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LIFE HISTORIES OF DEEPWATER CHONDRICHTHYANS



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All research activities were conducted under Great Barrier Reef Marine Park Authority Permit G10/33603.1 and Department of Agriculture and Fisheries Permits 55105 &147714.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee Approval Number A1566.

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ABSTRACT

As fisheries move into deeper waters the ability of deepwater chondrichthyans to sustain fishing is relatively unknown, although the limited information to date suggests most are inherently vulnerable to exploitation. Knowledge of deepwater chondrichthyans life history traits is required to enable effective management of deepwater chondrichthyans, as life history traits are important indicators of the productivity of species and consequently, species abilities to tolerate fishing pressure. This dissertation aimed to further knowledge of the life histories of deepwater chondrichthyans by assessing patterns in their traits and studying the life history of species taken as bycatch in a deepwater trawl fishery within the Great Barrier Reef Marine Park. It also addressed the issue of the inability to age many deepwater chondrichthyans through investigation of a novel approach to ageing, that is, by using near infrared spectroscopy.

The association of chondrichthyan life history traits and habitat was examined among the three main marine habitats of shelf, pelagic and deepwater, and also within the deepwater habitat. Life history traits were obtained from 226 populations of chondrichthyans across the three habitats. These traits were analysed for patterns using a linear mixed effects model that controlled for the correlation among species due to their common evolutionary history. Life history differences were identified between chondrichthyans from shelf, pelagic and deepwater habitats, and within the deep habitat down the continental slope. Deepwater species as a group, had lower growth rates, later age at maturity and higher longevity than both shelf and pelagic groups of species. In the deep habitat, with increasing depth, most species matured later, lived longer, had smaller litters and bred less frequently. The group of deepwater species also had a smaller body size than the groups of shelf and pelagic species, which indicates body size is not appropriate as a predictor of vulnerability in most deepwater chondrichthyans. The visual interaction hypothesis offers a potential explanation for these findings, and it is apparent habitat influences the trade-offs in allocation of energy for survival and reproduction. In general, deepwater chondrichthyans are more vulnerable to exploitation than shelf and pelagic species and this vulnerability markedly increases with increasing depth. The life history traits of the deepwater chondrichthyans as a group are unique from the shelf and pelagic groups of species, and reflect adaptations driven by both mortality and resource limitations of their habitat.

The chondrichthyan bycatch from the deepwater eastern king prawn fishery at the Swain Reefs, in the southern Great Barrier Reef Marine Park, was sampled onboard two commercial prawn trawlers. In all, 1533 individuals were collected from 11 deepwater chondrichthyan species, with a skate, *Dipturus polyommata*, most dominant by number at 50% of the bycatch. A

dogfish, *Squalus megalops* and a catshark, *Asymbolus pallidus* were the other dominant species accounting for 28% and 15% of the bycatch, respectively. They were followed by a gummy shark, *Mustelus walkeri* which accounted for 3% of the bycatch. The remainder of the species were captured infrequently, and included an angelshark (Squatinae), stingarees (Urolophidae) and a shortnose chimaerid (Chimaeridae). Preliminary biological data was obtained from all these infrequently caught species. *Dipturus polyommata*, *S. megalops* and *M. walkeri* all had reliable ageing structures and were taken in sufficient numbers to enable detailed life history studies. A fourth deepwater species (a dogfish, *Squalus montalbani*) that occurs in the Great Barrier Reef Marine Park but which was collected from New South Wales, was provided to this study and was also investigated for age, growth and reproduction life history information.

Dipturus polyommata was a small skate that was the shortest lived of the four species, with an observed maximum longevity of 10 years. It also had the fastest growth, with a von Bertalanffy growth completion parameter of $k = 0.208 \text{ year}^{-1}$ for combined sexes, and it matured at the earliest age, with males reaching maturity at 4.0 years and females at 5.1 years. *Mustelus walkeri* was a moderately sized shark that lived longer than *D. polyommata*, with the oldest male 9 years and oldest female 16 years. It also grew more slowly with a combined sexes $k = 0.033 \text{ year}^{-1}$, and matured later with males estimated to mature at 7–10 years and females at 10–14 years. The two dogfish species, *S. megalops* and *S. montalbani* were small and moderately sized dogfish, respectively. They had the slowest growth rates of all four species; with *S. megalops* combined sexes $k = 0.003 \text{ year}^{-1}$ and *S. montalbani* combined sexes $k = 0.007 \text{ year}^{-1}$. These dogfish were also longer lived than *D. polyommata* and *M. walkeri* with maximum observed ages for males and females of 18 and 25 years for *S. megalops*, and 28 and 27 years for *S. montalbani*. Further, they were the oldest at maturity with *S. megalops* males mature at 12.6 years and females at 19.1 years. *Squalus montalbani* males were mature at 21.8 years and females at 26 years.

All viviparous species had low fecundity with litter sizes of 5–7 for *M. walkeri*, 2–3 for *S. megalops* and 9–16 for *S. montalbani*. The oviparous *D. polyommata* had an average ovarian fecundity of 8 follicles which was low compared to other small–medium sized *Dipturus* species. The age, growth and reproduction of these four species corroborated the life history pattern analyses. Assuming that fishing mortality was the same among species, it is likely that the shallowest dwelling *D. polyommata* was the most productive, followed by the slightly deeper occurring *M. walkeri* and then the two deeper dwelling dogfish. *Squalus megalops* was likely more productive than the deepest occurring *S. montalbani*.

Reliable age information is essential to accurately predict the ability of chondrichthyan species to sustain exploitation, yet many deepwater chondrichthyans cannot be aged as they do not have reliable age structures. A novel approach to ageing, that is, using near infrared spectroscopy for ageing (NIRS), was first trialled on two coastal species, *Sphyrna mokarran* and *Carcharhinus sorrah*, both of which been previously age validated. NIRS successfully predicted their ages up to 10 years of age for both species, with the correlations between the known ages of the vertebrae and their near infrared spectra strong at R^2 values of 0.89 and 0.84 for *S. mokarran* and *C. sorrah*, respectively. The NIRS approach was then applied to three species of deepwater sharks using their dorsal fin spines, vertebrae and fin clips. Ages were successfully estimated for the two dogfish, *S. megalops* and *S. montalbani*, and NIRS spectra were correlated with body size in the catshark, *Asymbolus pallidus*. Correlations between estimated-ages of the dogfish dorsal fin spines and their NIRS spectra were good, with *S. megalops* $R^2 = 0.82$ and *S. montalbani* $R^2 = 0.73$. NIRS spectra from *S. megalops* vertebrae and fin clips that have no visible growth bands were correlated with estimated-ages, with $R^2 = 0.89$ and 0.76, respectively.

This study demonstrated that the NIRS approach to ageing was feasible for age estimation of sharks. The NIRS ageing approach is rapid, which is a major advantage of the method, and could enable large numbers of sharks to be aged quickly. This offers the fisheries management benefit of improving the reliability of age information for stock and risk assessments. NIRS also has the capacity to non-lethally estimate ages from fin spines and fin clips, and thus could significantly reduce the numbers of sharks that need to be lethally sampled for ageing studies. This NIRS approach is the first chemical assay approach investigated in shark ageing that is simple, rapid and cost-effective. The detection of ageing materials by NIRS in poorly calcified deepwater shark vertebrae that have no visible bands, could potentially enable ageing of this group of sharks that are vulnerable to exploitation.

This ageing and life history research has improved the understanding of deepwater chondrichthyans. This group of chondrichthyans have a unique suite of life history traits that render them more vulnerable to fishing pressure than their counterparts in shelf and pelagic waters, with their vulnerability increasing with depth. This knowledge is vitally important to fisheries management because the deeper the fishing, the less capacity the chondrichthyans have to recover. The findings of this dissertation can be used to facilitate more effective management and conservation strategies needed to ensure this group of chondrichthyans are sustainably fished and not placed at risk of extinction.

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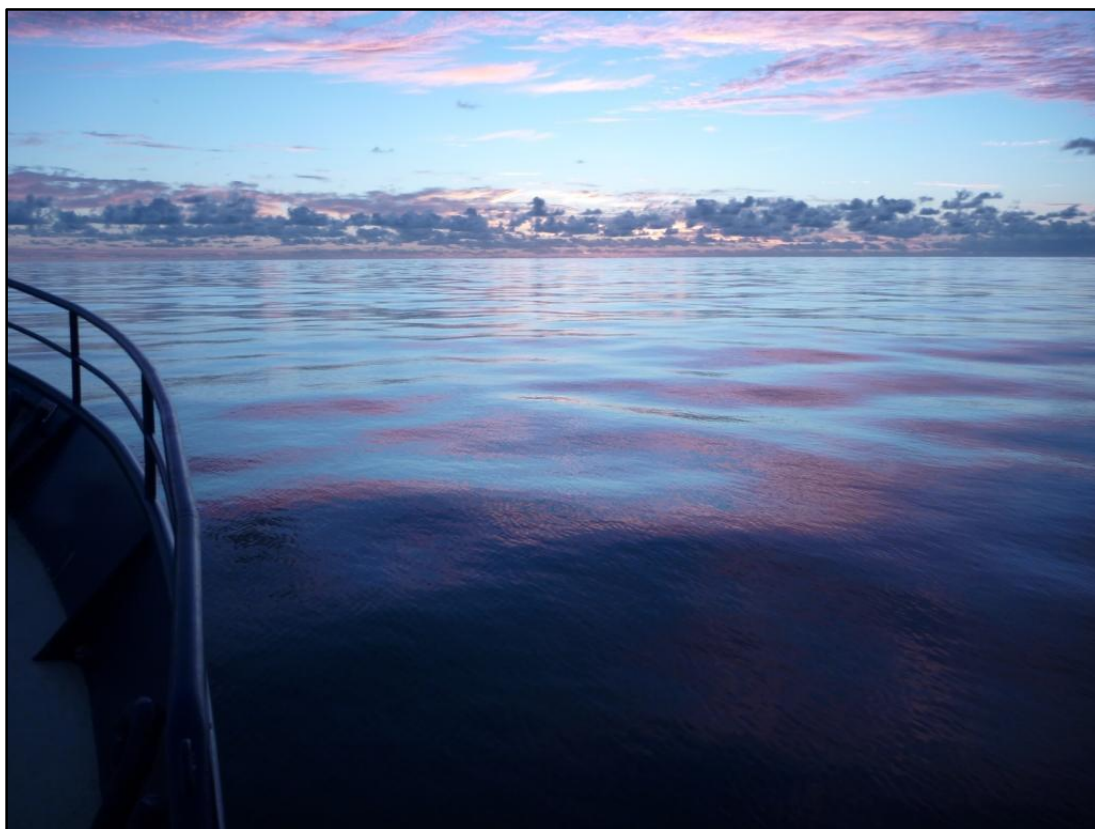
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Chapter 1 General introduction



Sunrise at sea

Fisheries are increasingly moving into deeper waters as coastal fisheries decline in response to greater fishing pressure (Norse *et al.* 2012; Watson and Morato 2013). Consequently, chondrichthyans (sharks, rays and chimaeras) that inhabit these deepwater areas are likely to experience increased exploitation (Morato *et al.* 2006b; Simpfendorfer and Kyne 2009). The ability of these deepwater chondrichthyans to sustain fishing and recover from depletion is relatively unknown as there is very little information on their life history traits of age, growth and reproduction. This is despite deepwater chondrichthyans accounting for almost half of the world's approximately 1200 chondrichthyan species (Kyne and Simpfendorfer 2010; Naylor *et al.* 2012). Life history information is critical to the assessment of productivity and vulnerability to fishing pressure and for stock assessment and development of effective management and conservation strategies (Cailliet *et al.* 2006; Dulvy and Forrest 2010; Goldman *et al.* 2012).

The deep sea is generally considered as waters below 200 metres depth and poses logistical difficulties with sampling that has limited the number of life history studies of deepwater chondrichthyans (Kyne and Simpfendorfer 2007). The majority of chondrichthyan life history data comes from the shallower shelf waters, and to a lesser extent from the pelagic open ocean. Chondrichthyans from these shelf and pelagic habitats are generally slow growing, late maturing, have low fecundity, long gestation periods and long life spans (Hoenig and Gruber 1990; Cortés 2000). This suite of life history traits result in much lower productivity relative to broadcast spawning taxa, such as teleost fishes, and an intrinsic vulnerability that is widely recognised (Cailliet *et al.* 1990; Field *et al.* 2009; Dulvy *et al.* 2014).

The few life history studies of deepwater chondrichthyans to date indicate that they have an even greater vulnerability to exploitation than shelf and pelagic chondrichthyans. Most chondrichthyans from the deep, dark and cold habitat where there is limited food (Angel 1997; Gartner Jr *et al.* 1997) exhibit slower growth rates, later ages at maturity and higher longevities than chondrichthyans from both shelf and pelagic waters (García *et al.* 2008; Bergstad 2013). This results in even lower biological productivity than their relatives in these other habitats (Simpfendorfer and Kyne 2009). Consequently, the extinction risk from fishing pressure of deepwater chondrichthyans is higher, with estimates that the fishing mortality that would drive deepwater species to extinction is 58% that of shelf species and just 38% that of pelagic species (García *et al.* 2008). There is also the suggestion that within the deepwater habitat this vulnerability to fishing increases with increasing depth down the continental slope (Simpfendorfer and Kyne 2009).

Large declines in the biomass of deepwater chondrichthyans that are commercially fished or taken as bycatch have been documented globally (Dulvy *et al.* 2003; Devine *et al.* 2006; Campbell *et al.* 2011). In Australia, dramatic population declines were recorded in deepwater chondrichthyans exposed to trawling in the Australian Southern and Eastern Scalefish and Shark Fishery on the New South Wales continental slope (Graham *et al.* 2001; Graham and Daley 2011). Two decades of intensive trawling caused the collapse of upper slope chondrichthyan populations with at least seven species known to have suffered declines of > 90% in relative abundance (Graham *et al.*, 2001). Recovery of some of these depleted species may take decades or even centuries (Daley *et al.* 2014).

The Great Barrier Reef Marine Park (GBRMP) in northeastern Australia has one third its area in deep water. These deep water areas have rarely been surveyed and are subject to some fishing pressure. This is of concern to both State fisheries managers and GBRMP managers, as the deepwater chondrichthyan fauna and their resilience to fishing pressure in the GBRMP are poorly known (GBRMPA 2009; Sumpton *et al.* 2013). An ecological risk assessment of trawling in the GBRMP identified deepwater chondrichthyans taken as bycatch as at high ecological risk and a priority for research (Pears *et al.* 2012). The risk assessment result was a precautionary rating based on the inherent vulnerability of most deepwater chondrichthyans, and a paucity of data on the species taken and their life histories. Some deepwater chondrichthyan species are captured in a deepwater trawl fishery that operates in the southern region of the GBRMP. Species composition and life history information are needed to more confidently assess the risks of this fishery to these deepwater chondrichthyans. The risks may be compounded by the high degree of endemism and restricted geographical and bathymetric ranges common among deepwater chondrichthyans (Kyne and Simpfendorfer 2010). This endemism and restricted distribution potentially further reduces the resilience of species to exploitation.

The limited deepwater chondrichthyan life history studies to date have mainly been on dogfish (Squaliformes) and skates (Rajiformes), which are among the dominant taxa of deepwater chondrichthyans. Traditional ageing methods rely on counts of periodic growth bands in calcified hard parts (Cailliet and Goldman 2004; Cailliet *et al.* 2006). In dogfish, these hard parts are the external dorsal fin spines which have visible and distinguishable bands. These fin spines have been proved to be reliable structures for ageing (Irvine *et al.* 2006a; Goldman *et al.* 2012). Some of the deepwater skates have visible banding in their vertebrae which can be reliably aged, while the caudal thorns of other deepwater skates have been shown to be reliable age structures in some, but not all, species (Kyne and Simpfendorfer 2007; Moura *et al.* 2007).

Age estimates are one of the most critical life history variables as they form the basis of many of the key parameters of fisheries and demographic assessments, such as growth rate, mortality rate and productivity (Campana 2001). Yet for numerous deepwater chondrichthyans, age estimations are not possible using traditional techniques as they have poorly calcified vertebrae that lack visible growth bands, and many do not have dorsal fin spines (Cailliet 1990; Cotton *et al.* 2014). Other ageing methods, such as captive growth and tag-recapture (Goldman *et al.* 2012) are limited in their suitability for deepwater chondrichthyans due to logistical difficulties in the deep sea (Cotton *et al.* 2014). There is a lack of age and growth estimates for the highly speciose catsharks (Scyliorhinidae), which besides dogfish and skates are the other dominant deepwater taxa (Kyne and Simpfendorfer 2010). Consequently, alternative ageing methods are required for many deepwater chondrichthyans to provide age information essential for their management and conservation (Gennari and Scacco 2007).

Considering the lack of knowledge of deepwater chondrichthyans and their vulnerability to exploitation, the primary aims of this research were to: 1) assess patterns in deepwater chondrichthyan life history traits and compare them to shelf and pelagic chondrichthyan traits, 2) identify chondrichthyans taken as bycatch in the southern GBRMP, 3) determine the age, growth and reproduction of those bycatch species, and 4) investigate novel approaches to ageing chondrichthyans. To accomplish these aims, the chondrichthyan life history traits were compared between deep, shelf and pelagic habitats, and examined within the deep habitat (Chapter 2). The deepwater eastern king prawn fishery was sampled for chondrichthyan bycatch and preliminary biological data presented (Chapter 3). For those species with adequate sample size and reliable ageing structures, age, growth and reproduction was determined (Chapters 4 and 5). A novel approach to ageing using near infrared spectroscopy was trialled on previously age validated coastal sharks (Chapter 6) then investigated with deepwater chondrichthyans (Chapter 7). The accumulated information was then used to evaluate and compare life histories of chondrichthyans species within the deepwater habitat and examine policy and management implications of the findings (Chapter 8). Each data chapter of the thesis forms a manuscript that is published (4 papers) or in review (2 papers). Chapters have been modified to minimise excessive repetition, although some repetition was unavoidable and included to facilitate readability.

