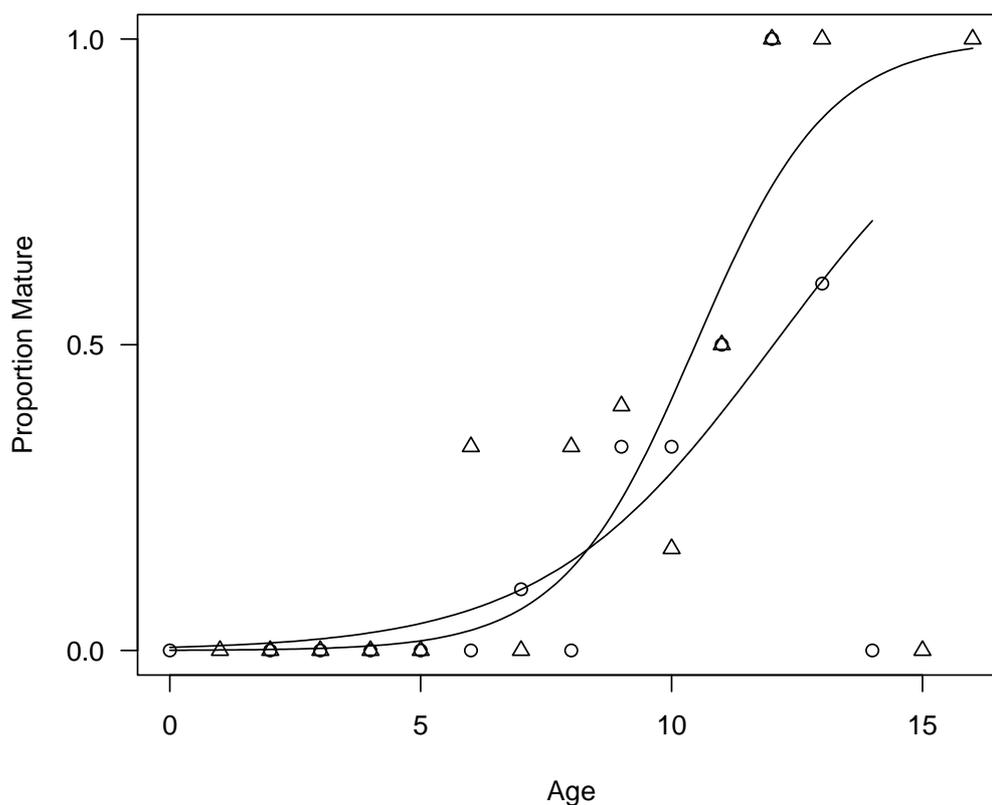
Of the 207 male lucifer dogfish, 111 (54 %) were mature (Table 6). The length at maturity ogives provided a very good fit to the observed proportion mature at length data (Figure 18). The mean length of maturity for males ( $L_{50}$ ) was estimated at 34.3 cm, which was 74 % of the maximum observed length. Of the 142 female lucifer dogfish collected, 34 (24 %) were mature (Table 7). The mean length of maturity for females ( $L_{50}$ ) was estimated at 40.3 cm, which was 83 % of the maximum observed length.



**Figure 18:** Logistic ogive fitted to the proportion mature in 2 cm length classes for males ( $\Delta$ ) ( $n = 207$ ) and females (O) ( $n = 142$ ) lucifer dogfish. Sharks assumed to be mature at Stage 3 and above.

#### *Age at maturity*

The estimated age at 50 % maturity ( $A_{50}$ ) for the males was 10.5 years, compared to 12.0 years for females (Figure 19). This is 61 % of the maximum observed age for males, and 86 % of the maximum observed age for females. The oldest immature male was estimated at 15 years (35.4 cm), similarly in females the oldest immature female was aged at 14 years (39.5 cm). These observations seem unlikely, but removing the immature male at age 14 and immature female at age 14 made little difference to the estimated  $A_{50}$  (changed the estimates by less than a year; males  $A_{50} = 10.5$  years; females  $A_{50} = 11.3$  years).



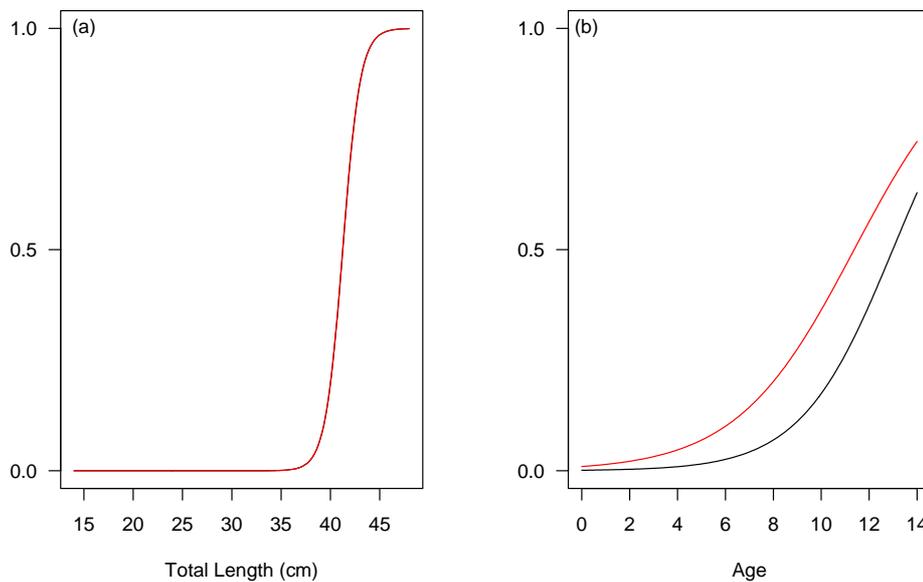
**Figure 19:** Logistic ogive fitted to the proportion mature in one year age classes for male ( $\Delta$ ) ( $n = 51$ ) and female (O) ( $n = 54$ ) lucifer dogfish. Sharks assumed to be mature at Stage 3 and above. The model is fitted using weighted least squares where the weights are assigned to the number of sharks in each age class.

#### *Using objective measures to assign maturity*

There was no difference in the logistic curve fits (Figure 20) to the proportion mature at length based on the macroscopic key, compared to the proportion mature at length based on the minimum right uterus width of a mature female (minimum right uterus width = 0.0107 cm).

There was a slight difference between the logistic curve fits to the proportion mature at age based on the macroscopic key (black line) compared to proportion mature at age based upon the minimum right uterus width for mature females. This difference did not, however, alter the parameter estimates markedly as the  $A_{50}$  based on the macroscopic key was 13 years and the  $A_{50}$  based on the right uterus

was 11.4 years. These results supported the use of the female macroscopic maturity key to assign maturity stages to lucifer dogfish females (Figure 20 a, b).