Chapter 2 Patterns in life history traits of deepwater chondrichthyans



Black shark *Dalatias licha*

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2.1 Introduction

Chondrichthyans are generally slow growing, late maturing, long lived and have low fecundity (Hoenig and Gruber 1990). This is a successful strategy for their environment where the main natural predator is larger sharks and they only need to produce a few young capable of reaching maturity to maintain population levels (Cailliet *et al.* 1990; Cortés 2000). Yet this is also a strategy that reduces their capacity to recover from exploitation and thereby increases their vulnerability to human disturbances (Stevens *et al.* 2000a; Devine *et al.* 2006; Field *et al.* 2009). There is a wide range of chondrichthyan life histories, and species studied to date vary in their degree of vulnerability (Smith *et al.* 1998; Cortés 2002; Dulvy and Forrest 2010), though this is mostly based on shelf and pelagic species with less knowledge of deepwater chondrichthyans. Life history traits are useful indicators of productivity (Simpfendorfer and Kyne 2009) and the increase in deepwater life history studies in recent years has provided an opportunity to more closely examine patterns in the traits of this group.

Evolution of life history traits is a selective and adaptive response to a complex interaction of density dependence, resource availability, environmental conditions and extrinsic mortality (Reznick *et al.* 2002), with on-going debate about the relative importance of these factors (Ricklefs 2000; Dulvy and Forrest 2010). Variations in resource availability, mortality and environmental conditions between marine habitats are hypothesised to play a major role in patterns of life history traits (García *et al.* 2008). Differences are apparent in both fish and chondrichthyan traits among three distinctive marine habitats: continental shelf, pelagic open ocean and deep sea (Koslow *et al.* 2000; Cailliet *et al.* 2001; Clarke *et al.* 2003; García *et al.* 2008; Norse *et al.* 2012). The continental shelf is the most productive and diverse habitat encompassing waters from the intertidal to 200 metres (m) depth and contains the majority of the world's chondrichthyan species (Compagno 1990). The pelagic open ocean, a far less diverse habitat, extends beyond the edge of the shelf and into the ocean basins with generally low productivity, except in some areas of near-surface waters where the abundant light contributes to primary productivity (Robison 2004). Pelagic chondrichthyans are highly mobile species that primarily inhabit the open ocean waters and account for ~ 2% of the global chondrichthyan diversity (Stevens 2010).

The deep sea reaches from the 200 m edge of the shelf to the maximum depths of the ocean and is a relatively stable habitat of low productivity, low temperatures, high pressures, dim to absent light and limited food (Angel 1997; Gartner Jr *et al.* 1997; Gibbs 1997). However it is not a completely uniform habitat as these parameters vary, particularly on the upper to mid

continental slope where a thermocline from 200 m down to 1000 m drops the temperature rapidly to just above freezing and varies with circulation patterns of the ocean, latitude and season (Marshall 1979). Light levels diminish down this slope to the limit of visible light at 1000 m, beyond which it is permanently dark (Angel 1997). Food availability declines rapidly down the slope and beyond as it sinks to the seafloor, yet this appears to vary not just with depth but also with season and region as it likely reflects seasonal surface productivity that varies among oceanic regions (Robison 2004; Drazen and Haedrich 2012; Norse *et al.* 2012).

Deepwater chondrichthyans rarely occur below 3000 m (Priede *et al.* 2006) and the currently 530 known species (Kyne and Simpfendorfer 2010) account for almost half of the world's estimated 1200 species of chondrichthyans. They are a diverse group dominated by dogfish (Squaliformes), skates (Rajidae, Arynchobatidae and Anacanthobatidae) and the highly speciose catsharks (Scyliorhinidae), with the majority of species geographically and bathymetrically restricted and high levels of endemism among the lantern sharks (Etmopteridae), catsharks and skates (Kyne and Simpfendorfer 2010). While life history data is lacking for most deepwater species, adequate data on dogfish, skates and some other taxa was previously available for analysis. This indicated that deepwater chondrichthyans have a set of life history traits common to the deep habitat and beyond phylogenetic relationships: they grow more slowly, mature later and live longer than their relatives in the shelf and pelagic habitats (García *et al.* 2008). They are considered to have even lower productivity and hence greater vulnerability to exploitation than the chondrichthyans in these shallower habitats (García *et al.* 2008; Simpfendorfer and Kyne 2009). Consequently, their extinction risk from fishing pressure is also higher. Garcia *et al.* (2008) estimated that the fishing mortality that would drive deepwater species to extinction was 58% of shelf species and just 38% of pelagic species. There is also evidence that within the deepwater habitat this vulnerability to fishing increases with increasing depth and that viviparous species in the deep habitat are more vulnerable than oviparous species (Simpfendorfer and Kyne 2009).

The association of life history traits with habitat and the lower productivity of deepwater chondrichthyans have been variously attributed to environmental conditions (temperature), resource availability (food) and mortality (predator-prey interactions) (García *et al.* 2008; Simpfendorfer and Kyne 2009). Low temperatures and limited food logically may result in slow growth rates that lead to late maturity and these factors along with possible effects of pressure and lower oxygen levels have also been offered as the cause of similar traits and reduced metabolism with depth in deepwater fish (Vetter and Lynn 1997; Cailliet *et al.* 2001; Gordon 2001; Drazen and Haedrich 2012). However, the observed decreases in metabolic rates and

growth rates often cannot be entirely accounted for by such parameters as low temperatures, limited food, increased pressure and lower oxygen (Robison 2004; Seibel and Drazen 2007). An alternative hypothesis suggested by Childress *et al.* (1980) was that declining light levels with depth reduce the reactive distances between predator and prey which relaxes the selective pressure on rapid locomotory capacity providing an opportunity for reduced energy expenditure and a decline in metabolic rates. Conversely, in the pelagic habitat with reasonable light levels and no refuges from predators, there is a need for strong locomotory capacity and much higher metabolic rates (Childress 1995). Shelf waters tend to be more turbid, providing more opportunities for refuge from predators and reducing the distance over which predators and prey interact and thus lessening the need for metabolic rates to be as high as those in pelagic habitats (Childress and Somero 1990; García *et al.* 2008). This visual interactions hypothesis is supported by differences in metabolic rates and other physiological characteristics with depth for visual and non-visual taxa. The metabolic rates of visual fauna such as fishes, cephalopods and active crustaceans decline rapidly in the first 500 m and then level off below around 1000 m where light is absent. In contrast, no such depth related declines in metabolic rates are evident in non-visual animals such as echinoderms, cnidarians and worms (Childress 1995; Seibel *et al.* 2000).

This hypothesis may not provide the only explanation for the observed patterns in traits. While it deduces that the decrease in metabolic and growth rates is not due to food availability, in the deep habitat where food is limited and creates a resource or energy poor environment it may be a relevant factor to the selection pressure on other life history traits. Life history theory is based on the concept that the finite energy available in the environment imposes constraints or trade-offs in the allocation of this energy among life history traits (Dulvy and Forrest 2010). Beverton and Holt (1959) identified that these trade-offs were expressed in relationships between growth, age and size at maturity and adult mortality rate (and hence longevity) that are relatively consistent among a wide range of taxa. These relationships are referred to as life history invariants, or 'rules of life', and provide insight into patterns in life history traits. Invariants have been published for some groups of sharks, elasmobranchs and skates (Cortés 2000; Frisk *et al.* 2001; Frisk 2010), but never for chondrichthyans as a whole.

We aimed to examine the association of habitat and life history traits among the three broad marine habitats and also within the deep habitat. To separate habitat from phylogenetic effects we used an analytical approach that controlled for the correlation among species due to their common evolutionary history (García *et al.* 2008; Chamberlain *et al.* 2012). Specifically we (1)

reassessed the association of chondrichthyans traits between shelf, pelagic and deep habitats with a larger and more diverse range of species than previously considered, (2) investigated the relation of traits within the deep habitat to depth and geographic region, (3) compared invariants and other relationships between traits among shelf, pelagic and deep habitats, (4) assessed whether body size varied among the three marine habitats and with increasing depth within the deep habitat, and (4) examined associations of reproductive mode, body size and habitat.

2.2 Methods

2.2.1 Data

Life history trait data were obtained from 226 populations (144 species) of chondrichthyans: 56 deep, 29 pelagic and 141 shelf populations. The maximum body size (S_{\max}), size at maturity (S_m), age at maturity (T_m), longevity (T_{\max}) (both observed $^{\circ}T_{\max}$ and theoretical $^T T_{\max}$) and von Bertalanffy growth constant (k) (von Bertalanffy 1938) were collated for females (F) and males (M) separately. Size at birth (S_{birth}), litter size (l), interbirth interval (I_i) (the interval in years between births) and reproductive mode (R_m) were collated by populations, though not all populations had available data for l or S_{birth} (Table A.1 in Appendix A). The data were organised at population level where available so as not to exclude the variability in life history traits exhibited by some species (Cortés 2000; Cope 2006). The area of occurrence of the species or population's life history data was described using the FAO Fishing Areas (the Food and Agriculture Organization of the United Nation's Major Fishing Areas for Statistical Purposes) with the taxonomic classification and species names used from Compagno (2005) and the Catalogue of Fishes (Eschmeyer 2012) (Table A.1 in Appendix A).

Where there was only one value available for each of the traits of S_{\max} , S_m , T_m , T_{\max} and k this value was used for both the female and male traits. The size and age at which 50% of the population reached maturity was used where available, otherwise either the reported value or the mid-point of a given range was used. When multiple studies were cited for a species or population, the median of the range of values for each life history parameter was used. Where T_m was not reported it was calculated from S_m and the von Bertalanffy growth model if available. Both $^{\circ}T_{\max}$ and $^T T_{\max}$ were included as the observed data often pertained to one study while the theoretical data may have represented a broader population. Where it was not reported, $^T T_{\max}$ was estimated using the method of Ricker (1975) based on the age at which $>95\%$ of L_{∞} was reached: $>95\%L_{\infty} = 5 * ((\ln 2)/k)$. Mean l was presented where available otherwise the mid-point of l range was used and where l was not available, ovarian fecundity

was used. Annual fecundity was presented for the oviparous Rajiiformes species, as this was the only available information.

Reproductive modes are diverse and were ascribed using terminology from Musick and Ellis (2005). The oviparous modes were either single (one egg is deposited at a time from each oviduct) or multiple (multiple egg cases retained in the oviduct) while the viviparous modes were categorised according to embryo nutritional source: the yolk-sac with no additional maternal input (lecithotrophic), other embryos (adelphophagic), unfertilised eggs (oophagic), a rich maternal secretion from the uteri (histotrophic), and placental.

The habitats for each population were defined as deep, pelagic or shelf based on the distribution of the population, or the habitat of the majority of the populations' life cycle. Deepwater chondrichthyans were defined as those at depths below 200m and included benthic and epibenthic species, those that occur on, or associated with, the bottom of the sea bed; and species that occur in the water column (Kyne and Simpfendorfer 2007). Pelagic chondrichthyans were considered those that spend the majority of their life cycle in the epipelagic zone; the open ocean to 200m depth and coastal chondrichthyans were those that are mostly confined to shelf waters at less than 200m depth. This information was compiled from field guides and primary literature, including Compagno *et al.* (2005), Kyne and Simpfendorfer (2007), Last and Stevens (2009) and IUCN (2012). The focus was on age and growth studies, with reproductive parameters, if not included in the same study, available for the same population. Patterns in life history traits within the deepwater habitat were examined in finer depth and geographic scales using the deepwater populations and their distribution by depth, regions and longitudinal and latitudinal ranges (Table A.2 in Appendix A). Depth was characterised as both the usual or 'typical' depth limit ($Depth_U$) at which the population has been reported to occur and the maximum depth ($Depth_M$) recorded for a population, as these two can sometimes be quite different. Depth ranges were also included in the analyses; the usual depth range ($DepthR_U$) and the maximum depth range ($DepthR_M$). Due to the smaller deep habitat dataset, the FAO Areas were combined into four regions: North Atlantic, South Atlantic, North Pacific and South Pacific. Some shelf habitat populations were included in the fine-scale deep habitat analyses as they occur in both shelf and deep water; they were piked dogfish *Squalus acanthias* Linnaeus 1758, spiny dogfish *S. suckleyi* (Girard 1855), Mediterranean starry ray *Raja asterias* Delaroche 1809 and school shark *Galeorhinus galeus* (Linnaeus 1758).

2.2.2 Data Analysis

2.2.2.1 All habitats

Patterns in the life history traits of k , T_m , $^O T_{max}$ and $^T T_{max}$ for female and males and l , S_{birth} and I_i were examined among the three habitats of deep, shelf and pelagic. To control for the non-independence of species a linear mixed effect model (LMEM) was applied with the taxonomy hierarchy included as random effect group variable (species nested in genera, genera in families, families in orders and orders in superorder). All LMEMs used in this study included taxonomic hierarchy as a random effect. The taxonomic, rather than phylogenetic classification was used to represent the relatedness of species, which is an alternate approach when a phylogenetic tree that includes all species in the analyses is not available (García *et al.* 2008; Chamberlain *et al.* 2012). This method takes into account patterns of variability associated with phylogenetic similarities when evaluating fixed effects. The fixed effects were each of the dependent life history variables with the independent variable of body size and independent factor of habitat. The same formulae was used to examine patterns in each of the life history variables among habitats, with each of the life history variables used as a separate response (dependent) variable; for example, to examine patterns in the female growth constant among the three habitats, the formula was $\ln k_F \sim S_{maxF} + \text{Habitat}$. All life history variables were log-transformed (\ln) to achieve normality. The statistical software S-Plus was used for these analyses.

To present the magnitude of difference in deep habitat traits from those in the other two habitats the LMEM resultant coefficient values of traits for the pelagic and shelf habitats were added to the intercept value of the traits for the deep habitat. These values were back-transformed and the predicted ratio of the deep to pelagic trait and deep to shelf trait reported, following the method of Garcia *et al.* (2008). This comparison controlled for the effect of S_{max} and phylogeny, that is, it is equivalent to comparing sharks of the same S_{max} in each habitat.

2.2.2 Deep habitat

Within the deep habitat patterns in life history traits of k , T_m , $^O T_{max}$, $^T T_{max}$ for females and males and l , S_{birth} and I_i were examined in relation to the four regions using the same LMEM approach described above. The relationship of these traits to depth ($Depth_U$ and $Depth_M$), depth ranges ($Depth_{RU}$ and $Depth_{RM}$) and longitudinal and latitudinal distribution was assessed using the LMEM with these habitat variables included as fixed effect independent variables with S_{max} ; for example, the formula used to examine patterns in the female growth constant with usual depth was $\ln k_F \sim S_{maxF} + Depth_U$. Across the regions S_{max} and S_{mat} were analysed by the LMEM with size as the dependent variable and region the independent variable. To increase the size of the dataset of S_{birth} and l for the deepwater species, additional populations were included that had data on S_{birth} , l and T_{mF} (but not k).

2.2.2.3 Invariant life history and other ratios

The mean ratios of relative size at maturity (S_m/S_{max}) and relative age at maturity (T_m/T_{max}) (observed, theoretical and combined longevity) were compared to published chondrichthyan life history invariants and tested for differences among the three habitats with a one-way ANOVA and Tukey-Kramer post-hoc comparison of means.

To determine if the relationship between each pair of life history traits varied among the three habitats while accounting for the non-independence of species the LMEM was again used. For example, to test whether habitat affects the relationship between S_{mF} and T_{mF} , the formula was $\ln S_{mF} \sim \text{Habitat} + \ln T_{mF} + \text{Habitat} : \ln T_{mF}$. The interaction tested for differences in the slope of the $\ln S_{mF} - \ln T_{mF}$ relationship among habitats. A significant interaction indicated the slope of the relationship between the two traits was different among habitats. If the interaction was not significant, it was removed and the LMEM run again to test for differences in the intercept. While the LMEM allowed for unbalanced designs, the results were interpreted with caution and plots of the raw data used to display the relationships to ensure they were not an artefact of the analyses. The high fecundities of the oviparous Rajiformes (Rajidae and Arynchobatidae species) biased the relationships of l and other traits and the analyses were run with and without this group.

2.2.2.4 Body size and depth

As S_{max} has been suggested as a proxy for vulnerability (Dulvy and Reynolds 2002) we examined the relationship of S_{max} and depth by: 1) Pearson's product moment correlation using $Depth_M$ as a covariate; 2) a one-way ANOVA of S_{max} among the three habitats (deep, pelagic and shelf) with Tukey-Kramer; and 3) LMEM of S_{max} among the three habitats; for example, $\ln S_{maxF} \sim \text{Habitat}$. Both the one-way ANOVA and the LMEM were also applied to just the deepwater species to examine changes in S_{max} with depth using the co-variables $Depth_M$ and $Depth_U$.

2.2.2.5 Reproductive mode, habitat and body size

To determine if R_m was associated with habitat, additional data were collated, that is, the R_m for 416 chondrichthyan species (184 deep, 19 pelagic and 213 shelf). The number of species with each R_m was compared among the three habitats. Within the deep habitat a chi-square test was used to assess if the proportion of oviparous to viviparous modes differed from 1:1. Within the deep habitat the pattern of R_m with depth was plotted. The relationship of S_{maxF} and R_m was investigated using the LMEM with S_{maxF} as the dependent variable and R_m the independent

factor applied to the 226 populations, and to just the deepwater species with oviparous and viviparous lecithotrophic modes.

2.3. Results

2.3.1 All habitats

Deep habitats had significantly lower k , later T_m and higher T_{max} than both shelf and pelagic habitats (Table 2.1 and Table A.3 in Appendix A) with the differences in these traits more pronounced between deep and pelagic habitats than deep and shelf habitats (Figure 2.1). The k_F and k_M of deepwater chondrichthyans was 0.62 and 0.59 respectively of pelagic species and 0.68 of shelf species (Table 2.1). T_m was approximately 1.6 times and 1.3 times higher in deepwater chondrichthyans than pelagic and shelf species, respectively (Table 2.1). T_{max} of deepwater species was 1.4-1.7 greater than pelagic species and 1.2-1.5 times greater than shelf species with all differences significant for ${}^T T_{max}$, but not ${}^O T_{max}$ (Table 2.1). The differences in traits among these three habitats were very similar for female and male populations. There were no significant differences in S_{birth} , l and I_i between habitats (Table A.4 in Appendix A).