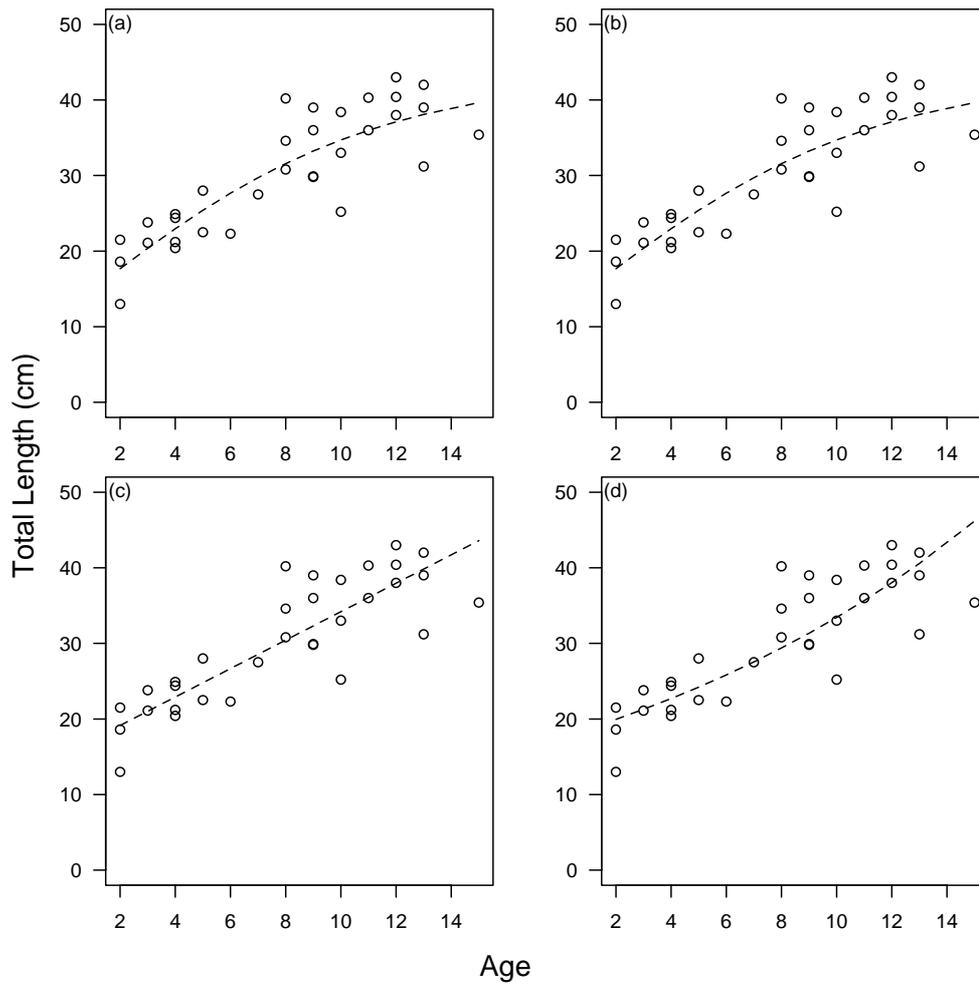


**Figure 20:** a) Fitted maturity ogive at a) length, and b) age, based on i) the minimum standardised right uterus width (red), ii) the macroscopic maturity scale (black line- hidden beneath the red in a). The model for the length-at-age data is fitted using weighted least squares where the weights are assigned to the number of sharks in each age class.

## Growth

### *Males*

Of the four cases of the Schnute growth model, and the two cases of the VBGF, Schnute growth model Case 4 had the lowest log-likelihood and AIC score indicating that it was the best fitting model, and estimated a slightly exponential growth pattern (Figure 21; Table 8). Cases 1 and 2 fitted the data with an asymptotic growth pattern (Figure 21 a, b), Case 3 fitted the data (Figure 21 c) as a linear growth pattern.



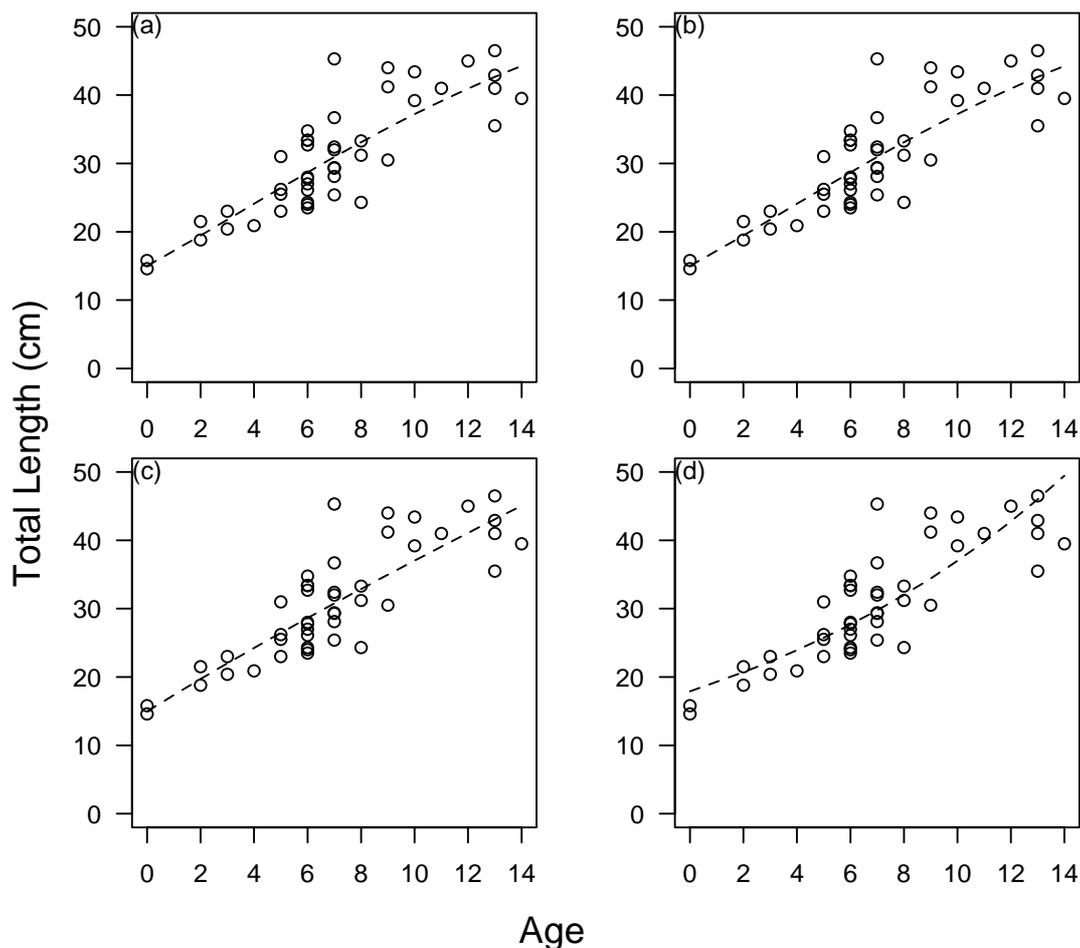
**Figure 21:** Growth modelled using four cases of the Schnute growth model fitted to length-at-age data obtained from internal spine band counts from a sample of 32 male lucifer dogfish. Schnute growth model: (a) Case 1, (b) Case 2, (c) Case 3, and (d) Case 4.

**Table 8:** Growth model selection for fits to length-at-age data of male lucifer dogfish. AIC = Akaike's information criterion.

Model	Case	# of parameters	Negative log-likelihood	AIC
<b>Schnute</b>	1	5	-17.94	45.88
	2	4	-17.94	43.88
	3	4	-16.60	41.20
	4	3	-14.47	34.93
<b>Von Bertalanffy (<math>t_0</math>)</b>	1	4	-17.85	43.71
<b>Von Bertalanffy (<math>L_0</math>)</b>	2	4	-17.85	43.71