Table 2.1 Predicted ratios of growth constant (k), age at maturity (T_m) and longevity (observed ${}^O T_{max}$ and theoretical ${}^T T_{max}$) for the deep to pelagic trait and deep to shelf trait with significance level.

Habitat	k		T_m		${}^O T_{max}$		${}^T T_{max}$	
	Female	Male	Female	Male	Female	Male	Female	Male
Pelagic	0.62	0.59	1.65	1.63	1.38	1.35	1.58	1.66
	p=0.011	p=0.009	p=0.004	p=0.002	p=0.027	p=0.056	p=0.018	p=0.011
Shelf	0.68	0.68	1.29	1.27	1.18	1.23	1.46	1.45
	p=0.002	p=0.003	p=0.021	p=0.024	p=0.083	p=0.050	p=0.003	p=0.004

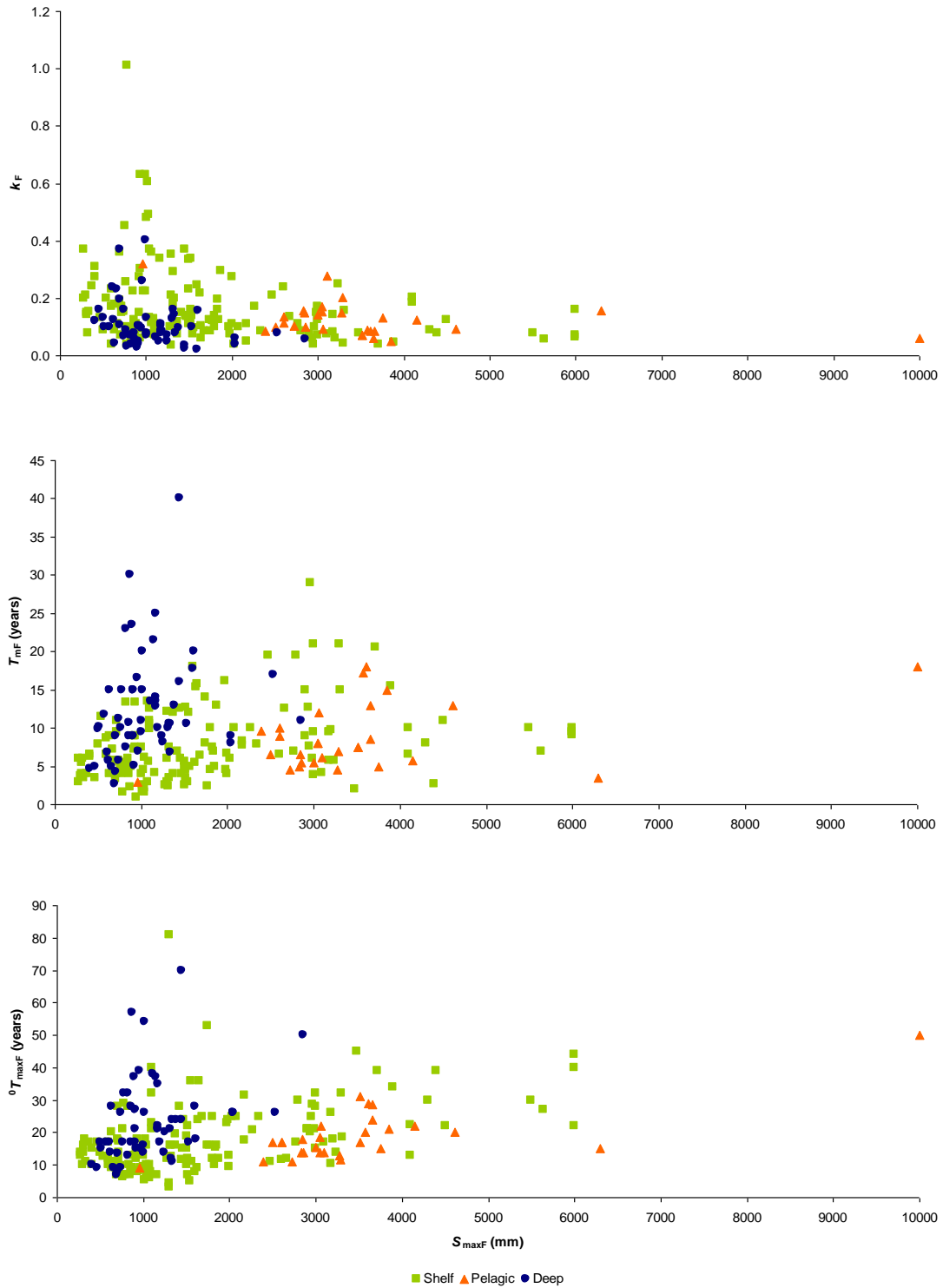


Figure 2.1 Female growth constant (k_F), age at maturity (T_{mF}) and longevity (${}^0T_{\max F}$) for deep, pelagic and shelf habitats against maximum size ($S_{\max F}$) (raw data).

2.3.2 Deep habitat

Within deepwater habitats there were significant differences in species life history traits with increasing depth and across the four geographic regions, but not across latitudinal or longitudinal ranges.

2.3.2.1 Depth

With increasing $Depth_U$ the T_{mF} ($F_{1,46}=4.6$, $p=0.037$), ${}^O T_{maxF}$ ($F_{1,46}=5.9$, $p=0.019$), ${}^O T_{maxM}$ ($F_{1,46}=5.2$, $p=0.027$) and S_{birth} ($F_{1,87}=6.9$, $p=0.018$) all significantly increased; k declined for both sexes although it was not significant. As the $Depth_{R_U}$ increased the ${}^O T_{maxF}$ ($F_{1,46} = 4.0$, $p=0.043$) and S_{birth} ($F_{1,87} = 4.7$, $p=0.033$) both significantly increased. When $Depth_M$ and $Depth_{R_M}$ were considered there were no significant differences in the life history traits, except that with increasing $Depth_{R_M}$ the I_i significantly increased ($F_{1,46}=5.2$, $p=0.027$) and l significantly decreased ($F_{1,29}=5.1$, $p=0.032$).

2.3.2.2 Regions

In the North Atlantic, the females had the fastest k , lowest ${}^T T_{max}$ and the S_{birth} was the smallest (Table 2.2). In contrast, South Atlantic females had the slowest k and highest ${}^T T_{max}$. The North Atlantic females grew 1.7 times and 1.5 times faster than in the South Atlantic and North Pacific, respectively, and ${}^T T_{maxF}$ was lower than in the South Atlantic (0.58) and North Pacific (0.67) (Table 2.2). The North Atlantic S_{birth} was smaller than the South Pacific (0.82) and Indian (0.75) which had the largest S_{birth} (Table 2.2). Litter size in the North Atlantic was the largest but only significantly different (at 1.9 times) from the smallest l in the South Atlantic ($t_{3,27}=2.6$ $p=0.017$) (Table A.5 in Appendix A). Other life history traits exhibit trends but no significant differences among regions; k_M showed a similar pattern among regions as the k_F (Table A.5) and the S_{max} , S_m , T_m and ${}^O T_{max}$ for both sexes were all smallest in the North Atlantic (Table A.6 in Appendix A).

Table 2.2 Regional patterns in deep habitat female growth constant (k_F), longevity (${}^T T_{maxF}$) and size at birth (S_{birth}) in relation to size at maturity (S_{mat}). The LMEM coefficient values (\pm se) are relative to the intercept value for the North Atlantic and the predicted ratios with the significance level are compared to the North Atlantic.

Region	k_F			${}^T T_{maxF}$			S_{birth}		
	Value LMEM	Value (k_F)	Ratio	Value LMEM	Value (yrs)	Ratio	Value LMEM	Value (mm)	Ratio
North Atlantic	-1.738	0.176		2.981	19.8		4.942	140.1	
Intercept	(0.295)			(0.296)			(0.146)		
North Pacific	-0.400	0.118	1.49	0.399	29.4	0.67	0.099	154.6	0.91
	(0.189)		$p=0.040$	(0.189)		$p=0.043$	(0.063)		$p=0.123$
South Atlantic	-0.554	0.101	1.74	0.553	34.3	0.58	0.099	154.7	0.91

	(0.222)		p=0.017	(0.222)		p=0.017	(0.071)		p=0.167
South Pacific	-0.086	0.161	1.09	0.085	21.4	0.92	0.203	171.6	0.82
	(0.204)		p=0.676	(0.200)		p=0.675	(0.059)		p<0.001
Indian							0.290	187.1	0.75
							(0.078)		p<0.001

2.3.3 Invariant life history and other ratios

The mean relative size at maturity (S_m/S_{max}) across the three habitats for females and males combined was 0.72 ± 0.01 . The S_m/S_{max} varied among habitats and was significantly higher in the deep at 0.76 ± 0.02 ($F_{2,449}=9.0$, $p<0.001$) than both other habitats: 0.68 ± 0.02 for the pelagic and 0.72 ± 0.01 for the shelf; the invariant followed this same trend across habitats for both sexes. The regression analyses also indicated that in the deep habitat the S_m was relatively larger than in the other two habitats and that the rate it increased with S_{max} was slower (Figure 2.2). The mean relative age at maturity (T_m/T_{max}) was 0.38 (for observed, theoretical and sexes combined) across the three habitats. As the value of $^T T_{max}$ was mostly greater than $^O T_{max}$ (Table A.1), it was not surprising that the invariant $T_m/^T T_{max}$ (0.29) was much lower than $T_m/^O T_{max}$ (0.47) (Table 2.3). The mean relative age at maturity (T_m/T_{max}) was also affected by habitat as it was significantly higher in the deep than both the pelagic and shelf habitats, using observed longevity ($^O T_{max}$) and combined longevity ($^{OT} T_{max}$) (Table 2.3). The separate female and male ratios followed the same pattern as that for combined sexes. The difference in habitat was also apparent in the regression in which the slopes were not significantly different but the intercepts were; the deep habitat had a significantly greater $T_m/^O T_{max}$ with the ratio higher for each of the sexes in the deep compared to the shelf (female $t_{2,168} = 2.8$, $p=0.006$, male $t_{2,168} = 2.6$, $p=0.011$) and pelagic (female $t_{2,168} = 2.0$, $p=0.048$, male $t_{2,168} = 2.2$, $p=0.028$) habitats.

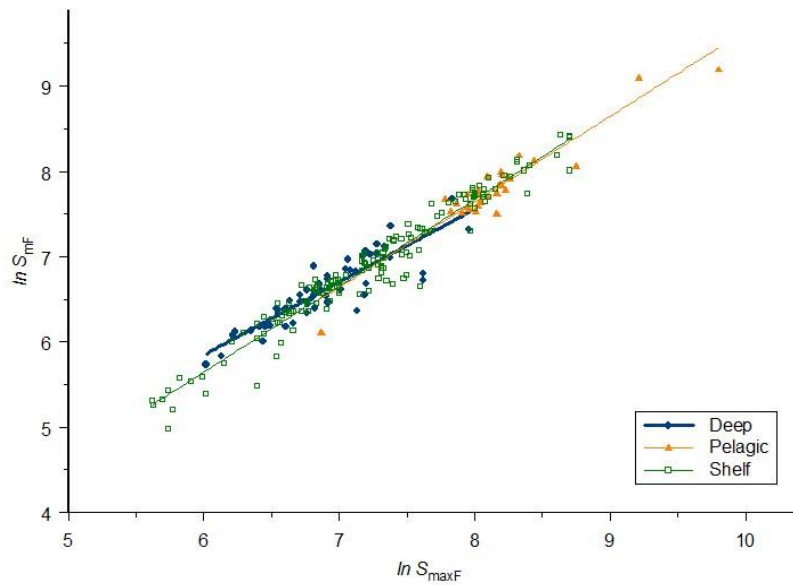


Figure 2.2 Relationship between female size at maturity (S_{mF}) and maximum size (S_{maxF}). The three habitats are shown separately with the plots from the raw data and the regression equations from the LMEM between S_{mF} and S_{maxF} and the levels of significance relative to deep habitat: Deep $\ln S_{mF} = 0.93 + 0.82 \cdot \ln S_{maxF}$; Pelagic $\ln S_{mF} = -0.13 + 0.97 \cdot \ln S_{maxF}$ $p = 0.111$, Shelf $\ln S_{mF} = -0.05 + 0.96 \cdot \ln S_{maxF}$ $p = 0.025$.

Table 2.3 Relative age at maturity invariant (T_m/T_{max}) (mean \pm se) across all habitats and for each habitat using observed longevity (${}^O T_{max}$), theoretical longevity (${}^T T_{max}$) and combined longevity for both sexes combined. The significance levels are for differences in the invariants relative to the deep habitat.

Habitat	$T_m / {}^O T_{max}$	$T_m / {}^T T_{max}$	$T_m / {}^{OT} T_{max}$
All	0.47 (0.01)	0.29 (0.01)	0.38 (0.01)
Deep	0.53 (0.01)	0.30 (0.01)	0.41 (0.01)
Pelagic	0.45 (0.03)	0.27 (0.01)	0.36 (0.02)
	$p < 0.001$	$p = 0.611$	$p = 0.016$
Shelf	0.45 (0.01)	0.29 (0.01)	0.37 (0.01)
	$p < 0.001$	$p = 0.611$	$p = 0.016$

Other relationships of pairs of traits that differed among habitats were the female to male ratios of T_{max} and k . The ${}^O T_{maxF} / {}^O T_{maxM}$ increased at a greater rate in the deep habitat with the greatest difference between deep and pelagic habitats (Figure 2.3). The slopes of the ${}^T T_{maxF} / {}^T T_{maxM}$ were not significantly different but the intercepts were, which indicated ${}^T T_{maxF}$ was relatively higher than ${}^T T_{maxM}$ in the deep habitat, with these differences most pronounced between the deep and shelf ($t_{2,168} = 2.4$, $p = 0.017$). The k_F was relatively slower than k_M in the deep, with this difference

significant between the deep and shelf waters ($t_{2,168} = 2.5$, $p=0.015$). When k was considered relative to ${}^{\circ}T_{\max}$ we found the k_F and k_M were both relatively slower in the deep with the difference greatest between deep and shelf habitats (female $t_{2,168} = 2.9$, $p=0.004$; male $t_{2,168} = 2.0$, $p=0.043$).

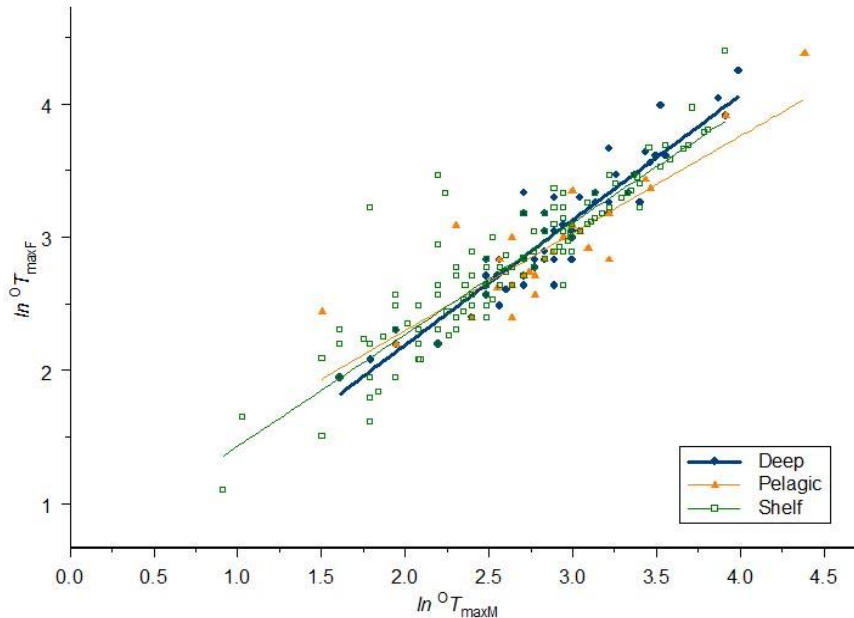


Figure 2.3 Relationship between female longevity (${}^{\circ}T_{\max F}$) and male longevity (${}^{\circ}T_{\max M}$). The three habitats are shown separately with the plots from the raw data and the regression equations from the LMEM between ${}^{\circ}T_{\max F}$ and ${}^{\circ}T_{\max M}$ and the levels of significance relative to deep habitat: Deep $\ln {}^{\circ}T_{\max F} = 0.55 + 0.90 * \ln {}^{\circ}T_{\max M}$; Pelagic $\ln {}^{\circ}T_{\max F} = 1.06 + 0.66 * \ln {}^{\circ}T_{\max M}$ $p=0.008$, Shelf $\ln {}^{\circ}T_{\max F} = 0.62 + 0.85 * \ln {}^{\circ}T_{\max M}$ $p=0.414$.

Another relationship that varied among habitats was l to $S_{\max F}$, but only when the highly fecund Rajiformes (Rajidae and Arynchobatidae species) were included. In that case the $l/S_{\max F}$ in the deep was larger than both shelf ($t_{2,126} = 2.3$, $p=0.026$) and pelagic ($t_{2,126} = 2.2$, $p=0.028$) habitats. The relationship of l and S_{birth} changed when relative S_{birth} was used, that is $S_{\text{birth}}/S_{\max F}$. The correlation of l and S_{birth} was weak, positive and not significant ($r = 0.086$, $p=0.291$) but for the correlation of l and $S_{\text{birth}}/S_{\max F}$, l significantly decreased as $S_{\text{birth}}/S_{\max F}$ increased ($r = -0.251$, $p=0.002$). Rajiformes affected the variation among habitats in l and $S_{\text{birth}}/S_{\max F}$, when they were included the l relative to $S_{\text{birth}}/S_{\max F}$ was significantly greater in the deep habitat and decreased at a greater rate than in the other two habitats ($t_{2,98} = 2.6$, $p=0.011$ and $t_{2,98} = 3.9$, $p<0.001$ pelagic and shelf respectively). Conversely with the oviparous Rajiformes excluded the deep habitat l relative to $S_{\text{birth}}/S_{\max F}$ was significantly smaller than the other two habitats and decreased (with increasing $S_{\text{birth}}/S_{\max F}$) at a similar rate to that in the pelagic habitat ($t_{2,98} = 2.1$, $p=0.040$ and $t_{2,98} =$

2.6, $p=0.011$ pelagic and shelf respectively). Regardless of the inclusion or exclusion of Rajiformes the $S_{\text{birth}}/S_{\text{maxF}}$ also significantly increased with k_F ($r = 0.208$, $p=0.01$) though this relationship did not vary among habitats.