## Females

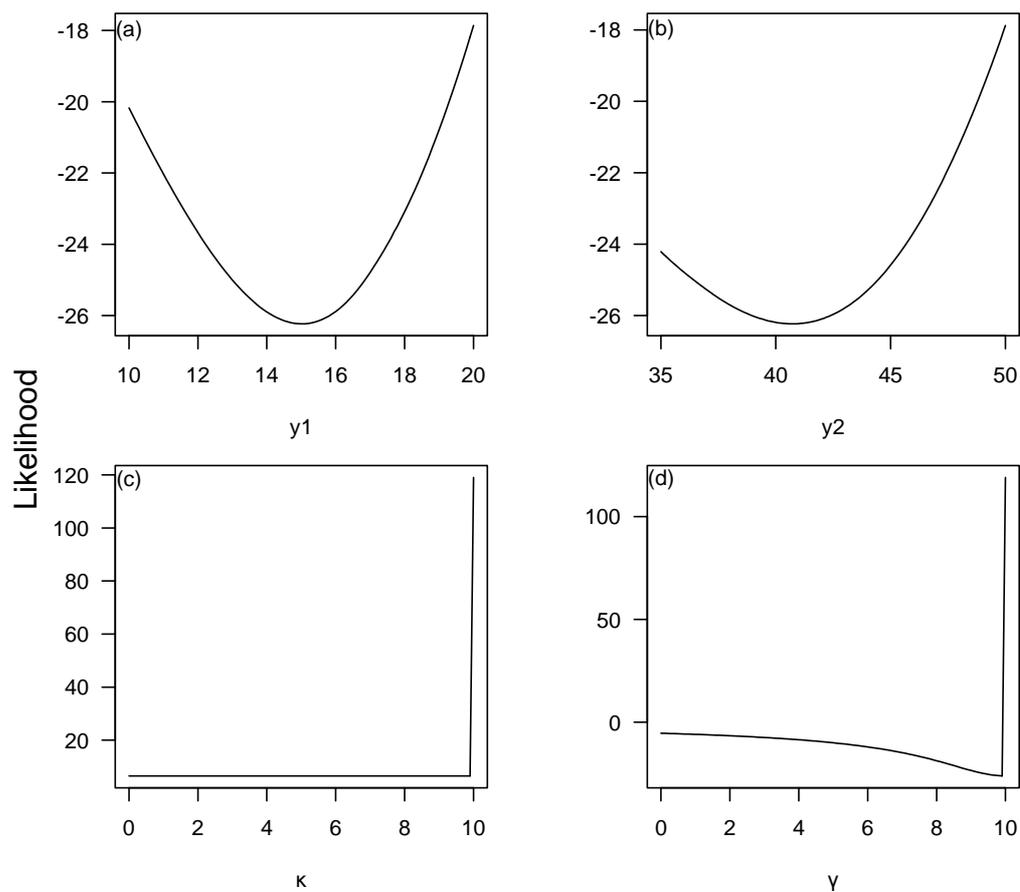
As with the males, Case 4 of the Schnute growth model provided the best fit to the length-at-age data, having the lowest log-likelihood value and AIC score (Table 9). The first three cases of the Schnute growth model provided a similar fit to the data, and all indicated near linear growth (Figure 22 a, b, c). Again, the asymptotic growth models provided the poorest fit to the data.



**Figure 22:** Growth modeled using four cases of the Schnute growth model fitted to length-at-age data obtained from internal spine band counts from a sample of 45 female lucifer dogfish. Schnute growth model: (a) Case 1, (b) Case 2, (c) Case 3, and (d) Case 4.

In Schnute growth model Case 1 for the female's growth data,  $\kappa$  and  $\gamma$  parameters were poorly determined with  $\kappa$  having a flat likelihood profile (Figure 23). This shows that these parameters cannot be estimated and suggests that this case is over-parameterised, and not credible for describing the growth of lucifer dogfish females

in the sample.  $\kappa$  was constrained by the bounds set in `optim`, with the estimate of  $\kappa$  always tending to the lower bound (Figure 23 c). Case 1 was therefore ignored from further consideration in the analysis, as the incorrect parameter estimates influenced the negative log likelihood and AIC values. Likelihood profiles were only estimated for Case 1 of the Schnute growth model, as this was the only model where problems in parameter estimation took place.

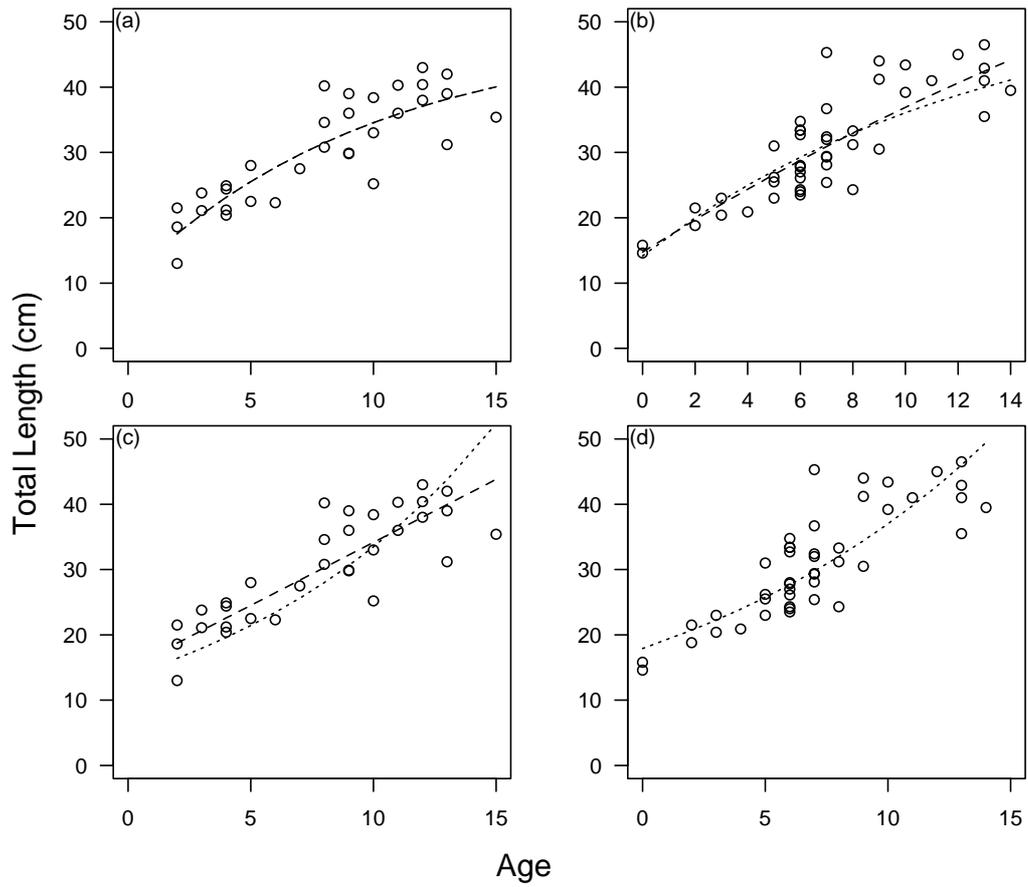


**Figure 23:** Likelihood profiles for Schnute growth model Case 1 fitted to female age data for lucifer dogfish, showing profiles for a)  $y_1$ , b)  $y_2$ , c)  $\kappa$  and d)  $\gamma$

**Table 9:** Growth model comparisons for fits to length-at-age data of female lucifer dogfish. AIC = Akaike's information criterion.

<b>Model</b>	<b>Case</b>	<b># of parameters</b>	<b>Negative log-likelihood</b>	<b>AIC</b>
<b>Schnute</b>	1	5	-26.23	62.47
	2	4	-26.23	60.47
	3	4	-25.94	59.88
	4	3	-22.33	50.65
<b>Von Bertalanffy (<math>t_0</math>)</b>	1	4	-24.62	57.23
<b>Von Bertalanffy (<math>L_0</math>)</b>	2	4	-25.96	59.91

The conventional VBGF model did not provide a better fit to the length-at-age data than Case 4 of the Schnute growth model, for either sex (Tables 8 and 9). The average length ( $L_\infty$ ), at the maximum age, was also over-estimated for both sexes in the VBGF (Figure 24 a, b; Table 10). The modified form of the VBGF (Table 8) fitted the male growth data the same as the traditional, whereas the modified form fitted the female growth data slightly worse than the traditional VBGF (Table 9). For the male growth data, Cases 3 and 4 of the Schnute growth model fitted better than both forms of the VBGF (Table 8), indicating that the male growth data demonstrated linear or increasing growth rate rather than asymptotic growth.



**Figure 24:** Traditional (-) and modified (...) Von Bertalanffy growth curve fitted to the length-at-age data for lucifer dogfish (a) males (n = 51) and (b) females (n = 54). The Schnute growth model cases that performed better than the VBGF c) males [case 3 (-), case 4(...)] and d) females [Case 4 (...)].

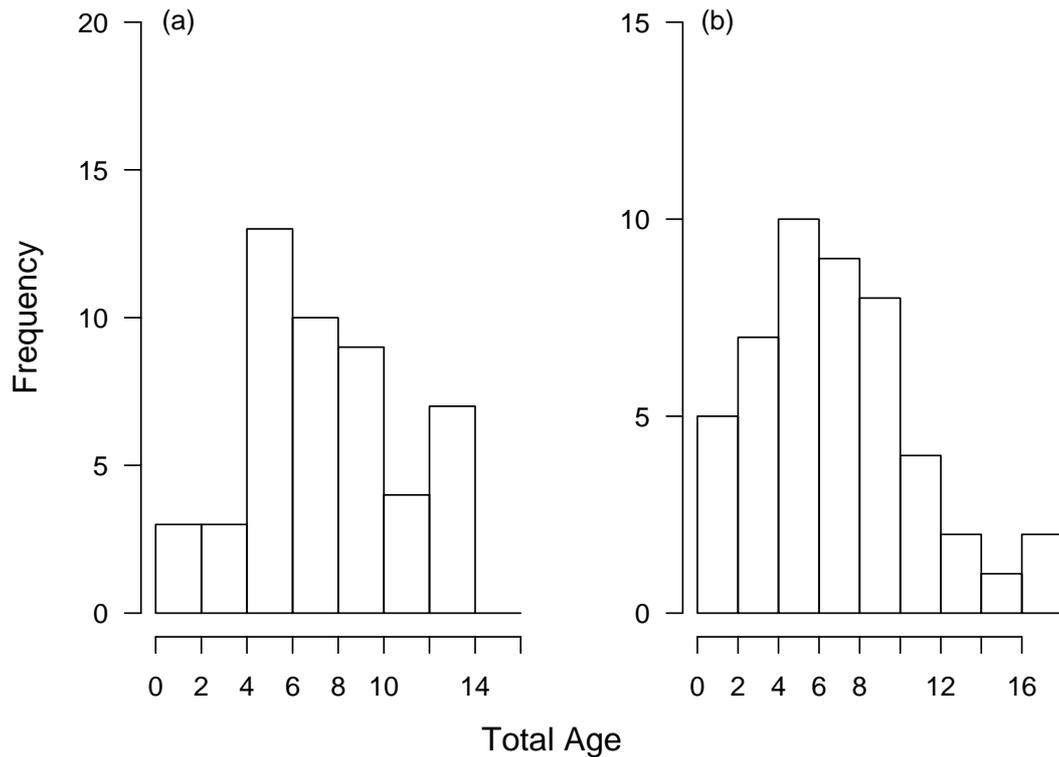
**Table 10:** Parameter estimates for the Schnute and Von Bertalanffy growth models fitted to the length-at-age data for lucifer dogfish.

Function	Parameters	Sex	
		Males	Females
<b>Schnute Model</b>	$y_1$	14.94	14.98
	$y_2$	40.80	44.28
	$\kappa$	0.17	0.10
	$\gamma$	<0.01	<0.01
	$\sigma^2$	0.14	0.14
<b>Case 2</b>	$y_1$	14.94	14.98
	$y_2$	40.80	44.28
	$\kappa$	0.17	0.10
	$\sigma^2$	0.14	0.14
<b>Case 3</b>	$y_1$	14.43	14.97
	$y_2$	35.41	45.07
	$\gamma$	1.06	1.19
	$\sigma^2$	0.14	0.14
<b>Case 4</b>	$y_1$	18.69	17.91
	$y_2$	52.54	49.46
	$\sigma^2$	0.15	0.15
<b>VBGF (traditional)</b>	$L_\infty$	48.74	55.00
	$k$	0.0098	0.077
	$t_0$	0.14	-3.87
	$\sigma^2$	0.14	0.14
<b>VBGF (modified)</b>	$L_\infty$	48.64	104.87
	$k$	0.10	0.03
	$L_0$	10.75	14.74
	$\sigma^2$	0.138	0.136

### Longevity and mortality

The ages estimated using internal band count data for lucifer dogfish ranged from 1 to 17 in the males (Figure 25 a) and 1 to 14 in the females (Figure 25 b). Within these age groups, for both males and females, five year old sharks were the most abundant. Using the maximum observed age of 17 years for males and 14 years for females, the total mortality rate was estimated using Hoenig's (1983) method as  $0.25 \text{ yr}^{-1}$  for males, and  $0.30 \text{ yr}^{-1}$  for females.

Assuming an estimated age at full recruitment of 6 years for females and 4 years for males, the Chapman-Robson estimator gave an estimate of total mortality rate for males of  $0.17 \text{ yr}^{-1}$  and females  $0.14 \text{ yr}^{-1}$ .



**Figure 25:** Age frequency distributions for lucifer dogfish collected in the 2012 Chatham Rise survey for (a) females (n = 54) (b) males (n = 51).

### **Diet of lucifer dogfish**

Of the 351 lucifer dogfish stomachs examined, 201 stomachs were empty (57.3 %), 92 contained liquid (fullness described as “trace”) and unidentifiable digested prey (26.2 %), 24 stomachs were half full (6.8 %) and 32 were considered full (9.1 %). The identifiable stomach contents were mesopelagic fishes, crustaceans, and squid (Table 11). The most common prey identified was *Lampanyctodes hectoris* (Figure 26) occurring in 29.9 % of the stomachs. Other mesopelagic fishes found in the sample included *Symbolophorus boops* and *Maurolicus australis*. Crustacean prey included the natant decapods *Oplophorus australis* and *Eusergestes articus*. Cephalopod prey contributed to only a small proportion of the sample’s gut contents with the only identifiable squid being *Iridotheus maoria*. Unidentifiable large pieces of fish flesh and cephalopod fragments were found in 6 % of the stomachs, which the shark may have sourced by scavenging or attacking prey while in the net.

**Table 11:** Percentage frequency of prey items in the stomachs of a sample of lucifer dogfish, collected in the 2012 Chatham Rise survey.

Prey Items	% Frequency
<b>Osteichthyes</b>	
<i>Diaphus danae</i>	1.5 %
<i>Diaphus ostenfeldi</i>	1.5 %
<i>Lampanyctodes hectoris</i>	29.9 %
<i>Maurollicus australis</i>	3.0 %
<i>Protomyctophus luciferum</i>	1.5 %
Stomiiformes order	1.5 %
<i>Symbolophorus boops</i>	6.0 %
Fish fragments	3.0 %
Unidentifiable fish	23.9 %
<b>Crustacea</b>	
<i>Eusergestes arcticus</i>	7.5 %
Caridean prawn	1.5 %
<i>Oplophorus novaeelandiae</i>	1.5 %
Unidentifiable natant decapod	6.0 %
Unidentifiable crustacean	1.5 %
<b>Cephalopoda</b>	
<i>Irodotheuthis maoria</i>	3.0 %
Squid fragments	3.0 %
Unidentifiable squid	4.5 %
<b>Unidentifiable</b>	11.9 %
<b>Number of stomachs with prey</b>	67
<b>Total number of stomachs</b>	351



**Figure 26:** *Lampanyctodes hectoris*; a mesopelagic fish removed from the gut contents of lucifer dogfish.

## Discussion

This study provides the first comprehensive data on the size, length-weight relationships, age, sexual maturity, growth and diet of lucifer dogfish, caught on Chatham Rise trawl surveys, at depths between 374 and 1028 metres.

The length at maturity estimates (34.3 cm in males and 40.3 cm in females) for lucifer dogfish from New Zealand were broadly similar to those reported in other studies from other regions (Last & Stevens, 2009; Ebert et al., 2013). Last and Stevens (2009), in their book on Australian sharks and rays, stated that male lucifer dogfish reach maturity at about 30 cm and females at about 34 cm. Ebert et al. (2013), for lucifer dogfish, from an unknown origin, also stated that males are thought to mature between 29 and 42 cm (midpoint = 35 cm) and females greater than 34 cm. The differences in estimated length at maturity between these studies may be attributable to variations in sampling methods, sample size, or other factors that may be affecting growth and maturity, such as environmental differences between the study areas (Porcu et al., 2014b). Sexual dimorphism is common in shark species and has been demonstrated within the *Etmopterus* genus (Irvine, 2004; Porcu et al., 2014b).