2.3.4 Body size and depth

2.3.4.1 All habitats

S_{max} decreased with depth when assessed using correlations, one-way ANOVA and the LMEM. Correlations indicated that S_{max} decreased significantly with depth for both sexes, though the strength of the correlations was not strong ($r = -0.17$, $p=0.012$ for both females and males). The one-way ANOVA found the S_{max} was significantly smaller in the deep than both other habitats, with the largest size in pelagic (female $F_{2, 223}=39.3$, $p<0.001$, male $F_{2, 223}=41.8$, $p<0.001$). When taxonomy was taken into account with the LMEM the deep habitat S_{max} is between that of shelf and pelagic, with the females significantly larger than those on the shelf ($t_{2, 169}=2.3$, $p=0.026$). However when the Rajiformes are excluded, the S_{max} is smallest in the deep habitat and significantly different to the pelagic habitat that has the largest sizes (female $t_{2, 113}=3.17$, $p=0.002$, male $t_{2, 113}=2.95$, $p=0.004$). When examined more closely by taxa, the Squaliformes, Chimaeriformes and Carcharhiniformes deep median S_{max} are smaller than those of the other habitats, but the median S_{max} of Rajiformes is larger in the deep than in the shelf waters.

2.3.4.2 Deep habitat

Deepwater species decreased significantly in S_{max} with increasing depth when analysed with a one-way ANOVA, but not with the LMEM. Decreasing S_{max} with increasing depth was apparent with the ANOVA of $Depth_M$ (female $F_{1, 64}=4.9$, $p=0.031$, male $F_{1, 64}=4.9$, $p=0.030$). When the analyses included the effect of taxonomy the decrease in S_{max} with depth was not significant suggesting that taxonomic differences between habitats may account for the differences observed in the ANOVA. The LMEM was rerun with a larger dataset of deepwater taxa (127 populations) and there was still no significant difference in S_{max} down the slope, rather there was an opposite trend of increasing S_{max} with depth; there is a large degree of variability in S_{max} within the deepwater habitat.

2.3.5 Reproductive mode, habitat and body size

2.3.5.1 Reproductive mode and habitat

In the deep habitat there was a dominance of oviparous and lecithotrophic viviparity modes and the types of R_m were less diverse than in the shelf habitat, but more diverse than the pelagic habitat (Table 2.4). When just oviparous and viviparous modes are compared among the three habitats, deep species have an almost equal proportion of each (48% oviparous and 52 %

viviparous) that is not significantly different from 1:1 ($X^2=0.196$, $df=1$, $p=0.658$), pelagic species are all viviparous and shelf species are predominantly viviparous (23% oviparous and 77 % viviparous).

Table 2.4 The number of chondrichthyan species with each type of reproductive mode (R_m); O - oviparous single, Om - oviparous multiple, Va, Vh, Vl, Vo, Vp refer to adelphophagic, histotrophic, lecithotrophic, oophagic and placental viviparity respectively.

R_m	Deep	Pelagic	Shelf
O	82	0	41
Om	7	0	8
Va	0	0	1
Vh	2	3	32
Vl	87	3	61
Vo	3	10	1
Vp	3	3	69
Total	184	19	213

For the deepwater species, there appeared to be no pattern in R_m with depth as both oviparous and viviparous modes occurred at all depths (Figure 2.4). Of the deepwater viviparous species, 87 were lecithotrophic, with just two species that were histotrophs (both Rajiformes), three that were oophagic (all Lamniformes) and three that were placental (all Carcharhiniformes) (Figure 2.4, Table A.1). There was no pattern of matrotrophic viviparity with depth, as these species occurred in a wide range of depths, even down to 2200 m for the placental Carcharhiniformes, bigeye houndshark *Iago omanensis* (Norman 1939). All deepwater families except Rajidae and Scyliorhinidae only exhibited one type of R_m (Table A.1). The Rajidae were all oviparous, though some have multiple oviparity while the Scyliorhinidae included both single and multiple oviparous species and some viviparous lecithotrophic species. Within the deepwater chondrichthyans R_m is strongly associated with phylogeny and does not appear to be driven by depth.

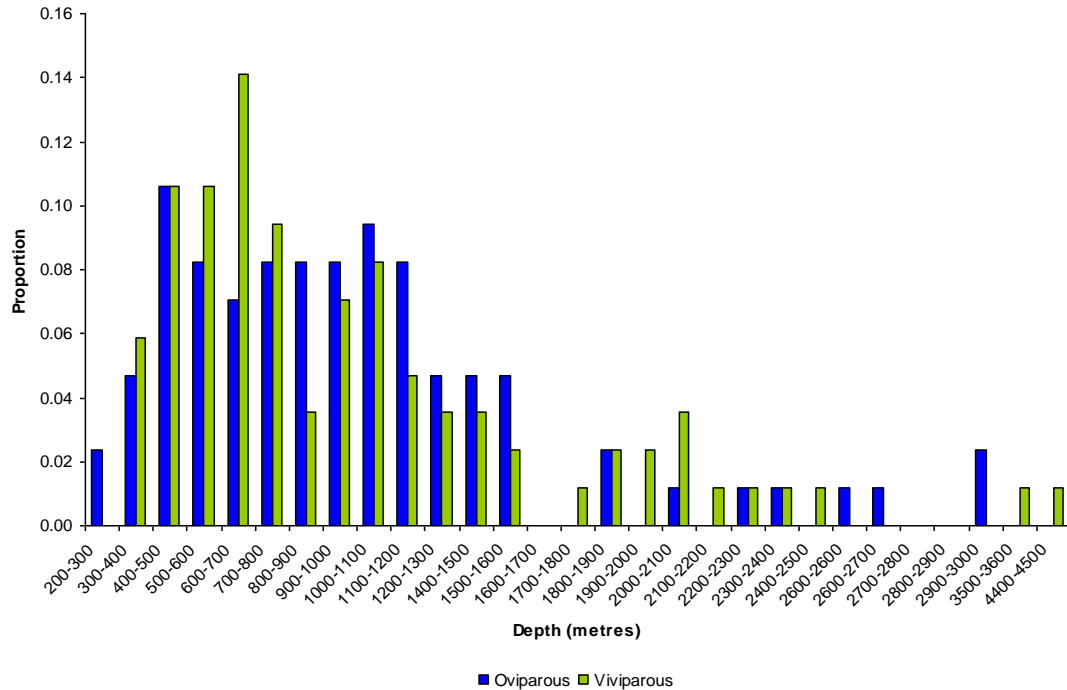


Figure 2.4 The proportion of oviparous and viviparous species (as a ratio of the total number of oviparous and viviparous species respectively) in each 100 m depth interval from 200 to 4500 m.

2.3.5.2 Reproductive mode and body size

S_{\max} of chondrichthyans appeared to vary with the different R_m . Those species that were oviparous had the smallest S_{\max} and those that were viviparous oophagic had the largest S_{\max} with single oviparous species significantly smaller than both viviparous lecithotrophic and viviparous oophagic species, at 41% and 16% of the size respectively ($t_{6, 168} = 2.2, p=0.033$ and $t_{6, 18} = 3.1, p=0.006$, respectively). Species that were single oviparous were also significantly smaller than those with multiple oviparity ($t_{6, 168}=2.4, p=0.020$) at 56% their size, though this result warrants further investigation as data becomes available; there are few multiple oviparous species in this dataset and it is influenced by the large size of the multiple oviparous big skate *Raja binoculata* Girard 1855. Among just the deepwater species there was no significant difference in S_{\max} for the two R_m of oviparous single and viviparous lecithotrophic.

2.4 Discussion

The results of this study demonstrated that chondrichthyan life history traits are associated with broad-scale habitats - species from deep habitats on average grew more slowly, matured later and lived longer than those in the shelf and pelagic habitats. Similar observations in the changes in life history between broad habitat types have previously been reported by Garcia *et al.* (2008) and Simpfendorfer and Kyne (2009). The present study was able to strengthen these

observations by substantially increasing the sample sizes for the deep habitat, and demonstrated for the first time that within the deep habitat that there were differences in life history traits associated with habitat changes down the continental slope. With increasing depth, the species matured later, lived longer, had smaller litters and bred less frequently. This combination of traits indicates a marked decline in productivity with depth and further explains the finding by Simpfendorfer and Kyne (2009) that the capacity of deepwater chondrichthyan populations to recover from exploitation decreased with increasing depth. They found the differences in these traits resulted in deepwater chondrichthyans having rates of population increase less than half those of species from other habitats and, in agreement with Garcia *et al.* (2008), that they had a higher extinction risk than shelf and pelagic species. Our study has compounded the evidence for the vulnerability to exploitation of deepwater chondrichthyans and identified the specific life history traits that increase their vulnerability with increasing depth.

The different life history in the deep habitat is also evident in teleosts, where a similar suite of traits to those of the chondrichthyans are well documented as typical for deepwater fish, a group for which far more work on differences between habitats has been completed (Koslow *et al.* 2000; Cailliet *et al.* 2001; Clarke *et al.* 2003; Morato *et al.* 2006a; Morato *et al.* 2006b; Drazen and Haedrich 2012). Fewer studies though have directly investigated the habitat effects on traits and taken phylogenetic relatedness into account to separate the influence of habitat from the effect of phylogeny (Chamberlain *et al.* 2012), whereby differences in the distribution of taxa between habitats can drive apparent trends in traits and confound the effect of habitat on these traits. Phylogeny was taken into account in our study which, combined with our findings, strengthened the paradigm that habitat influences life history.

The visual interactions hypothesis offers an explanation for the association of life history traits with habitat. The hypothesis predicts metabolism is slowest in the deep habitat due to an energy saving response to reduced light levels affecting predator prey interactions (Childress *et al.* 1980) and that the pelagic habitat has the highest metabolic rates (Childress 1995). Our finding that differences in traits were strongest between the deep and pelagic habitats, and that the growth constant was lowest in the deep habitat which, by the 'rules of life', affects age at maturity and longevity (Beverton 1992), provide support for this hypothesis. Additionally, a recent study of metabolic rates in deepwater elasmobranchs found they decline with depth in a pattern that closely follows the predictions of this visual interactions hypothesis (Condon *et al.* 2012). The role of visual predator-prey interactions for chondrichthyans in the light limited deep sea is not yet fully understood, however it is highly likely that they use their visual senses in conjunction with electroreceptors. Their eyes exhibit an array of specialisations that

accommodate vision in the deep sea and they have the lowest number, yet greatest diversity in position, of electrosensory pores compared to other habitats (Bleckmann and Hofmann 1999; Kajiura *et al.* 2010). Additionally, deep sea kitefin and lantern sharks use luminescent ventral photophores and tissues, most likely as a visual camouflage mechanism known as counter-illumination that is used by other mid-water taxa (Claes and Mallefet 2008; Claes *et al.* 2012).

The visual interactions hypothesis predicates that mortality via the response to predation is a key driving force and other life history theories also hypothesize mortality to be among the main selective forces in sharks' life history, primarily through their effects on the juvenile stages (Cortés 2004; Dulvy and Forrest 2010). However it is unlikely that a single hypothesis can explain all the observed variation in traits between habitats, particularly as there is considerable debate over the merit of different theories to explain chondrichthyan life history evolution (Hoenig and Gruber 1990; Koslow 1996; Reznick *et al.* 2002; Clarke *et al.* 2003; Cortés 2004; Winemiller 2005). Resource availability affects the degree of density dependence, which in turn affects mortality, and along with environmental fluctuations are also important selective factors in chondrichthyan life histories (Reznick *et al.* 2002) and are likely to also have a role in variation in traits between habitats and among deepwater chondrichthyans.

There is a need to better understand the relative importance of the different selective factors that drive chondrichthyan life histories and some insight into the mechanism of these forces and the trade-offs deepwater chondrichthyans make to maximise fitness are provided by our review of the invariant life history ratios. The relative size and age at maturity (0.72 and 0.38, respectively) from this study concurred closely with previously reported values for sharks (Cortés 2000; Clarke *et al.* 2003; Graham and Daley 2011), rays (Frisk 2010) and elasmobranchs (Frisk *et al.* 2001). This corroborates the consistent nature of these invariants for chondrichthyans, particularly as our work was based on a greater and more diverse range of species than previously used and it included all groups simultaneously (sharks, rays and chimaeras).

The invariants of both relative size and age at maturity were higher in the deep habitat than pelagic and shelf habitats. Considering that life history strategies are shaped by the optimal allocation of the available energy in the habitat for survival and reproduction (Roff 1992), it is apparent that the deep habitat species partition a greater amount of energy and time in growth before reproductive age is reached. In the resource limited deep habitat the relatively larger size at maturity may enable the females to be of sufficient size to have the energy to support the production of fewer larger young, which would increase the likelihood of juvenile survival

(Frisk *et al.* 2001; Hussey *et al.* 2010; Deakos 2012). Strategies to reduce predation on the most vulnerable juvenile stage are considered favoured by k-selected life history traits exhibited by most chondrichthyans (Stearns 1992; Frisk *et al.* 2001; Dulvy and Forrest 2010). Little is known about juvenile mortality in deepwater chondrichthyans (Forrest and Walters 2009) though increasing the size of the young may reduce the risk of predation (Cortés 2000; Hussey *et al.* 2010). Larger young may also be a response to limited food resources where a larger size offers a competitive advantage, as has been shown in some species of fish in low resource habitats (Bashey 2008; Riesch *et al.* 2012). The larger size would also lower metabolic demand (per unit of weight) (Drazen and Seibel 2007; Papiol *et al.* 2012) with the consequent need to feed less frequently which would be an advantage in the deep habitat limited resource environment. Such a conclusion is consistent with other studies that have found large sized fish in the deep sea are associated with limited food availability (Collins *et al.* 2005; Papiol *et al.* 2012).

Maternal investment in reproduction is predicted by life history theory to be a balance between survival of the offspring and maintenance of their own survival and future reproductive potential (Frisk *et al.* 2005; Hussey *et al.* 2010). In deep habitats the relatively larger female size and age at maturity may not be solely for production of larger young, it could also be a mechanism to maintain maternal health in a resource limited environment while expending energy to provide nourishment via yolk reserves to the developing embryos during gestation (Shine 1988), which can be a long period in deepwater chondrichthyans (Kyne and Simpfendorfer 2010). This late onset of breeding has been reported in deepwater dogfish sharks (Graham and Daley 2011; Irvine *et al.* 2012) where some species reach maturity when almost fully grown. It may also assist with continuous breeding cycles that have been reported for some deepwater dogfish sharks and many deepwater skates (Watson and Smale 1998; McLaughlin and Morrissey 2005; Kyne and Simpfendorfer 2010; Graham and Daley 2011) which would require considerable energy investment to sustain the concurrent development of follicles and embryos. Despite the relatively larger maternal size in the deep, the litters were smaller relative to the size of young than in other habitats. As life history theory predicts a reproductive trade-off between litter size and size at birth (Winemiller and Rose 1992; Cortés 2000; Laptikhovskiy 2006) this could be a response to lesser energy available in the deep to partition between the two traits as has been reported for deepwater fish (Norse *et al.* 2012).

In the absence of information, body size, an easily measurable trait, has been suggested as a predictor of extinction risk for chondrichthyans with the hypothesis that larger species have lower potential population increases and are more vulnerable to exploitation (Jennings *et al.*

1999a; Frisk *et al.* 2001; Dulvy and Reynolds 2002; Reynolds *et al.* 2005). This hypothesis is not appropriate for deepwater chondrichthyans as they have smaller body size than species in other habitats yet they have a lower productivity and less resilience (Walker 1998; Simpfendorfer and Kyne 2009). The only deepwater group for which it may be appropriate is skates, with our study confirming previous findings that skates increase in size with depth (Dulvy and Reynolds 2002). Age at maturity has been suggested as an alternative predictor of extinction risk (Reynolds *et al.* 2005; Hutchings *et al.* 2012), but perhaps relative size or relative age at maturity would be more relevant for deepwater chondrichthyans as we found these invariants were markedly higher in the deep habitat.

Reproductive mode has also been found to be associated with extinction risk; it is lowest for oviparous chondrichthyans, increases for lecithotrophic viviparity and is highest in matrotrophic viviparity (García *et al.* 2008). This latter mode has the highest energetic cost to females and they tend to breed less frequently or have smaller litters than those with oviparous and lecithotrophic modes, lowering their reproductive output and rebound potential and increasing extinction risk (García *et al.* 2008; Simpfendorfer and Kyne 2009). The offset to this energetic cost of viviparity is the benefit of increased offspring survival (Goodwin *et al.* 2002; Frisk *et al.* 2005). There were very few species with this mode in the deep habitat which was dominated by oviparous and lecithotrophic modes in equal proportions. The higher energetic costs of matrotrophic viviparity associated with supplying nutrients through placental and uterine secretory structures (Goodwin *et al.* 2002) may be too great for the energy limited deep habitat. Lecithotrophic viviparity also has a higher energetic cost than oviparity and this may be the reason it has not become a dominant mode in the deep habitat. The occurrence of oviparous and lecithotrophic viviparous modes within the deep habitat showed no pattern with depth, an observation that has been made for elasmobranchs in general (Goodwin *et al.* 2005) and it appears phylogeny rather than depth drives the types of reproductive modes in the deep sea.