In this study, male and female lucifer dogfish reached maturity at 74 % and 83% of their maximum length respectively. This finding of late maturation relative to maximum size (Table 12) has been demonstrated in other deepwater shark studies (Graham & Daley, 2011; Irvine, 2004).

**Table 12:** Examples of estimates of length at maturity ( $L_{50}$ ) compared with maximum length ( $L_{max}$ ) from selected studies on elasmobranchs.

Species	$L_{50}/L_{max}$ (%)	Reference
Southern Lantern shark ( <i>Etmopterus granulosus</i> )	75-79 %	Wetherbee (1996)
Baxter's dogfish ( <i>Etmopterus baxteri</i> )	71-75 %	Irvine (2004)
Lucifer dogfish ( <i>Etmopterus lucifer</i> )	74-83 %	2012 Chatham Rise Survey

If we accept the validity of the age estimates, lucifer dogfish also has a late estimated age at 50 % maturity ( $A_{50}$ ), of 61 % and 86 % of the maximum age for males and females, respectively. Previous age data for lucifer dogfish do not exist in the scientific literature, however data have been obtained for related genera (Irvine, 2004). Irvine (2004) observed an age at maturity of Baxter's dogfish at between 42 % to 52 % of the maximum observed age, which she considered to be a relatively late age at maturity (Males  $A_{50}$  = 20 years, Females  $A_{50}$  = 30 years). Irvine (2004) suggested that late age at maturity is an indicator of low productivity, making Baxter's dogfish more vulnerable to overexploitation. Given the relatively late age at maturity also observed here (Males  $A_{50}$  = 10.5 years, females  $A_{50}$  = 12 years), this inference would also apply to lucifer dogfish in this study.

The age at which a shark reaches sexual maturity is an important parameter in fisheries management, as it has a significant effect on the productivity of a species (Parker & Francis, 2012). It has been demonstrated that shark species that mature at a younger age are better able to recover from overfishing than late maturing species (Smith et al., 1998; Stevens et al., 2000; Francis & Duffy, 2004), with Stevens et al. (2000) reporting that age at maturity was the strongest single predictor of a shark populations' ability to recover from overfishing.

The differences in the age of maturity between males and females observed in this study, and that of Irvine (2004), have also been demonstrated in other shark studies (Bishop et al., 2006, Parker & Francis, 2012). Bishop et al. (2006), in their study of shortfin mako (*Isurus oxyrinchus*), obtained  $A_{50}$  estimates of 8 years for males and 18 years for females. The maximum ages from band counts were 29 and 28 years for males and females respectively. Parker & Francis (2012), studied the productivity of two deepwater shark species (birdbeak dogfish and leafscale gulper shark (*Centrophorus squamosus*)) from New Zealand, and also observed a substantial difference in the  $A_{50}$  estimates for birdbeak dogfish males and females of 8.7 and 20.4 years respectively, with a maximum age observed from dorsal-fin spine band counts of 23 years for a mature female. It is hypothesised that females mature at a greater age than males, and as a result their period of fast immature growth lasts

longer, enabling them to attain a larger size in order to support pup development (Francis & Duffy, 2004). Therefore the difference in the age of maturity between males and females lucifer dogfish in this study is expected, however the age at maturity relative to maximum age seems to be late in comparison to other studies. 86 % of the maximum age is a very unproductive life-strategy, and I suggest that the reason for this vastly late age at maturity may be because either inner bands underestimate ages, and/or there were not enough samples of lucifer dogfish to be able to capture an older animal from the population.

There are both costs and benefits associated with late maturation in sharks. Benefits associated with late maturity include sharks being able to maintain growth for longer and reach a larger size before maturation, and thus decrease their risk of predation (Frisk et al. 2001). In female sharks, late maturity allows for additional growth of the abdominal cavity to enhance the quality and size of the pups (Porcu et al., 2014a). There are, however, costs associated with late maturation, including potentially reduced lifetime fecundity and increased natural mortality (Poos et al., 2011), making sharks increasingly vulnerable to overfishing.

The differences in length at maturity observed between sexes within this, and other studies, and within sexes and between studies, could also be due to variations in the techniques used to determine maturity (Porcu et al., 2014a), causing bias in maturity estimates (Flammang et. al., 2008). In this study, the level of clasper calcification, together with inner clasper length and testes length, and testes weight, were used to describe maturity. The condition of the claspers and the testes are characteristics that are commonly used to determine male shark maturity subjectively (Stehmann, 2002; Irvine, 2004). Baremore & Passerotti (2013), in their study of blacktip sharks (*Carcharhinus limbatus*), used clasper calcification alone as a measure of maturity. The use of clasper calcification as a sole measure of determining maturity has been questioned, as the difference between a partially and a fully calcified clasper is highly subjective (Awruch, 2007). It has also been noted that for some species of sharks claspers do not become calcified until late into maturity (Ebert, 2002).

The inner clasper length proved to be a successful objective measure as it agreed with our macroscopic key. Awruch (2007) also chose clasper length as an indicator of the onset of sexual maturity in the draughtboard shark (*Cephaloscyllium laticeps*), and similarly found it increased progressively with maturity. Girard & Buit (1999) also advocated the use of clasper length as an indicator of maturity in their study on two deepwater shark species, Portuguese dogfish (*Centrosymnus coelolepsius*) and leaf scale gulper shark.

In this study vas deferens was also examined. Moreno & Moron (1992) used the level of clasper calcification and the degree of folding of the deferent ducts to determine maturity of the bigeye thresher shark (*Alopias superciliosus*), and concluded that the most reliable method was examination of the degree of folding of the deferent ducts.

Although there was a slight overlap in each of the objective measures between the macroscopic maturity stages, these measures, particularly inner clasper length, provided an objective measure of maturity. The degree of coiling of the vas deferens enabled mature and immature individuals to be distinguished from one another, but was not useful for differentiating between Stage 2 (maturing) and Stage 3 (mature) individuals. Testes weight, especially, was not an overly informative objective measure as there were no clear-cut differences between the different maturity levels, unlike the testes length and inner clasper length measurements. Testes weight and length were relatively difficult to measure for Stage 1 males, as the testes were small. This means that there is more uncertainty in these measurements. The difficulty in using qualitative measures on their own, as indicators of maturity, is that they can be highly subjective (Baremore & Passerotti, 2013).

The maturity of females was based upon the condition of the ovaries and the uterus. Differentiating between the maturity stages involved both qualitative and quantitative measures, specifically by assessing uterine and oviducal gland width, number and diameter of oocyte, and oocyte colour. Some researchers (Irvine, 2004; Parker & Francis, 2012) used oocyte colour as a measure of female maturity,

however they did so in combination with other objective measures to support their findings. However, the sizes and colour of oocytes are not easily distinguishable between the different maturity stages (Clarke, 2000; Baremore & Passerotti, 2013), which was also found in this study, with Stage 6 resting mature sharks and Stage 2 developing juveniles having similar sized and coloured ova. It would seem then that the colour of oocytes is only useful in distinguishing Stages 1 and 2 from Stage 3 individuals.

Awruch (2007) used oviducal gland width to determine maturity in a study of the Australian swellshark (*Cephaloscyllium laticeps*). Oviducal gland width was used because, unlike the other female measures such as uterine width, this measurement progressively increases throughout maturity, and is independent of the reproductive cycle (Awruch, 2007). Unfortunately, oviducal gland width could not be used as the sole measure for determining female maturity stages in this lucifer dogfish study. This was because the oviducal gland was not always clearly visible in Stage 1 and 2 individuals, making it impossible to take credible measurements, and difficult to distinguish these stages from one another.