Life history traits are known to change in response to fishing pressure as the most vulnerable species decrease in abundance (Casey and Myers 1998; Walker and Hislop 1998; Jennings *et al.* 1999b; Dulvy *et al.* 2000; Sosebee 2005). We found regional differences in deepwater chondrichthyan life history traits; the North Atlantic had the highest growth constant and through the link between growth and theoretical longevity in the von Bertalanffy growth model, also the lowest longevity. The reasons for these regional differences are unknown: they may be the result of differences in the suite of species in each region for which age and growth data were available; they may reflect naturally occurring variations in oceanic environmental parameters and zoogeography (Angel 1997; Cope 2006); they may be the result of differences

in fishing pressure as the North Atlantic is a region where fishing has occurred deeper for longer than other regions, and there have been high levels of deepwater fishing (Gordon 2003; Morato *et al.* 2006b). This finding raises the question of whether the effects of different degrees of fishing pressure are already apparent in the deepwater chondrichthyan communities on a regional scale and warrants further investigation as more deepwater life history data across regions becomes available.

The deepwater chondrichthyan life histories are considered adaptations to maximising fitness with the most efficient energy expenditure driven by both mortality and resource availability: an energy saving growth response to low light levels driven by predation and optimal investment of energy in reproduction more likely driven by limited resources. These adaptations have led to a life history that causes deepwater chondrichthyans to be inherently more vulnerable than their counterparts in shelf and pelagic habitats with this vulnerability increasing with depth, a finding substantially strengthened by this study. We reiterate earlier warnings that the deeper the fishing, the less capacity the chondrichthyans have to recover; and have now identified the life history traits that drive these patterns. To further our understanding of patterns in life history traits of deepwater chondrichthyans there is a need for more age and growth data, particularly from the deeper waters (>1000 m) and especially for catsharks, the most speciose group of deepwater chondrichthyans for which we have very limited life history information.

Chapter 3 Deepwater chondrichthyans of the southern Great Barrier Reef, Australia



Ogilby's ghostshark *Hydrolagus lemures*

Rigby, C.L., White, W.T., Simpfendorfer, C. A. (in review) Deepwater chondrichthyans of the southern Great Barrier Reef. *PLOS ONE*.

3.1 Introduction

Deepwater chondrichthyans are defined as those species whose distribution is predominantly at (or restricted to) depths below 200m, or those that spend the majority of their lifecycle below this depth (Kyne and Simpfendorfer 2007). Most of the chondrichthyans reported from deep habitats of the Great Barrier Reef Marine Park (GBRMP) were collected in research trawl surveys by the FRV *Soela* in the mid 1980's (Last *et al.* 2014). To date, 54 species of deepwater chondrichthyans are known to occur in the GBRMP (Chin *et al.* 2010; Table B1 in Appendix B). Thirty five of these deepwater species are endemic to Australia with 19 of the endemics occurring only in waters offshore from Queensland, and a further eight species restricted to the east coast of Australia (Table B1 in Appendix B).

There is a general lack of life history data on deepwater chondrichthyan species in the GBRMP with a number of the species listed as Threatened by the IUCN and almost half listed as Data Deficient (Table B1 in Appendix B). They are considered at risk in the GBRMP due to the lack of biological information, their intrinsic vulnerability and their capture as bycatch by fisheries (Pears *et al.* 2012; GBRMPA 2014). A number of deepwater line fisheries and a trawl fishery operate within the GBRMP. The line fisheries are dispersed across the GBRMP with generally low and sporadic effort and deepwater chondrichthyan catches poorly reported, though there are concerns about increasing effort and the effect on these deepwater species (Sumpton *et al.* 2013). In contrast, the deepwater eastern king prawn (EKP) trawl fishery operates in one area of the southern GBRMP, around the Swain Reefs, with high levels of effort (Pears *et al.* 2012). The area is a poorly known upper continental slope habitat where any chondrichthyans present have been rated as being at high risk as a precaution due to the trawl effort and paucity of knowledge of their biology (Pears *et al.* 2012). The trawl fishery deploys turtle excluder and bycatch reduction devices in the nets that generally exclude larger chondrichthyans (greater than about one metre in length) but have a minimal effect on reducing the catch of the smaller individuals and species which include many of the deepwater chondrichthyans (Brewer *et al.* 2006; Courtney *et al.* 2007; Courtney *et al.* 2014). Information on the catch of deepwater chondrichthyans in this fishery and their life histories is required to ensure their sustainability.

Given the need for better data on deepwater chondrichthyans to help improve management, the present study aimed to provide information on the species composition and biology of chondrichthyans captured in the deepwater EKP fishery. This will improve knowledge of the species encountered in the deeper waters of the GBRMP and advance information on the life history of these species. It will also facilitate management to more confidently assess the risks of the deepwater trawl fishery to the southern GBRMP.

3.2 Materials and Methods

3.2.1 Sampling

The chondrichthyan bycatch of the deepwater EKP fishery around the Swain Reefs was observed on two commercial prawn trawlers during their normal trawling activities. On each vessel a five week trip was undertaken: 1 June–6 July 2011 and 14 March–18 April 2012. Demersal trawl fishing gear comprised three otter trawl nets of 15 fathoms each (i.e. head rope length of 27 m) with cod end meshes of 44.5 mm and a Turtle Excluder Device that was a top-opening metal grid and square mesh panel Bycatch Reduction Device. Trawling was from dusk till dawn with each trawl shot in one direction. The date, time, depth (m) and latitude and longitude (WGS 84) of the start and end of each shot were recorded. The start and end of each shot was taken from when the trawl nets reached and left the seafloor, respectively.

All deepwater chondrichthyans captured during the two, five week trips were deceased upon landing on the vessel and were identified, sexed and labelled. They were snap frozen whole, retained and upon completion of each trip were transported frozen to the laboratory where they were stored frozen until processed. Any shelf chondrichthyans landed were identified, sexed, measured for stretched total length (L_{ST}) or disc width (W_D), photographed and returned to the sea. The majority of the shelf chondrichthyans were alive when returned. Fisheries Queensland, Department of Agriculture and Fisheries donated some deepwater chondrichthyan specimens retained from their commercial deepwater EKP fishery observer surveys at the Swain Reefs.

3.2.2 Specimen identification

All chondrichthyans were identified by taxonomic features at sea using the keys and illustrations in Last and Stevens (2009). A tissue sample (fin clip) was collected from a subsample of specimens of each deepwater chondrichthyan species for molecular species identification. The samples were analysed as part of an ongoing National Science Foundation project: Chondrichthyan Tree of Life, led by the College of Charleston in the United States. The methodology for these molecular analyses sequenced for the mitochondrial NADH2 gene as described in Naylor et al. (2015). In addition, four tissue samples of eastern spotted gummy shark *Mustelus walkeri* White & Last 2008 were sequenced for two mitochondrial genes, COI and ND2 (Jessica Boomer, Macquarie University, pers. comm. 2012; Boomer *et al.* 2012). Representative specimens of each deepwater species were lodged as voucher specimens at the Australian National Fish Collection (CSIRO, Hobart). All shelf chondrichthyan species identifications were confirmed by one of the authors (WW) from the photographs taken at sea.

3.2.4 Deepwater chondrichthyan processing

All specimens were thawed, sexed, weighed (W_{BT}) (± 0.1 g) and measured (± 1 mm) following Francis (2006b): total length (L_T) and disc width (W_D) for batoids; stretched total length (L_{ST}) and fork length (L_F) for sharks; and chimaera length (L_C - snout to posterior end of supracaudal fin), precaudal length (L_{PC} - snout to anterior edge of supracaudal fin) and snout to vent length (L_{SV}) for the chimaera. Differences in the sex ratio were tested by Chi-square test with Yates' correction. Where sample sizes were sufficient, the relationships between L_{ST} and L_F and L_{ST} and W_D were examined using linear regression.

Specimens were dissected to remove ageing structures and to investigate their reproductive biology. Dorsal fin spines were removed from the piked spurdog *Squalus megalops* (Macleay 1881)(Chapter 5) and a segment of 5-10 vertebrae excised from under the first dorsal fin of all the sharks and blackfin ghostshark *Hydrolagus lemures* (Whitley 1939) and from the anterior region of the abdominal cavity of all the batoids. These ageing structures were labelled and frozen. For the investigation of a novel approach to ageing using near infrared spectroscopy (Chapter 7), the left pectoral fin of all *S. megalops* and pale spotted catshark *Asymbolus pallidus* Last, Gomon & Gledhill 1999 were removed, labelled and frozen. A white muscle tissue sample was removed from below the first dorsal fin from all specimens and retained frozen for potential future collaborative isotope studies. Heads were retained, frozen and provided to the University of Western Australia for sensory studies of deepwater chondrichthyans. Tail spines from the Urolophids were removed, frozen and provided to University of Giessen (Germany) for a study on venom.

The stomachs and livers were removed from all specimens and weighed (W_S , W_L) (± 0.1 g). Reproductive staging of all species was adapted from Ebert (2005) and Walker (2007). Males were classed immature (claspers pliable and shorter than pelvic fins), adolescent (claspers extended past the pelvic fins but still pliable), and mature (claspers extended past the pelvic fins and were rigid and fully calcified, testes were developed and epididymides were coiled). The presence of sperm in the epididymides was noted.

Females were classed as immature (undifferentiated ovaries, undeveloped oviducal glands and thin uteri), adolescent (developing ovaries with white follicles, developing oviducal glands, slightly expanded uteri), and mature (yolked follicles, fully developed oviducal gland and uteri). For those species with sufficient sample sizes, estimates of population length at 50% maturity (L_{ST50}) with 95% confidence intervals were determined for males and females separately using a generalised linear model with a binomial error structure and logit-link function within the

statistical package ‘R’ (R Development Core Team 2014). For other species the range of length at maturity was reported. The L_{ST50} or mid-point of the range of length at maturity were used to determine the life history invariant ratio of relative length at maturity (L_{ST50}/L_{ST}) (Dulvy and Forrest 2010). For the invariant ratios, where the range of length of maturity was large, the length of maturity from the literature was used and the maximum length of the males and females from the literature was used when it was greater than that sampled in this study.

Reproductive systems were removed and left and right testes and ovaries (including epigonal organs) weighed separately (M_G) (± 0.1 g). The number of yolked follicles in each ovary and the maximum follicle diameter (D_{Fmax}) (± 1 mm) were recorded. The number of yolked follicles can be used as a measure of ovarian fecundity; a proxy for fecundity as egg laying rates of oviparous species are difficult to define (Kyne and Simpfendorfer 2010). Where there were sufficient data, relationships between the total length and total ovary weight (M_G), D_{Fmax} and number of yolked follicles were examined by linear regression. When present, the number of embryos and the sex, presence of internal or external yolk, uterus (left or right), total length (± 0.1 mm) and mass (± 0.1 g) of each embryo were noted. When present, the number of egg cases and uterus (left or right) and mass (± 0.1 g) were noted and egg case length (L_{EC}) (± 0.1 mm) taken following Ebert and Davis (2007). All egg cases were labelled, frozen and retained. Any recently born elasmobranchs were noted and could be mostly distinguished as neonates by the presence of an umbilical scar on their ventral body surface in the region between the pectoral fins.

3.3 Results

3.3.1 Sampling

A total of 211 trawl shots were observed across a depth range of 117–280 m over the entire trawl grounds (referred to as ‘trawl grounds’) (Figure 3.1). The majority of the trawls were between 150–200 m on the shelf in the main deepwater EKP fishery trawl grounds (referred to as ‘main trawl grounds’) with six shots in deeper waters (203–280 m) to the south of the main trawl grounds (Figure 3.1). Deepwater chondrichthyans were observed in 72% of the trawl shots. There were an average of four shots per night, though in rough weather trawling ceased and over the two, five weeks trips 105 shots were observed on Trip 1 and 106 shots on Trip 2. The trawl shots had an average duration of 2.5 hours and speed of 2.9 knots.

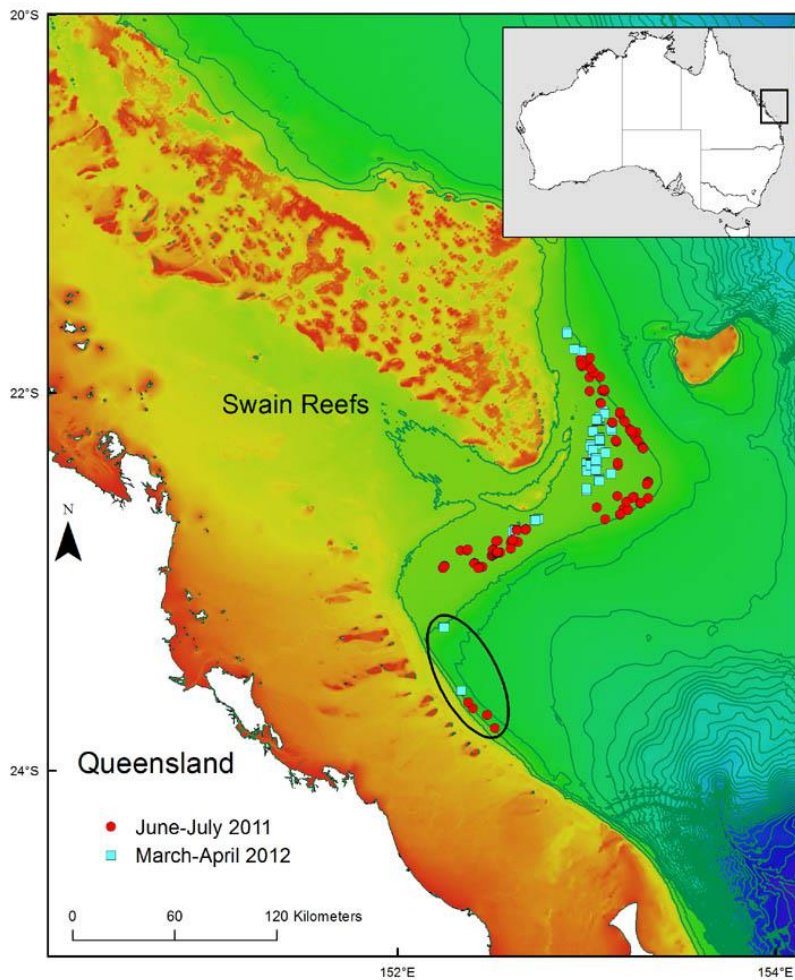


Figure 3.1 Sample locations with contours at 100 metre depth intervals. The six shots south of the main trawl grounds are circled.

3.3.2 Species composition

A total of 1675 individuals were observed from eleven species of deepwater chondrichthyans and thirteen species of shelf chondrichthyans (Table 3.1). The deepwater chondrichthyans ($n = 1533$ individuals) were far more abundant than shelf species ($n = 142$) (Table 3.1). Argus skate *Dipturus polyommata* (Ogilby 1910) dominated the bycatch by number at 50.1% of the deepwater species bycatch and 45.9% of the combined deepwater and shelf species bycatch (Table 3.1). Along with the next two most dominant bycatch species, *S. megalops* and *A. pallidus*, these three species accounted for 92.3% of the deepwater bycatch (Table 3.1

Table 3.1 Observed deepwater and chondrichthyan species.

Scientific name and authority	Common name	Male (n)	Female (n)	Total (n)	Depth range (m)	Length range (L_{ST}/L_T mm)	% deep water bycatch	% total bycatch
Deepwater species								
<i>D. polyommata</i> (Ogilby 1910)	Argus skate	366	402	768	135-280	95-371	50.1	45.9
<i>Squalus megalops</i> (Macleay 1881)	Piked spurdog	117	305	422	187-280	253-505	27.5	25.2
<i>Asymbolus pallidus</i> Last, Gomon & Gledhill 1999	Pale spotted catshark	110	115	225	174-280	141-436	14.7	13.4
<i>Mustelus walkeri</i> White & Last 2008	Eastern spotted gummy shark	14	34	48	124-242	410-1050	3.1	2.9
<i>Urolophus piperatus</i> Séret & Last 2003	Coral sea stingaree	10	8	18	123-216	158-367	1.2	1.1
<i>Hydrolagus lemures</i> (Whitley 1939)	Blackfin ghostshark	8	9	17	203-242	465-820 L_C	1.1	1.0
<i>Urolophus bucculentus</i> Macleay 1884	Sandyback stingaree	4	10	14	159-242	175-690	0.9	0.8
<i>Squatina albiguttata</i> Last & White 2008	Eastern angelshark	4	7	11	132-242	510-1160	0.7	0.7
<i>Dipturus apricus</i> Last, White & Pogonoski 2008	Pale tropical skate	5	3	8	237-280	177-279	0.5	0.5
<i>Cephaloscyllium variegatum</i> Last & White 2008	Saddled swellshark	0	1	1	215	675	0.1	0.1
<i>Pristiophorus delicatus</i> Yearsley, Last & White 2008	Tropical sawshark	0	1	1	176	949	0.1	0.1
Total abundance deepwater species				1533				
Shelf species								
<i>Hemigaleus australiensis</i> White, Last & Compagno 2005	Australian weasel shark	15	31	46	117-137	450-820		2.7
<i>Brachaelurus colcloughi</i> Ogilby 1908	Colclough's shark	17	10	27	128-157	410-880		1.6
<i>Aptychotrema rostrata</i> (Shaw 1794)	Eastern shovelnose ray	9	9	18	123-150	490-900		1.1
<i>Carcharhinus coatesi</i> (Whitley 1939)	Whitecheek shark	8	7	15	128-137	520-600		0.9
<i>Carcharhinus plumbeus</i> (Nardo 1827)	Sandbar shark	7	6	13	135-196	720-1620		0.8
<i>Orectolobus maculatus</i> (Bonaterre 1788)	Spotted wobbegong	5	6	11	128-242	820-1420		0.7
<i>Gymnura australis</i> (Ramsay & Ogilby 1886)	Australian butterfly ray	2	3	5	117-137	520-840 W_D		0.3

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<i>Carcharhinus amblyrhynchoides</i> (Whitley 1934)	Graceful shark	1	1	2	146-152	1490-1760	0.1
<i>Carcharhinus falciformis</i> (Müller & Henle 1839)	Silky shark	0	1	1	139	1230	0.1
<i>Carcharhinus sorrah</i> (Müller & Henle 1839)	Spot-tail shark	1	0	1	133	1310	0.1
<i>Chiloscyllium punctatum</i> Müller & Henle 1838	Grey carpetshark	0	1	1	126	520	0.1
<i>Dasyatis thetidis</i> Ogilby 1899	black stingray	0	1	1	190	400 DW	0.1
<i>Rhynchobatus palpebratus</i> Compagno & Last 2008	eyebrow wedgefish	0	1	1	136	1200	0.1
Total abundance shelf species				142			
Total abundance all chondrichthyans				1675			

All lengths are for L_{ST} or L_T unless otherwise specified as chimaera length (L_C)

The results from this study added an additional four deepwater species to the known chondrichthyan fauna in the regions of the deepwater EKP fishery: *S. megalops*, Coral Sea stingaree *Urolophus piperatus* Séret & Last 2003, eastern angelshark *Squatina albipunctata* Last & White 2008 and tropical sawshark *Pristiophorus delicatus* Yearsley, Last & White 2008. In addition, this study found it is likely that all previously recorded patchwork stingaree *Urolophus flavomosaicus* Last & Gomon 1987 were actually the sandyback stingaree *Urolophus bucculentus* Macleay 1884 (Section 3.3.3 and Table B.1 in Appendix B). This study added *Squalus megalops* to the known deepwater species in the GBRMP (Table B.1 in Appendix B). Six additional shelf species were recorded in this study that had not previously been reported from the deepwater EKP fishery within the GBRMP: Australian weasel shark *Hemigaleus australiensis* White, Last & Compagno 2005, graceful shark *Carcharhinus amblyrhynchoides* (Whitley 1934), silky shark *Carcharhinus falciformis* (Müller & Henle 1839), spot-tail shark *Carcharhinus sorrah* (Müller & Henle 1839), black stingray *Dasyatis thetidis* Ogilby 1899 and eyebrow wedgefish *Rhynchobatus palpebratus* Compagno & Last 2008 (Pears *et al.* 2012).

Shelf species will not be further described, though it is worth noting that the maximum length and depth of Colcough's shark *Brachaelurus colcloughi* Ogilby 1908 was extended from 770 mm to 880 mm and 100 m to 157 m, respectively (Kyne 2008; Last and Stevens 2009). The known maximum depth of three other bottom dwelling shelf species was also extended: spotted wobbegong *Orectobolus maculatus* (Bonaterre 1788) from 218 m to 242 m, grey carpetshark *Chiloscyllium punctatum* Müller & Henle 1838 from at least 85 m to 126 m, and *R. palpebratus* from 60 m to 136 m (Last and Stevens 2009).

3.3.3 Specimen identification

The molecular analyses confirmed the morphological identifications of *S. megalops*, *A. pallidus*, *U. piperatus*, *S. albipunctata*, pale tropical skate *Dipturus apricus* Last, White & Pogonoski 2008, saddled swellshark *Cephaloscyllium variegatum* Last & White 2008 and *P. delicatus*. NADH2 sequences for *D. polyommata* were almost identical with those for its sister species Endeavour skate *Dipturus endeavouri* Last, 2008 from further south in Queensland. These two species differ in colour pattern and subtle morphology (Last 2008), and the sequence data suggested they are very close and possibly only relatively recently separated from one another. Similarly, *Mustelus walkeri* sequences were almost identical with those of gummy shark *Mustelus antarcticus* Günther 1870 in southern Australia. Although the molecular data did not distinguish them using the NADH2 gene, these two species differ in some morphological features (White and Last, 2008) and life history traits (Chapter 4). One of the

morphological features that separates these two species, the extent of the buccopharyngeal denticles on the roof and floor of the mouth (White and Last 2008), was examined in all *M. walkeri* specimens collected in this study. Furthermore, extensive tagging work indicated that *M. antarcticus* does not extend into Queensland waters (Walker 2007). The sequences of *H. lemures* were identical to samples from Western Australia, Tasmania, the Tasman Sea and New South Wales which have been identified as both *H. lemures* and Ogilby's ghostshark *Hydrolagus ogilbyi* Waite 1898. The key morphological characteristics of the specimens recorded in this study aligned well with those provided by Last and Stevens (2009) for *H. lemures* rather than *H. ogilbyi*. This species belongs to a poorly defined *lemures-ogilbyi* species complex which needs a detailed taxonomic investigation to resolve.

The sequences from specimens of a reticulated *Urolophus*, which were identified in the field as patchwork stingaree *Urolophus flavomosaicus* Last & Gomon 1987 based on their colour pattern, grouped close to but distinct from *U. flavomosaicus* from Western Australia. These sequences were identical to a sequence from a *U. bucculentus* specimens collected off New South Wales (G. Naylor, unpubl. data). The *Urolophus* specimens obtained in this study possessed the complex pattern of reticulations and large white spots typical of *U. flavomosaicus*, but not over the central disc region. The central disc area of these specimens more closely resembled that of typical *U. bucculentus* specimens, i.e. small white spots and fine reticulations (Last and Stevens 2009). Thus, we consider these specimens to be conspecific with *U. bucculentus* and not *U. flavomosaicus*. Further taxonomic investigation is required to elucidate whether *U. flavomosaicus* records from eastern Australia are actually just a northern colour variant of *U. bucculentus*, with these being sister species.

3.3.4 Distribution

The majority of deepwater chondrichthyans were taken in the six trawl shots to the south of the main trawl grounds that were all in waters > 200 m deep (Figure 3.2). The only species that was caught often and also across the main trawl grounds was *D. polyommata*. Other species also present in the main trawl grounds but not frequently captured were *M. walkeri*, *S. albipunctata*, *U. piperatus*, and *P. delicatus*. Nearly all the *S. megalops* and *A. pallidus* were taken south of the main trawl grounds with the small numbers of those in the trawl grounds (7% of the total number of *S. megalops* and 12% of total *A. pallidus*) present in the same area at the edge of the shelf in the eastern extremity of the deepwater EKP fishery area sampled (Figure 3.2). All the deepwater chondrichthyans observed as bycatch are endemic to Australia, except *S. megalops*, with five of the ten endemics only occurring in waters offshore from Queensland (Table B.2 in

Appendix B). All the Queensland endemics have wider distribution than the Swain Reefs deepwater EKP fishery area (Table B.2 in Appendix B).

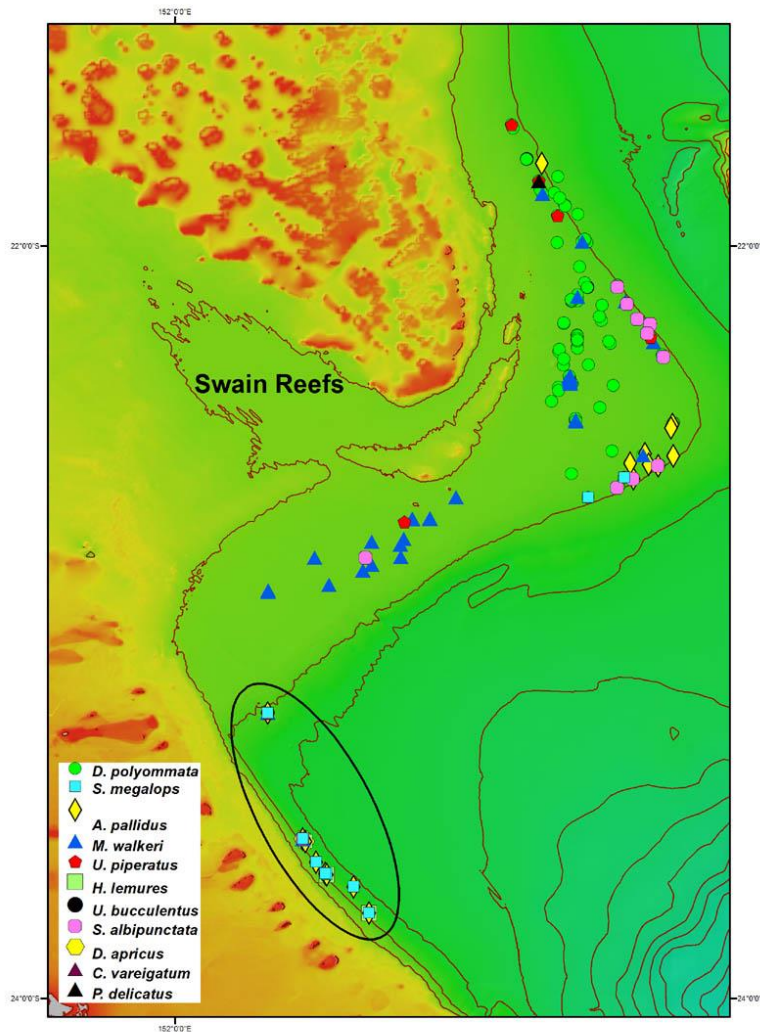


Figure 3.2 Distribution of deepwater chondrichthyans captured in the Eastern King Prawn fishery at Swain Reefs. The six shots south of main trawl ground are circled with all species present in these six shots except *Pristiophorus delicatus*.

3.3.4.1 New distribution and depth records

The *P. delicatus* collected extended the known northern distribution of this species slightly, from off Rockhampton (22° 10' S) to the Swain Reefs (21° 49' S) and the 207 m depth of capture (in the north of the trawl grounds, Figure 3.2) raised the upper depth limit of occurrence from the previously recorded 245 m (Yearsley and White 2008; Last and Stevens 2009). The individual was 960 mm TL which also increased the known maximum length from 840 mm (Last and Stevens 2009). The likely revision of *U. flavomosaicus* to *U. bucculentus* would extend the northern distribution of *U. bucculentus* from Stradbroke Island, Queensland (27°

35°) to the Swain Reefs (21° 41' S) (Last and Stevens 2009). Two other species had records for their upper depth limit extended by this study: *A. pallidus* from 225 m to 174 m and *U. piperatus* from 171 m to 123 m (Last *et al.* 1999; Seret and Last 2003).

3.3.5 Biological aspects

The extent of biological data varied greatly between the deepwater species collected. Three species had adequate sample sizes and reliable age structures that enabled age, growth and reproductive studies: *D. polyommata*, *S. megalops* and *M. walkeri*. The results from those studies are described in Chapters 4 and 5 and summarised in Table 3.2. Preliminary biological data were available for *A. pallidus*, *U. piperatus*, *U. bucculentus*, *H. lemures* and *S. albipunctata* and are described below and summarised in Table 3.2.

Table 3.2 Biological data for deepwater chondrichthyans captured in the Eastern King Prawn fishery at Swain Reefs. Length at maturity are range estimates unless stated as L_{ST50} = estimates of population length at 50% maturity, LC = chimaera length. NA = no information available from the individuals collected in this study.

	Max. length (L_{ST}) (mm)		Length at maturity (mm)		Relative length at maturity		Length at birth (mm)	Litter size	Ovarian fecundity
	Male	Female	Male	Female	Male	Female			
<i>D. polyommata</i> ^a	369	371	278 L_{ST50}	303 L_{ST50}	0.73	0.80	89-111	NA	7.6
<i>S. megalops</i> ^b	407	505	352 L_{ST50}	422 L_{ST50}	0.81	0.84	158	2.5	
<i>A. pallidus</i>	428	436	330 L_{ST50}	352 L_{ST50}	0.75	0.75	~140	NA	8.5
<i>M. walkeri</i> ^a	805	1050	670-805	833-1012	0.92	0.83	273-295	5-7	
<i>U. piperatus</i>	289	367	205-273	233-366	0.48	0.56	NA	3	
<i>H. lemures</i>	620 L_C	820 L_C	500-533 L_C	625-718 L_C	0.83	0.82	NA	NA	3-11
<i>U. bucculentus</i>	507	690	<447	300-466	0.62	0.53	NA	2-4	
<i>S. albipunctata</i>	706	1160	NA	720-1160	NA	0.82	NA	4	
<i>D. apricus</i>	279	232	NA	NA	NA	NA	NA	NA	
<i>C. variegatum</i>	NA	675	NA	NA	NA	NA	NA	NA	
<i>P. delicatus</i>	NA	949	NA	NA	NA	NA	NA	NA	

^aChapter 4, ^bChapter 5.

3.3.5.1 *Asymbolus pallidus*

A total of 225 *A. pallidus* was collected: 110 males (314–428 mm L_{ST}) and 115 females (141–436 mm L_{ST}) (Table 3.2), with the sex ratio across all trawls not significantly different from parity ($\chi^2 = 2.76$, d.f = 1, $p = 0.10$). Fork length was not measured on this species due to the elongated shape of the caudal fin. Two males and three females were lodged as voucher specimens at the Australian National Fish Collection (CSIRO) with the remainder dissected. The specimens were dominated by mature males and females (Figure 3.3).

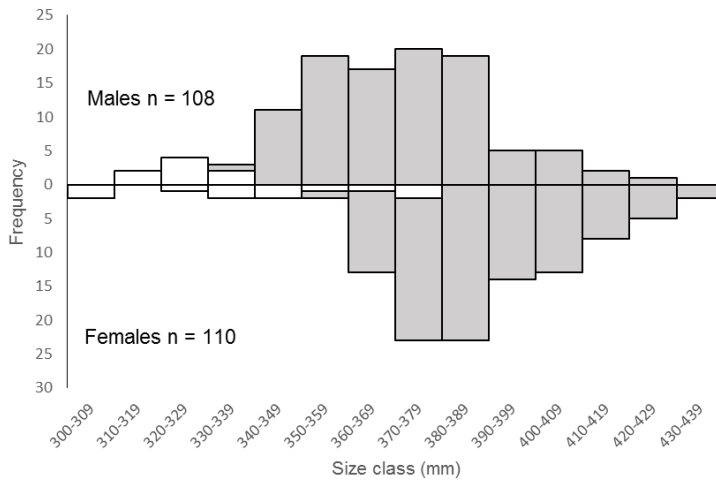


Figure 3.3 Length-frequency of immature (white) and mature (grey) *Asymbolus pallidus* individuals.

Although there were sufficient numbers of *A. pallidus* for an age study, the species had no reliable ageing structure as growth bands were not discernible on either whole or sectioned vertebrae and it had no other hard parts for ageing. Trials with a number of stains failed to enhance vertebral growth band visibility, that is, Alizarin red S (Officer *et al.* 1996), crystal violet and silver nitrate (Schwartz 1983), cobalt nitrate (Hoenig and Brown 1988; Gennari and Scacco 2007), graphite powder (Ferreira and Vooren 1991), ninhydrin (Davenport and Stevens 1988), nitric acid (Correia and Figueiredo 1997), and Mayer’s haematoxylin (modified technique of Bubley *et al.* (2012).

Length at maturity data were available for 108 males with all males mature at ≥ 339 mm. Estimate of L_{ST50} (with 95% CI) was 330.3 ± 0.0 mm (Table 3.2, Figure 3.4). This was very similar to the reported value of 320 mm (Last and Stevens 2009). Females matured at a larger length than males; the length at maturity data for 110 females indicated the smallest mature female was 351 mm and the largest immature female 371 mm. Estimate of L_{ST50} (with 95% CI) was 351.6 at ± 6.6 mm (Table 3.2, Figure 3.4). This is the first length at maturity estimate for females of this species. The invariants of relative length at maturity were 0.75 for both males and females (Table 3.2), and were calculated with the reported maximum length of 439 mm and 467 for males and females, respectively (Last *et al.* 1999) .

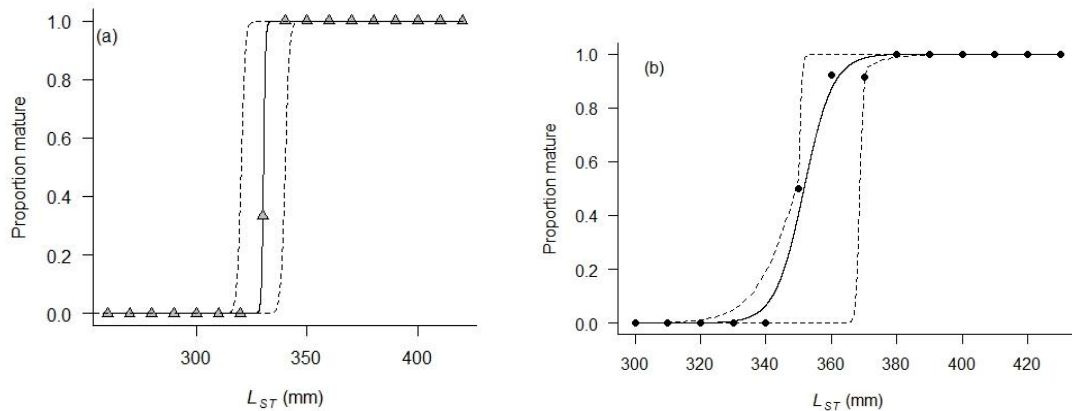


Figure 3.4 Length-based maturity ogives for *Asymbolus pallidus* (a) males and (b) females. Dashed lines are 95% confidence intervals.

Only the right ovary was functional as reported for other catsharks (Ebert *et al.* 2006; Flammang *et al.* 2008). In mature females the mean \pm se total number of yolked follicles in the right ovary was 8.5 ± 0.2 (range 2-15). The yolked follicles ranged in diameter from 4–23 mm. The ovary weight (M_G) and maximum follicle diameter D_{Fmax} increased rapidly after maturity (Figure 3.5). In mature females there were significant relationships between M_G and L_{ST} : $M_G = 0.09 L_{ST} - 25.42$ ($R^2 = 0.33$, D.f. = 98, $p < 0.001$) but the relationship was not significant for D_{Fmax} and L_{ST} : $D_{Fmax} = 0.017 L_{ST} + 8.55$ ($R^2 = 0.02$, D.f. = 98, $p = 0.16$). The number of yolked follicles increased significantly with length in mature females: number of follicles = $0.04 L_{ST} - 7.06$ ($R^2 = 0.12$, d.f. = 98, $p < 0.001$) (Figure 3.5).