While most of the objective and subjective measures were useful in describing the maturity of lucifer dogfish, there were some measurements that were not particularly instructive. These included testes weight, oviducal gland width, and the colouration and size of oocytes. While testes weight and oviducal gland width were not explicitly used to describe different maturity stages, oocyte colouration and size was. The use of oocyte colouration and size may have resulted in errors in maturity classification, especially in distinguishing between Stage 2 and Stage 6 females (or at least it did not help).

The potentially unrepresentative nature of the sample in this study may mean that not all stages were seen at the true (population) frequency, and so interpretation of the maturity stages could be biased. Assessing maturity will be most precise when a large number of immature, maturing and mature animals can be observed in the sample (Musick & Bonfil, 2005).

There was a paucity of apparently mature females, particularly pregnant females, collected in the 2012 Chatham Rise survey. A similar observation was made by Baba et al. (1987) for lucifer dogfish off the Japanese coast. A paucity of pregnant females has also been observed in a number of other deepwater shark species (Figueiredo et al., 2008; Parker & Francis, 2012; Wetherbee, 1996). Parker & Francis (2012), in their study of the deepwater shark species birdbeak and leafscale gulper shark, hypothesised that the lack of pregnant females could be because they became more pelagic or moved deeper into the water column (i.e. depth segregation), thus avoiding capture (Parker & Francis, 2012). Figueiredo et al. (2008), in their study of leafscale gulper shark, on the Portuguese coast, inferred that the limited number of pregnant females being caught may benefit the spawning stock biomass as there were females elsewhere who could potentially produce more offspring. Wetherbee (1996) investigated the distribution and reproduction of the southern lanternshark (*Etmopterus granulosus* = *E. baxteri* studied by Irvine 2004; Irvine et al., 2006 a), on Chatham Rise. He also observed a lack of pregnant females, proposing a similar hypothesis to that of Parker & Francis (2012), with pregnant females moving to another depth. Moura et al. (2014) observed spatial segregation by sex, in three species of deepwater sharks, with pregnant females occupying much shallower and/or warmer waters in all three species.

As our study observed similar maximum lengths of female lucifer dogfish to other studies (Last & Stevens, 2009; Ebert et al., 2013) it would seem highly unlikely that pregnant females were in some way avoiding the surveys. Another, more realistic hypothesis, proposed to explain the absence of mature females, is that lucifer dogfish may have an asynchronous reproductive cycle, with 2012 being a year in which they did not reproduce, so one would expect to observe a higher percentage of females in the 2013 and 2014 surveys. Hoffmayer et al. (2013) examined the variability in the reproductive biology of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), and observed an asynchronous reproductive cycle, with females collected in the survey possessing embryos at varying developmental stages, from recently fertilised oocytes to 150 mm total length embryos. Hoffmayer et al. (2013) concluded that, as several reproductive parameters are required for

stock assessment models, any changes in these parameters, such as an asynchronous reproductive cycle, could significantly change the outcome of these assessments.

Given these previous studies, it seems likely that the 2012 Chatham Rise survey was unrepresentative of the entire lucifer dogfish population, with the limited number of pregnant females collected making it difficult to determine their reproductive life history. Surveys over multiple years, and wider areas would be required where a single year's data is not adequate to determine life history parameters. If this sample is in fact representative of the population and there is a paucity of adult females, then the population is at risk of overexploitation.

The age of deepwater sharks has previously been determined by counting the growth bands on the external surface of the dorsal spine, or by counting internal growth bands on a dorsal spine cross-section (Irvine et al., 2006a, 2006b; Ramos, 2007). Irvine (2004), in a personal observation, noted the presence of bands on the external surface of the dorsal spine of lucifer dogfish. Despite Irvine's observation, in this study, and after repeated examination of the spine, and the use of a number of staining techniques known to enhance banding (e.g. silver nitrate and alizarin red), there was no clear evidence of external banding. Irvine et al. (2006a, b) successfully aged Baxter's dogfish and golden dogfish using external growth bands on dorsal fin spines. In both species, Irvine et al. (2006b) considered that the external bands provided a more reliable estimate of age because internal dentine appeared to stop forming in adults, whereas external band formation continued (Irvine et al., 2006a). She reached this conclusion using work previously done by Fenton (2001) on golden dogfish. The annual formation of external bands was partially validated using radiometric age estimates from research previously done on the species by Fenton (2001) using a small sample of vertebrae. Using this method, ages ranged from 26-43 years old, which were similar to the number of external growth bands on Irvine's (2006a) sample, who found the oldest male and female were 48 and 57 years, respectively. No validation work was done on the internal bands in Irvine et al. (2006a, b) studies.

In many deepwater sharks, the external enamel layer of dorsal fin spines is not well developed and the bands are poorly defined, making age determination difficult (Parker & Francis, 2012). This has necessitated the use of internal growth band counts to estimate age (Clarke et al. 2002; Parker & Francis 2012). Similar to this study, Clarke et al. (2002) estimated the age of the leafscale gulper shark, using internal bands, due to the absence of clear external banding on the dorsal fin spine. Parker & Francis (2012) also successfully used the internal dentine layer to determine the age of the deepwater sharks, birdbeak dogfish and leafscale gulper shark. Although the inner bands have been considered less reliable than the external bands (Irvine et al. 2006) as they may not continue to form in later life, they probably do not always provide vastly different age estimates (Tova-Avila et al., 2009). Tova-Avila et al. (2009) determined the age of Port Jackson shark (*Heterodontus portujacksoni*) using sectioned and whole vertebrae and dorsal spines, and found that there was good agreement between the number of external bands and internal bands, indicating that either could be used to determine age. Calliet & Goldman (2004) recommended the use of transverse or sagittally sectioned spines rather than whole structures due to the risk of under-estimating age due to erosion of the external surface of the spine, compared with the internal spine. This demonstrates that both inner and external bands could potentially provide similar age estimates, and that the method used here should not be rejected. However we cannot be sure as to the accuracy of the estimates until age validation studies have been performed.

Interpretation of the growth bands has proved problematic in many deepwater shark studies (Clarke, 2000; Parker & Francis, 2012). Key issues outlined in the literature include the concern as to whether there is a middle dentine band present in the internal section of the spine, and identifying the correct location of the trunk primordium (starting point for counting) when there is limited band clarity. In this study, inner, middle and outer dentine layers were identified in the dorsal fin spines of lucifer dogfish. Growth bands in the inner dentine layer were chosen for counting as the band spacing was the widest and the bands had high clarity compared with the middle and outer layers. Parker & Francis (2012) also used the inner layer to

estimate the ages of two deepwater sharks, proposing that the full growth history is only apparent in the inner layer of the cross section. Furthermore the authors of Clarke and Irvine (2007) were in disagreement about the middle dentine layers.

Clarke (2000), however, could not identify a middle dentine layer on the dorsal spines of the three deepwater shark species he was investigating, instead determining age by counting within the entire internal section, including what in this study, and Parker & Francis's (2012) study, define as the middle dentine layer where some banding can be observed but it is not clear on meaning. Clarke (2000) suggested that studies that identified a middle dentine layer and did not count it had the potential of under-estimating the shark's age. This suggestion by Clarke (2000) may imply that age could have been under-estimated in this study. However by following the more recent methods, as described by Irvine et al. (2006a, b) and Parker & Francis (2012), who have been clear in their expectation that the full growth history only occurs in the inner section of the dorsal spine, the age estimates for lucifer dogfish in this study may be more accurate and are consistent with current methodologies. In this study, we also occasionally had difficulty identifying the location of the trunk primordium, as did Parker & Francis (2012) in their study, and these would have got a poor readability score.

Formal age validation techniques were beyond the scope of this study. Without this information, the best approach for evaluating the interpretation of growth bands was to examine precision of age estimates (Parker & Francis, 2012). The estimate of precision for this study, within-readers (CV= 12.71 %) and between-readers (CV = 11.98 %) was similar to the level commonly documented as being acceptable for fish ageing studies of 10 % (ICES, 2013a). However the level of precision accepted has been shown to vary from this pre-defined level according to the fish species and the nature of the study, with CVs for shark ageing studies rarely being less than 10 % (Campana, 2001). Irvine et al. (2006a, b), in their study of Baxter's dogfish, set an upper limit for the CV at 20 %, with ages not included in the growth analysis if the CV was greater than this. The average CV of readable counts obtained in Irvine's study was a very low CV of 1.45 %. The low coefficient of variation obtained in this lucifer

dogfish study indicates an acceptable level of precision within the age estimates. But precision will remain unknown until validation takes place. Accurate age estimations are essential in age and growth studies, as biases can strongly influence productivity estimates, resulting in the overexploitation of a species (Campana, 2001). While validation was outside the scope of this study, there has been some evidence that the use of near infrared spectrometry (NIRS) could be useful for validating the ages of lucifer dogfish. Rigby et al. (2014), were successful in validating the ages of two species of deepwater squaloid sharks, the shortnose spurdog, (*Squalus megalops*), and the Phillipines spurdog, (*Squalus montalbani*) using NIRS on the dorsal fin spines.

Of the four cases of the Schnute growth model and the traditional and modified VBGF, fitted to the lucifer dogfish length-at-age data, Case 4 of the Schnute growth model provided the best statistical fit. This case of the Schnute growth model resembles exponential growth. The third case of the Schnute model, representing linear growth, also provided a good fit to the female growth data.

Exponential growth is considered realistic in the early life of sharks, however, like most other vertebrates, growth is later forced to asymptote for a variety of reasons including the switch to gamete production (maturity), and carrying capacity of the environment (Gedamke et al., 2007). Linear growth in sharks has also been observed in some shark species (Barker & Schluessel, 2005; Bishop et al., 2006). Barker & Schluessel (2005), examined the spatial and ontogenetic variation in the growth of neonate and juvenile lemon sharks (*Negaprion brevirostris*), and found that for the first three years of life, lemon sharks exhibited a linear growth pattern. Bishop et al. (2006), in their study of the short fin mako also demonstrated that females exhibited a near-linear growth pattern through most of their female data points. Cotton et al. (2011), in their study of the growth of the shortspine spurdog (*Squalus cf. mitsukurii*), found that female growth did not reach an asymptotic size as expected; they attributed this phenomenon to the paucity of older females in the sample. Nevertheless, persistent linear or exponential growth is considered unrealistic in most shark ageing studies, so these growth models are often excluded from data analysis (Natanson et al., 2013). The failure to observe asymptotic growth in lucifer

dogfish in this study could be caused by either the lack of older ages observed in the sample or that sharks are no longer living as long as they previously have. The latter may suggest a substantial rate of fishing mortality.

In this study, the traditional VBGF provided a poorer fit to the length-at-age data. The traditional VBGF is the most commonly used model to describe chondrichthyan growth (Cailliet et al., 2006). The model has been successfully used to describe the growth of a number of shark species. Lessa et al. (2004) and Natanson (2001) used the traditional VBGF to describe the growth of blue sharks (*Prionace glauca*) and the shortfin mako respectively. In both studies the AIC was the lowest for the traditional VBGF when compared to other models, indicating that it provided the best fit to the length-at-age data.

Despite its universal use, a number of authors have indicated that the VBGF may not always be the most useful descriptor of growth for all elasmobranch species (Cailliet et al., 2006; Katsanevakis & Maravelias, 2008; Barreto et al., 2011). This is because  $t_0$  (age at length 0) in the traditional VBGF is considered to have little biological meaning:  $t_0$  is difficult to interpret because it is the age of zero length; which implies negative time (Cailliet et al., 2006). Cailliet et al. (2006) recommended the use of a re-parameterised version of the VBGF (referred to as the modified VBGF), which is mathematically equivalent to the traditional VBGF, but replaces  $t_0$  with  $L_0$  (length at birth). This function was applied to the growth data of the white spotted bamboo shark (*Chiloscyllium plagiosum*) by Chen et al. (2007). Using AIC, the modified VBGF in Chen et al's (2007) study provided the best fit of the growth data. Another study by Fernandez-Carvalho et al. (2011), compared the performance of the traditional VBGF with the modified VBGF, to describe the growth of the bigeye thresher shark. While Fernandez-Carvalho observed that the traditional VBGF provided a better fit of the data, as evidenced by the lower AIC value, they chose to use the modified VBGF as  $L_0$  was the more biologically meaningful parameter for describing growth than  $t_0$ . In this study on lucifer dogfish, the modified VBGF did not provide a better fit of the growth data compared to the traditional model. The  $L_0$  of 10-15 cm was,

however, consistent with the sizes of pups seen in the Stage 5 females (11.1 – 13.0 cm TL).

In this study,  $L_{\infty}$  estimated from the traditional and the modified VBGF were much larger than the maximum observed length ( $L_{max}$ ) for both sexes. Unrealistic parameter estimates derived from the VBGF have been demonstrated in a number of shark studies (Wintner & Cliff, 1999; Manning & Francis, 2005; Bishop et al., 2006; Tribuzio et al., 2010;). The unrealistic parameter estimates have been linked to small sample sizes and a paucity of younger and older individuals in the sample resulting in insufficient curvature in the growth model (Wintner & Cliff, 1999; Bishop et al., 2006; Tribuzio et al., 2010).

Tribuzio et al. (2010), in their study of the age and growth of the spiny dogfish, hypothesised that the age at transition ( $t_h$ ) for their two-phase VBGF was underestimated due to the limited number of small sharks in the sample. Wintner & Cliff (1999), in their study on the white shark, observed a low estimate of  $L_{\infty}$  compared to the value of  $L_{max}$ , which they hypothesised as being due to the lack of larger sharks in their sample. Bishop et al. (2006), in their study on the short fin mako, observed a high  $L_{\infty}$  value for females, assuming that this was caused by the lack of older females within the sample. It is postulated that the unrealistic parameter estimates observed in this study on lucifer dogfish, using both forms of the VBGF, is most likely to be due to the lack of older females within the sample, and also potentially inaccurate age estimates (biased low).

Natural mortality is defined by Pauly (1980) as 'all the possible causes of fish death except deaths induced by fishing'. Both natural mortality and fishing mortality make up the total mortality. Despite the significance of understanding mortality, especially for fisheries management, it is often poorly known (Simpfendorfer et al., 2005).

Assuming that the age estimates are valid, the lucifer dogfish sample had a moderate mortality rate, ranging from  $0.15 \text{ yr}^{-1}$  (Chapman-Robson estimator, 1960) to  $0.27 \text{ yr}^{-1}$  (Hoenig 1983). Mortality estimates have not been published for lucifer

dogfish, however we can compare the estimates with the estimates for other deepwater sharks (Parker & Francis, 2012).

Parker and Francis (2009) estimated the total mortality of two species of deepwater sharks, birdbeak dogfish and leafscale gulper shark, using the Chapman Robson (1980) estimator, and found that total mortality for birdbeak dogfish ranged between  $0.41 \text{ yr}^{-1}$  and  $0.46 \text{ yr}^{-1}$  on Chatham Rise, and  $0.32 \text{ yr}^{-1}$  to  $0.41 \text{ yr}^{-1}$  for the Sub-Antarctic survey. These estimates were much higher than the mortality estimates found in this study as there was a high level of fishing mortality in these stocks. Leafscale gulper sharks had a similar level of mortality to lucifer dogfish of between  $0.10 \text{ yr}^{-1}$  and  $0.14 \text{ yr}^{-1}$ , which Parker & Francis put down to the lower levels of fishing mortality of this stock.