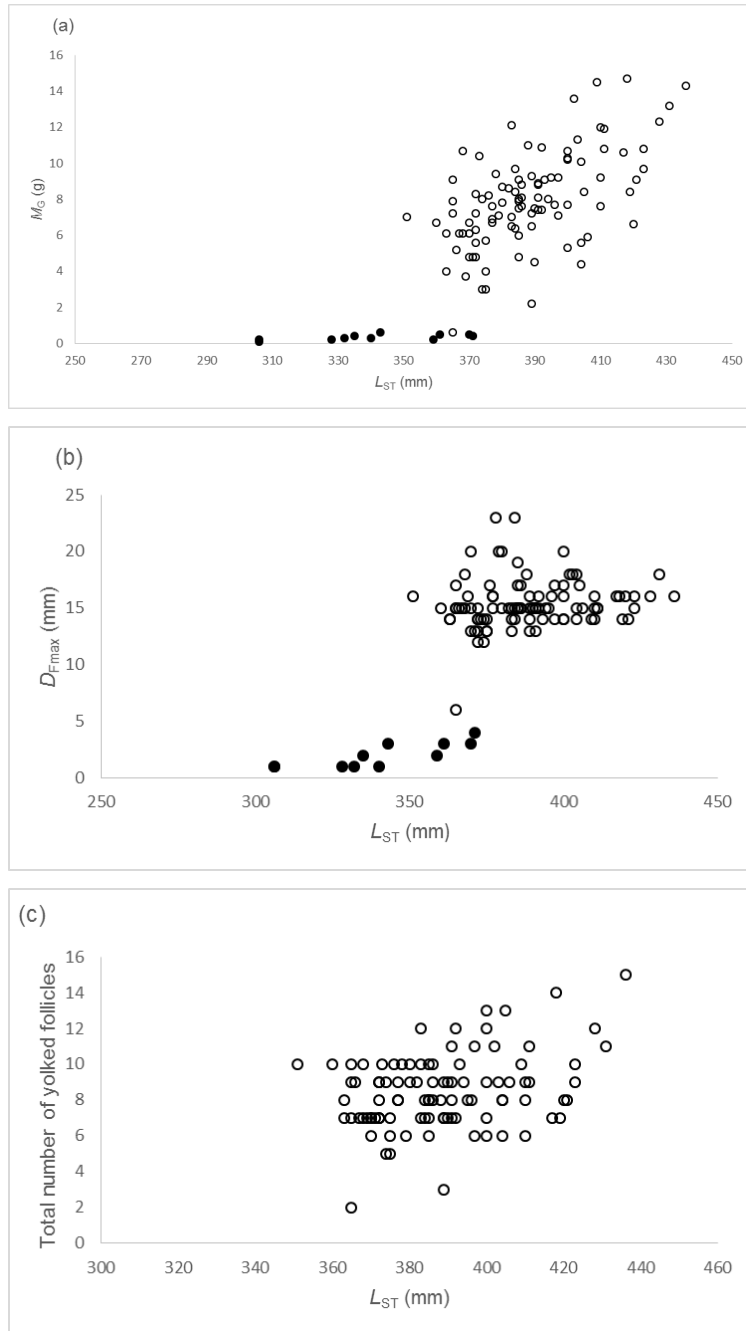


Figure 3.5 The relationship between stretched total length (L_{ST}) and reproductive indices of *Asymbolus pallidus* females (a) L_{ST} and total ovary weight (M_G), (b) L_{ST} and maximum follicle diameter (D_{Fmax}) and (c) L_{ST} and number of yolked follicles. Immature (closed circle) and mature (open circle).

Females with egg cases *in utero* were collected on both sampling trips with a total of 22 collected; the smallest gravid female was 366 mm L_{ST} . The proportion of mature females that were gravid was similar on both trips: 22% and 25% on trips 1 and 2, respectively. Gravid females were not segregated as they were collected in the same trawl shots as immature and mature non-gravid females and immature and mature males. The majority of the 22 gravid

females were in depths >200 m (203–280 m) south of the main trawl grounds with only 4 gravid females collected in the trawl grounds at depths < 200 m, i.e. at 174–196 m. All 22 gravid females had 6–10 yolked follicles in the right ovary with a diameter of 5–23 mm, and an egg case in each uterus. The egg cases were golden (Figure 3.6) and ranged in length from 44.6–51.5 mm L_{EC} and 2.5–4.0 g; there were no visible embryos within any of the egg cases. A free swimming female neonate of 141 mm L_{ST} was collected from 215 m depth south of the main trawl ground. The neonate had been feeding, evidenced by fish scales and a vertebra in the stomach. This extends the length of hatching from the previously reported 190 mm (Last and Stevens 2009) to 140–190 mm L_{ST} (Table 3.2).



Figure 3.6 Egg case from a 423 mm stretched total length *Asymbolus pallidus*. Anterior end at left of image (49.3 mm egg case length).

3.3.5.2 *Urolophus piperatus*

A total of 18 *U. piperatus* was collected with similar numbers of males and females: 10 males (205–289 mm L_T) and 8 females (158–367 mm L_T) (Table 3.2). The relationship between L_{ST} and W_D for sexes combined was: $L_T = 1.52 W_D - 15.19$ ($R^2 = 0.98$, d.f. = 17, $p < 0.001$). The smallest male was immature and captured in the main trawl grounds at 192 m. The remainder of males (273–289 mm L_T) were mature with sperm present in the epididymides and were all captured in one trawl shot to the south of the main fishing grounds in 215 m. Hence, males mature between 205–273 mm L_T which encompassed the reported length at maturity of 230 mm (Last and Stevens 2009).

Five of the females were immature (158–233 mm L_T) and three mature, two of which were pregnant and one *post partum* (366–367 mm L_T). Hence, females mature between 233–366 mm L_T (Table 3.2) which includes the previously reported length of maturity of 270 mm based on one female (Seret and Last 2003; Last and Stevens 2009). The life history invariants of relative

length at maturity were 0.48 and 0.56 for males and females, respectively (Table 3.2). The maximum length (484 mm L_T) and the length at maturity were used from the literature (Seret and Last 2003; Last and Stevens 2009).

The two pregnant females were caught in two consecutive trawl shots in the trawl grounds in 177 m. The *post partum* female was also caught in the trawl grounds at 129 m. Only the left ovary and uterus were functional, which is typical for urolophids (Trinnie *et al.* 2012). All three females had yolked follicles in the left ovary ($n = 5, 6, 10$) with a diameter of 5–15 mm and an expanded left uterus thickened with villi. One female aborted two embryos upon capture and retained one embryo (1 male, 2 female) and upon capture the other female aborted all three embryos (2 male, 1 female) (Table 3.2). All embryos had external yolk sacs attached and were 50.0–72.9 mm L_T and 1.2–3.3 g.

3.3.5.3 *Urolophus bucculentus*

A total of 14 *U. bucculentus* was collected with more females than males: 4 males (447–507 mm L_T) and 10 females (175–690 mm L_T) (Table 3.2). The relationship between L_T and W_D for sexes combined was: $L_T = 1.20 W_D + 21.51$ ($R^2 = 0.99$, d.f. = 12, $p < 0.001$). All males were mature and captured in one trawl shot to the south of the main fishing grounds in 215 m, where they occurred together with females of all life cycle stages. All mature males had sperm present in the epididymides. The life history invariant of relative length at maturity was 0.62 (Table 3.2) and was calculated using the length at maturity (414 mm) and maximum length of males (672 mm) from the literature (Trinnie *et al.* 2012)

Six of the females were immature (175–300 mm L_T) and four mature, two of which were pregnant and two *post partum* (466–690 mm L_T). Females mature between 300–466 mm L_T (Table 3.2). The females in this study were mature at a smaller length than the previously reported 478–522 mm ($L_{T50} = 502$ mm) (Trinnie *et al.* 2012). The life history invariant of relative length at maturity was 0.53 (Table 3.2) and was calculated using the minimum sampled length at maturity from this study (466 mm) and maximum length of females (885 mm) from the literature (Trinnie *et al.* 2012).

One pregnant female was caught in the trawl grounds at 175 m and the other south of the trawl grounds at 215 m where it was taken together with a *post partum* female. The other *post partum* female was caught in the trawl grounds on its own at 162 m. None of the pregnant or *post partum* females had yolked follicles in the left ovary and all had an expanded left uterus thickened with villi. Both females aborted upon capture, one aborted two embryos (1 male, 1

female) and the other four embryos (2 male, 2 female) (Table 3.2). All embryos had external yolk sacs attached and were 63.0–98.0 mm L_{ST} and 2.4–9.1 g.

3.3.5.4 *Hydrolagus lemures*

A total of 17 *H. lemures* was collected with similar numbers of males and females: 8 males (465–620 L_C) and 9 females (480–820 L_C) (Table 3.2). The combined sexes relationship for: L_C and L_{PC} was: $L_C = 1.053 L_{PC} + 35.47$ ($R^2 = 0.99$, d.f. = 13, $p < 0.001$); and for L_C and L_{SV} was: $L_C = 1.55 L_{SV} + 173.03$ ($R^2 = 0.98$, d.f. = 13, $p < 0.001$). This study extended the maximum recorded length from 530 mm to 820 mm L_C (Last and Stevens 2009). Two males were immature at 465–500 mm L_C and the rest mature (all with sperm present) (533–620 mm L_C), hence males mature between 500–533 mm L_C which concurs with the reported 500 mm (Last and Stevens 2009). Six females were immature (480–540 mm L_C), one adolescent (625 mm L_C) and two mature (718–820 mm L_C), hence females mature at 625–718 mm L_C (Table 3.2). This is the first length at maturity data for females of this species. The mature females had yolked follicles in the right and left ovaries ($n = 3–11$) with a diameter of 10–36 mm.

The invariant relative lengths at maturity were similar for males and females (0.83 and 0.82 respectively, Table 3.2) and were calculated with the midpoint of the lengths of maturity and maximum lengths of the males and females from this study. All the males were caught in the same area south of the main trawl grounds with the immature females in 203–280 m. The adolescent and mature females were all caught together in the one trawl shot at 242 m.

3.3.5.5 *Squatina albipunctata*

A total of 11 *S. albipunctata* was collected with more females than males: 4 males (592–706 mm L_{ST}) and 7 females (510–1160 mm L_{ST}) (Table 3.2). The relationship between L_{ST} and L_F for sexes combined was: $L_{ST} = 1.034 L_F + 16.12$ ($R^2 = 0.98$, d.f. = 9, $p < 0.001$). All males were immature and taken in the trawl grounds on the shelf edge at 190–196 m. Six of the females were immature (510–720 mm L_{ST}) and caught in the trawl grounds with the immature males at depths of 190–196 m, except the smallest female that was caught south of the main trawl grounds in 238 m. The one mature female (1160 mm L_{ST}) was pregnant and was caught on its own, in the trawl grounds at a shallower depth (133 m) than all other *S. albipunctata* encountered. Hence the length at maturity is 720–1160 which includes the known length at maturity of 1070 mm (Last and Stevens 2009). The relative length at maturity was 0.82 (Table 3.2) calculated from the literature maximum length of 1300 mm and known length of maturity (Last and Stevens 2009). Only the left ovary appeared functional which is the case in some, but not all species of *Squatina* (Bridge *et al.* 1998). The ovary had numerous small follicles, but

none were yolked. There were four embryos (Table 3.2), two in the left uterus and two in the right uterus. They all had external yolk sacs and were too small to sex at 49.5–54.7 mm L_{ST} and 0.8–1.7 g.

3.4 Discussion

This study increased the number of deepwater chondrichthyan species known to occur in the deepwater EKP fishery around the Swain Reefs. The bycatch community of sympatric deepwater chondrichthyans in this area of the fishery displayed life history traits typical of deepwater chondrichthyans (Garcia *et al.* 2008; Chapter 2). However, there was some variability evident in these life history traits and patterns of depth and spatial distribution. Three species of chondrichthyans had sufficient sample sizes and reliable ageing structures for age and growth studies: two shark species (*S. megalops* and *M. walkeri*) which were both relatively slow growing, long lived with late age at maturity and small litters; and a skate (*D. polyommata*) that was moderately fast growing with a shorter life span and younger age at maturity but low ovarian fecundity (Chapters 4 and 5). The preliminary biological data from the other species indicated they had relatively large lengths at maturity, small litters, low ovarian fecundity and in some cases non-continuous reproductive cycles which are a combination of traits suggestive of low productivity (Clarke *et al.* 2003).

Sexual dimorphism and life history invariants

Sexual dimorphism, whereby the females were of a larger length and had a length at maturity larger than the males, was apparent in all of the deepwater chondrichthyans collected in this study and is typical of many chondrichthyans (Cailliet and Goldman 2004; Cortés 2004). It has been attributed to the need for females to partition more time and energy into growth before reproductive age is reached to be of sufficient length to support the production of relatively large young (Cailliet *et al.* 1990; Frisk *et al.* 2001). This dimorphism has been reported in other small-medium bodied skates closely related to *D. polyommata* (Treloar 2008), in other populations of *S. megalops* (Braccini *et al.* 2006a) and in *Mustelus* species (Chapters 4 and 5).

Among the catsharks, length at maturity is often similar for both sexes (Ebert *et al.* 2006), though the dimorphism of *A. pallidus* has also been noted for the closely related orange spotted catshark *A. rubiginosus* Last, Gomon & Gledhill 1999 that occurs further south in Queensland and in some other catshark species (Castro *et al.* 1988; Francis 2006a; Capapé *et al.* 2008; Kyne *et al.* 2011). The length at maturity of *A. pallidus* males and females was similar to that of another small sized catshark New Zealand catshark *Bythaelurus dawsoni* (Springer 1971) (Francis 2006a). Dimorphism is also known among urolophids (White *et al.* 2001; White

and Potter 2005; Trinnie *et al.* 2012), chimaerids (Moura *et al.* 2004; Barnett *et al.* 2009a) and squatinids (Bridge *et al.* 1998; Capapé *et al.* 2002; Capapé *et al.* 2005).

The relatively large invariant length at maturity was evident for nearly all the deepwater species sampled. It reflects a relatively large length for onset of breeding and is typical of deepwater chondrichthyans for which the mean invariant length at maturity across all deepwater taxa has been reported as 0.76 and ranged to 0.90 (Ebert *et al.* 2006; Graham and Daley 2011; Irvine *et al.* 2012) (Chapter 2). The exceptions were the two urolophids, *U. piperatus* and *U. bucculentus*. The only other urolophid present in deepwater, the wide stingaree *Urolophus expansus* McCulloch 1916, has a typical deepwater length at maturity invariant of 0.74 (Kyne and Simpfendorfer 2007), hence the relatively smaller length at maturity for the female *U. bucculentus* may be a reflection of the smaller length at maturity reported for this northern population compared to that from southern Australian waters (Trinnie *et al.* 2012). The smaller invariant of *U. piperatus* may be attributed to the small sample size used from the literature to assess maturity and more samples may be required (Seret and Last 2003).

Reproduction

All the deepwater chondrichthyans sampled had low biological productivity characteristic of deep habitats (Kyne and Simpfendorfer 2007; García *et al.* 2008), with a combination of reproductive traits that varied from long cycles and small litters to shorter continuous reproductive cycles (where yolked follicles are present in pregnant females) with low fecundity. The viviparous species all had small litters and included both continuous and non-continuous cycles. The *S. megalops* litter sizes and continuous reproduction was similar to that previously reported for this species that is known to have a long biennial cycle (Braccini *et al.* 2006a). The only other species for which the reproductive cycle was formerly known, *U. bucculentus*, also has a long biennial cycle, with the non-continuous reproduction and litter sizes observed in this study concurring with that previously described (Trinnie *et al.* 2012). *Squatina albipunctata* appeared to have a non-continuous reproductive cycle with litter sizes similar to those cited before, and also likely has a longer biennial cycle, as this has been reported for the three other deepwater *Squatina* species (Bridge *et al.* 1998; Capapé *et al.* 2005; Vooren and Chiamonte 2006). *Mustelus walkeri* and *U. piperatus* both appear to have a continuous cycle that may be annual as the cycles were annual in other species of their genera (Walker 2007; Trinnie *et al.* 2012). The litters of *M. walkeri* were smaller than the closely related *M. antarcticus* and other aplacental *Mustelus* species (Walker 2007). In contrast, the *U. piperatus* litter size was typical of *Urolophus* species, which mostly have small litters of only 2 to 5 (White and Potter 2005; Trinnie *et al.* 2012).

The two gravid oviparous species, *D. polyommata* and *A. pallidus* both appeared to have a continuous reproductive cycle. Year round oviposition is common among skates and has previously been reported for other *Dipturus* species (Ruocco *et al.* 2006; Kyne *et al.* 2008; Treloar 2008). *Dipturus polyommata* was the least fecund of the *Dipturus* species for which ovarian fecundity data was available with body length unlikely to be the reason, as one of the species, *D. endeavouri*, was of similar length to *D. polyommata* (Kyne *et al.* 2008; Treloar 2008). This present study confirmed *A. pallidus* as single oviparous (one egg case per uterus), similar to its close relatives which also show year round oviposition, though the proportion of females carrying egg cases was lower than reported in other species of catsharks (Richardson *et al.* 2000; Francis 2006a; Kyne *et al.* 2011). The *A. pallidus* ovarian fecundity was also lower than that of two close relatives further south in Queensland (Kyne *et al.* 2011). However, these relatives were both larger bodied and the *A. pallidus* fecundity was similar to another small sized deepwater catshark, *B. dawsoni* (Francis 2006a). For *H. lemures*, the ovarian fecundity range was similar to other chimaerids for which it has been reported (Moura *et al.* 2004; Barnett *et al.* 2009a). Although all these bycatch species generally have low productivity, they present a variety of reproductive types and lengths of cycles that likely lead to varying degrees of resilience. This was apparent even within a genus, for e.g. both urolophids had low fecundity but *U. piperatus* likely has an annual cycle whereas *U. bucculentus* is biennial and so is probably less resilient to fishing pressure. This highlights the need for species to be individually assessed to accurately determine their productivity and susceptibility to commercial fishing.