The differences between the mortality estimates from the two methods used in this study, have also been reported by Simpfendorfer (1998). Using a number of direct and indirect estimators, Simpfendorfer (1998) determined the mortality of a non-fished sample of Australian sharpnose shark (*Rhizoprionodon taylori*). He found that the mortality estimates ranged from  $0.6 \text{ yr}^{-1}$  to  $1.65 \text{ yr}^{-1}$  between different estimators. Simpfendorfer (1998) suggested that this large variability in mortality estimates may be related to the Australian sharpnose shark's short life span and fast growth. Determining mortality is difficult and without direct evidence, such as in-situ tagging experiments, we cannot be sure as to which estimator provides us with the most accurate mortality measure.

A number of estimators have been developed to predict mortality based on empirical evidence from growth studies (Hoenig, 1980; Pauly, 1980), making it difficult to determine the most appropriate estimator (Maunder and Wong, 2011). Dunn et al. (1999) and Simpfendorfer (1998) examined the performance of different estimators in their studies. Dunn et al. (1999) compared the performance of the Chapman Robson (1960) estimator against other regression based indicators. After testing the performance of the estimators in a number of scenarios, the Chapman

Robson (1960) was identified as the best estimator as it had the lowest root mean square error and a lower bias than the other estimators.

The estimated maximum age of male lucifer dogfish (17 years) was higher than the females (14 years). A higher age for males could be due to the unrepresentative sampling (Table 8, 9). A similar observation was reported by Francis et al. (2007), in their study of the porbeagle shark (*Lamna nasus*), due to the assumed paucity of mature females, especially pregnant females, in their sample survey. No longevity estimates are known for lucifer dogfish, however data have been obtained for related genera (Coelho & Erzini, 2007; Coelho et al., 2014). In contrast to our results, Coelho & Erzini (2007) and Coelho et al. (2014), in their studies of two deepwater lantern sharks, smooth lanternshark and velvet belly lanternshark (*Etmopterus spinax*), found that the maximum age of females for both species was higher than the males maximum age. They estimated a maximum age of 13 years for male smooth lanternshark and 17 years for the females, with male velvet belly lanternshark attaining a maximum age of 8 years, and females 11 years. The difference in the maximum ages observed between males and females between these studies and the previous study is again hypothesised to be caused by the relative absence of mature females in the lucifer dogfish sample.

This study provided the first description of prey species consumed by lucifer dogfish on Chatham Rise. Myctophids were the most frequently observed prey species in the stomach contents of the lucifer dogfish sample. Baba et al. (1987), also observed that myctophids were an important dietary component for lucifer dogfish caught off the coast of Japan, but not as important as the small squid species, sparkling enope squid (*Watsenia scintillans*). Baba et al. (1987) also found an ontogenic change in the diet of lucifer dogfish, from euphausiids and crustaceans in the small individuals, to squid in the larger sharks. There were insufficient samples to examine this in the present study.

A number of lucifer dogfish stomachs contained unidentified fish flesh and squid arm fragments. This was interpreted as the sharks either feeding while in the net or as

evidence of scavenging, or the less likely conclusion, that the flesh was obtained by sharks taking bites out of larger prey like cookie cutter sharks (Goto et al. 2009). Dunn et al. (2010) studied the diet of a number of deepwater shark species on Chatham Rise and observed unidentifiable flesh in the stomach contents, which they suggested was sourced either by scavenging or by prey being attacked, but not fully ingested. Dunn et al. (2013) also reached similar conclusions, that scavenging may be commonly occurring in deepwater sharks.

## **Conclusion**

### *Implications for Management*

As the global demand for fish products intensified, fishing fleets moved into deeper waters as coastal fisheries become depleted (Kyne & Simpfendorfer, 2007).

Deepwater shark species have a higher risk of overexploitation than their pelagic counterparts because of their relatively late age at maturity, their low growth rate, and their low fecundity (Kyne & Simpfendorfer, 2007). Fishing fleets are exploiting the last refuges of these vulnerable deepwater species (Watson & Morato, 2013). Understanding species-specific life histories is crucial for providing scientific advice for effective management of deepwater sharks (Hamady et al., 2014; Moura et al., 2014).

A shark population's risk of overexploitation is dependent on both its vulnerability to fishing, its population size, and its productivity (Stevens et al., 2000). Whilst this study emphasizes that the larger females and older fishes were missed through unrepresentative sampling, there remains a possibility that the population is being subjected to a high mortality rate due to overfishing. If this is correct, then lucifer dogfish are at risk of overexploitation and unnoticed localized depletion, as there are few reproductive adults in the population. While lucifer dogfish is not directly targeted in New Zealand waters and there is no evidence of total population declines (Doonan & Dunn, 2011; O'Driscoll et al., 2011; Bagley et al., 2013) it is still recommended that the level of bycatch of lucifer dogfish should be carefully

monitored. This may mean that the IUCN Red List classification of lucifer dogfish as of 'Least Concern' should be re-evaluated.

### *Recommendations*

- Improve commercial fishers and scientific observer's identification and reporting of bycatch at the species level in order to get credible catch estimates, allowing more accurate estimates of stock status, and therefore ensure more efficient management of vulnerable deepwater shark species.
- Future research into the maturity of lucifer dogfish could include the use of microscopic measures, such as differences in the development of spermatocysts and follicles, to validate macroscopic measures. Microscopic analysis of maturity was beyond the scope of this study, and also not conducted in this study as samples were collected two years prior to the analysis; maturity staging from frozen specimens can introduce errors (ICES, 2013b).
- Future research into the validation of spine ages, and training of readers to ensure precision and accuracy is needed. Although this study provided the first described age estimates of lucifer dogfish, these estimates should be examined with caution, as the growth bands for a number of the samples were unclear and the age estimates were not validated. A novel validation technique for lucifer dogfish ages could include the use of Near Infrared Spectrometry (Rigby et al. 2014).
- Instead of fishing in deepwater habitats there needs to be more effort put into restoring and sustainably fishing populations that recover quickly in shallower, more productive nearshore ecosystems (Norse et al., 2012).

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# Appendices

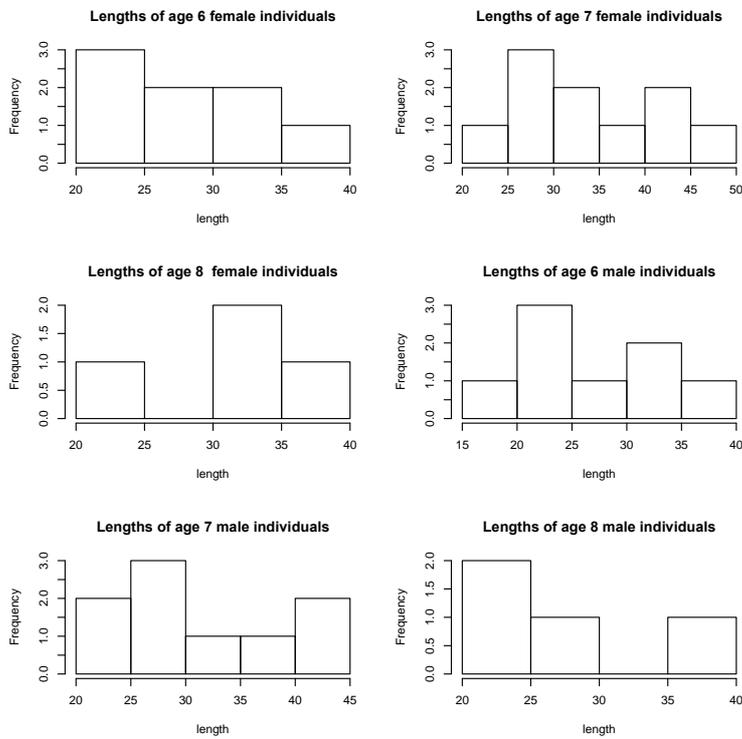


Figure A1: Histograms of the length-at-age for a selected number of common ages featured in the age data set of a sample of lucifer dogfish, subdivided into males and females.

Most ages (female 6, 7; male 6, 7, 8) tended to show a skew to the right-hand side. This would be consistent with a log normal (skewed) rather than normal (symmetrical) distribution.