Fishery effects

The majority of deepwater chondrichthyans taken as bycatch in this study were caught outside the main trawl grounds. This is not unexpected as the Swain Reefs EKP fishery is generally concentrated on the shelf, with some fishing on the upper slope habitat. Most observations of deepwater species on the shelf were of *D. polyommata* which dominated the bycatch. Skates are susceptible to capture by trawl gear (Ebert and Sulikowski 2007) and a closely related skate, *D. endeavouri* was also the most dominant species in the bycatch of the deepwater EKP fishery further south in Queensland (Courtney *et al.* 2007).

The fishery interacted with all life stages of *D. polyommata*, from newly hatched juveniles to mature and gravid adults with no sexual, maturity or length segregation evident. This lack of spatial segregation has been observed in temperate Australian *Dipturus* species and is common among other Rajiformes (Ebert 2005; Ebert *et al.* 2008a; Treloar 2008). Although this increases the potential impact of the fishery on *D. polyommata*, of all the deepwater chondrichthyans

encountered, *D. polyommata* may be more resilient to fishing pressure as it grows moderately fast, has moderate longevity and a continuous reproductive cycle (Chapter 4). This combination of traits in other small skates has been linked to increased resilience to fishing pressure (Frisk *et al.* 2002). *Dipturus polyommata* also has refuge in deeper waters and to the north of the Swain Reefs, as the fishery is at the southern edge of the species' range.

Another dominant bycatch species, *A. pallidus* consisted mostly of adults with limited numbers of immature specimens captured and other than the neonate, no animals <314 mm L_{ST} were taken. Two other species of catshark, including *A. rubiginosus*, were dominant in the bycatch of deepwater EKP fishery further south where there was also a lack of immature specimens (Courtney *et al.* 2007; Kyne *et al.* 2011). Gear selectivity was discounted as the cause of small individuals, as the small trawl mesh should retain small sharks. This suggests that immature animals may occupy deeper waters than adults (Kyne *et al.* 2011). Conversely, where length segregation has been observed in other catsharks, the young are usually shallower than adults (Richardson *et al.* 2000; Capapé *et al.* 2008) and their absence in trawls has been attributed to their movement up into the water column after birth (Ebert *et al.* 2006). Despite mostly adult *A. pallidus* being captured in the EKP fishery, this species also has a refuge in deeper waters and although it has a restricted distribution in offshore waters of Queensland, it also has refuge to the north of Swain Reefs because, similar to *D. polyommata*, the fishery is at the southern edge of the species range.

The other three species with distributions restricted to waters offshore of Queensland, *P. delicatus*, *M. walkeri* and *U. piperatus* all have refuge outside the fishery both spatially and at depth and were also all infrequently caught. However, the *M. walkeri* life history traits of slow growth, late maturity, high longevity and small litters (Chapter 4) are associated with a reduced capacity to recover from exploitation (García *et al.* 2008; Simpfendorfer and Kyne 2009). The *U. piperatus* also likely has low productivity because despite the continuous and possibly annual reproductive cycle, litters were small and high abortion rates on capture were evident and are typical of urolophids and can lead to reduced population viability (White *et al.* 2001; Trinnie *et al.* 2012). The likely low productivity of these deepwater chondrichthyans highlights the need to monitor catches of these species within the trawl fishery.

Two of the other deepwater chondrichthyans encountered that have broader Australian distributions, *U. bucculentus* and *S. albipunctata* are listed as Vulnerable on the IUCN Red List of Threatened Species due to heavy fishing pressure in the southeast Australia and documented declines in abundance (Graham *et al.* 2001; Pogonoski and Pollard 2003; Last and Marshall

2006). *Squatina albipunctata* has depth refuge from the deepwater EKP fishery and was caught infrequently however, this study has shown they have small litters and likely a non-continuous breeding cycle which indicates low biological productivity. The depth distribution of *U. bucculentus* (65-265 m) does not provide refuge from the Swain Reefs deepwater EKP trawl fishery. This study extended the known distribution of *U. bucculentus* from southern Queensland further north to Swain Reefs and while it has not been previously reported from the deepwater EKP fishery (either at the Swain Reefs or further south), *U. flavomosaicus* has been recorded, which was the field identification of *U. bucculentus* in this study. This study provides some evidence that *U. flavomosaicus* may not occur in eastern Australia, with the patterned form present in Queensland probably a colour variant of *U. bucculentus*. As *U. bucculentus* also occurs on the shelf in shallower depths it may be exposed to fishing pressure from other sectors of the Queensland East Coast Otter Trawl Fishery. However, it has not yet been recorded as a bycatch of the fishery, nor has *U. flavomosaicus* (Courtney *et al.* 2007; Pears *et al.* 2012).

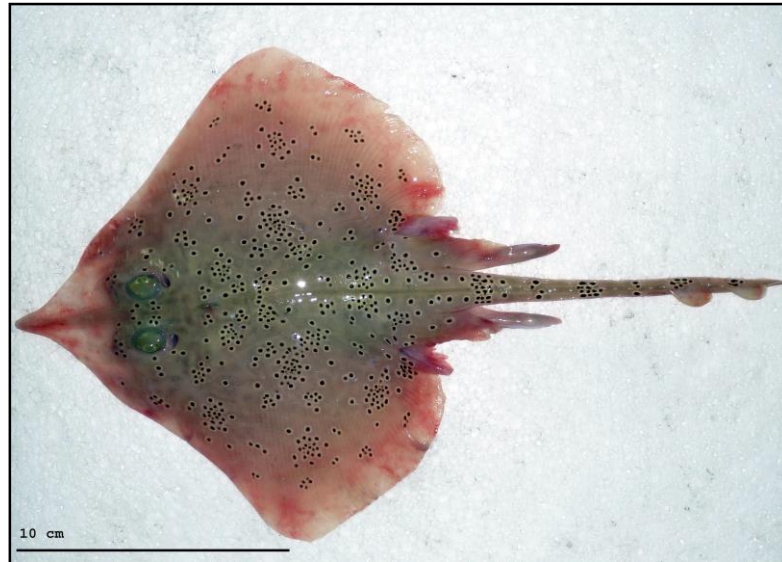
One of the shelf species captured in this study, *B. colcloughi* is listed as Vulnerable on the IUCN Red List due to its rarity of occurrence and restricted spatial and bathymetric distribution within mainly inshore waters of Queensland that are subject to a range of fisheries (Compagno *et al.* 2009). This study extended the known depth range of this species and indicated it may not be as rare as originally believed as it was the second most commonly captured shelf chondrichthyan.

The deepwater chondrichthyans bycatch observed in this study may not be fully representative of all species that occur in the deepwater EKP fishery trawl grounds as there were only two sampling occasions and the trawl gear may have caused length selective sampling bias. This could have affected both the lengths of species collected and the species composition as some larger deepwater chondrichthyans may have been excluded by the Turtle Excluder and Bycatch Reduction Devices, that generally allow animals over 1000 mm in length to escape the net (Brewer *et al.* 2006; Courtney *et al.* 2014).

This study has increased the knowledge of the life history of deepwater chondrichthyans taken as bycatch of the Swain Reefs deepwater EKP fishery and present in the southern GBRMP. The species all have life history traits typical of deep habitats and indicative of low biological productivity, though variability in their life history and distributions result in varying degrees of resilience to fishing pressure. This highlights the need for each species to be individually assessed for risk from the fishery. More information is required on the catches of some species

to ensure their sustainability. As such, ongoing monitoring of the deepwater chondrichthyan species taken as bycatch within the deepwater EKP fishery is recommended.

Chapter 4 Life history of two deepwater elasmobranchs endemic to the Great Barrier Reef: Argus skate *Dipturus polyommata* and eastern spotted gummy shark *Mustelus walkeri*



Argus skate *Dipturus polyommata* and eastern spotted gummy shark *Mustelus walkeri*

Rigby, C.L., White, W.T., Simpfendorfer (in review) Life history of two deepwater elasmobranchs endemic to the Great Barrier Reef: Argus skate and Eastern spotted gummy shark. *Journal of Fish Biology*.

4.1 Introduction

The Great Barrier Reef Marine Park (GBRMP) has one third of its area in deepwater and elasmobranchs encountered as bycatch in fisheries that operate in these areas have been identified as a priority for research. There is a general lack of data on these species and as such they are considered at risk as a precaution due to inherent vulnerability of deepwater elasmobranchs (GBRMPA, 2009: 2014). *Dipturus polyommata* and *M. walkeri* are two such species that both occur in GBRMP waters and are taken as bycatch in trawl and line fisheries (Pears *et al.* 2012). They are endemic to eastern Australia with sympatric restricted distributions. There is no published information on their life histories. *Dipturus polyommata* is a small skate found in a restricted area of tropical north Queensland from about Rockhampton to Townsville, and possibly further north, that inhabits the outer continental shelf and upper continental slope in depths of 135–320 m (Last and Stevens 2009). Historically, it has been confused with the *D. endeavouri* which occurs further south. These species were separated based on subtle morphological and colour differences (Last 2008). Biological and distributional information available for *D. polyommata* from southern Queensland (Courtney *et al.* 2007; Kyne *et al.* 2008) are referable to *D. endeavouri*.

Mustelus walkeri is currently known to occur from Moreton Island in southern Queensland to Hinchinbrook Island in northern Queensland. It is a demersal species, found on the continental shelf and the upper continental slope at depths of 52–403 m (White and Last 2008; Last and Stevens 2009). It is a relatively recently described species of gummy shark (genus *Mustelus*) that belongs to a subgroup of morphologically very similar white-spotted species which includes the *M. antarcticus* (southern Australia), western spotted gummy shark *M. stevensi* White & Last 2009 (northwestern Australia), Indo-West Pacific spotted estuary smooth-hound *M. lenticulatus* Philipps 1932 and starspotted smooth-hound *M. manazo* Bleeker 1855 (White and Last 2008).

Dipturus polyommata and *M. walkeri* are both captured in the deepwater eastern king prawn (EKP) trawl fishery which operates in the Swain Reefs area of the southern GBRMP. In a precautionary assessment, all deepwater elasmobranchs in this area were identified as at high risk due to potentially low resilience and the high trawl effort (Pears *et al.* 2012). The trawl fishery deploys turtle excluder and bycatch reduction devices in the nets that generally exclude larger elasmobranchs (greater than about one metre in length) but have a minimal effect on reducing the catch of the smaller sharks and rays. These devices were demonstrated to have no impact on the catch of the small *D. endeavouri* which is the closest relative of *D. polyommata* (Brewer *et al.* 2006; Courtney *et al.* 2007; Courtney *et al.* 2014). This deepwater EKP fishery is

currently the fishery with the highest effort that overlaps the distributional range of *D. polyommata* and *M. walkeri*.

Another trawl fishery that may have previously caught both species used to operate within the Commonwealth managed Coral Sea Fishery (CSF) that lies mostly to the east of their distribution with only partial overlap of their ranges. Any catches would have likely been minimal as the trawl effort was historically very low in the CSF and there has been no trawling since 2007 (Georgeson *et al.* 2014). The demersal line sector of the Coral Sea Fishery is still operational and while a line fishery is unlikely to interact with *D. polyommata* it may catch *M. walkeri*. Deepwater sharks have some level of protection in the Coral Seas Fishery; catch limits and the requirement that all deepwater sharks brought aboard live must be released alive were introduced in 2010 as precautionary management measures for sharks taken from below 200 m (AFMA 2010). The effort in the line sector of the fishery has been low since the implementation of these measures with only two active vessels and low catches of shark (approximately 1.7 tonne in 2011-12 and 2012-13) (Georgeson *et al.* 2014). This has made the effectiveness of these measures difficult to assess. The Coral Sea Fishery is currently under consideration for a Commonwealth Marine Reserve and depending on the outcomes, future harvest strategy trigger limits or bycatch mitigation measures such as best practice for handling of sharks may be implemented (AFMA 2012a). The other fisheries within the known range of these two species are the Queensland managed line fisheries (commercial, recreational and charter) in which *M. walkeri* has been recorded by observers and gummy sharks are a reported catch. Problems with species identification and logbook records, improved fishing technology and increasing deepwater effort have raised concerns for the sustainability of these fisheries (Sumpton *et al.* 2013).

Life history information is needed for the *D. polyommata* and *M. walkeri* to inform their management and assess their vulnerability to fishing pressure. *Dipturus polyommata* and *M. walkeri* both have restricted distributions that are sympatric and exposed to the same trawl fishery. However, they are from differing taxa with contrasting ray and shark morphologies. The present study provides the opportunity to describe and compare life histories of two contrasting deepwater taxa, relate the life histories to the potential effects of fishing, and assess whether they have differing resilience to fishing pressure.

4.2 Materials and Methods

4.2.1 Sampling

Specimens of *D. polyommata* and *M. walkeri* were obtained from the bycatch of commercial prawn trawlers operating at Swain Reefs in the deepwater EKP trawl fishery (Figure 4.1, Chapter 3). All *D. polyommata* and *M. walkeri* landed during the two, five week trawl sampling trips (June–July 2011 and March–April 2012) were retained and frozen whole. Queensland Fisheries observers donated 21 *D. polyommata* specimens collected from the same fishery in October 2010. All *D. polyommata* were collected over the depth range 135–280 m and *M. walkeri* over 124–242 m.

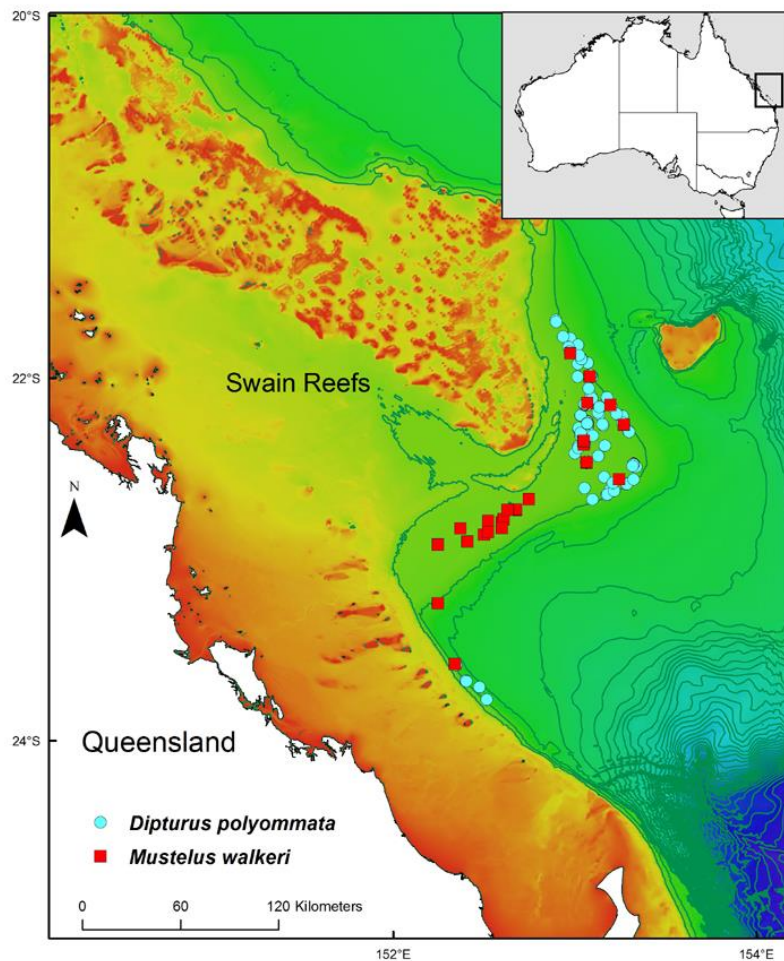


Figure 4.1 Sample locations with contours at 100 metre depth intervals.

4.2.2 Sample Preparation

All *D. polyommata* and *M. walkeri* were sexed, weighed (W_{BT}) (± 0.1 g) and measured for total length (L_T) and disc width (W_D) for *D. polyommata*, and stretched total length (L_{ST}) and fork length (L_F) (± 1 mm) for *M. walkeri* following Francis (2006b). Differences in the sex ratio were tested by a Chi-square test with Yates' correction. The relationships between L_T and W_D ,

and L_{ST} and L_F were examined using linear regression with differences in the slopes of the relationships between the sexes tested by analysis of covariance (ANCOVA). A segment of 8–10 vertebrae was excised from the anterior region of the abdominal cavity of *D. polyommata* and from below the first dorsal fin of *M. walkeri*. The neural and haemal arches were removed and the centra cleaned by trimming off cartilage and tissue after immersion in hot water for one minute. The centra were then soaked in 4% sodium hypochlorite for 5–20 minutes to remove any remaining tissue, rinsed thoroughly in tap water, air dried and stored in vials.

A number of stains and image analysis were tested to enhance visibility of the centra growth bands of both species: Alizarin red S (Officer *et al.* 1996), crystal violet and silver nitrate (Schwartz 1983), cobalt nitrate (Hoenig and Brown 1988; Gennari and Scacco 2007), ninhydrin (Davenport and Stevens 1988), nitric acid (Correia and Figueiredo 1997), and Mayer's haematoxylin (modified technique of Bublely *et al.* (2012). Sagittal sections (~ 300 μm) from centra embedded in polyester resin were taken through the focus of the centrum using a low speed diamond blade saw, rinsed in tap water, air-dried then stained. For image analysis, sections were fixed to a glass slide using resin (Campana 2014). All sections were examined with a dissecting microscope (x10). The most effective treatment for growth band enhancement was silver nitrate for *D. polyommata* and crystal violet for *M. walkeri* and these respective stains were applied to all centra sections of each species. Centra of neonate and *D. polyommata* less than 200 mm L_T were <1.0 mm diameter and too difficult to section. They were so small that they remain joined through the cleaning process and the segment of five cleaned centra were fixed longitudinally to slides with Crystal Bond™ and sanded using successively finer grades of 3M™ aluminium oxide lapping film to just above the focus, heated, turned over and sanded till they were readable (McPhie and Campana 2009). They were then stained with silver nitrate.

4.2.3 Age estimation

Centrum sections were placed in distilled water and examined under a dissecting microscope (10x) using transmitted light. Ages were estimated by counting the pairs of alternating translucent and opaque bands along the corpus calcareum (Cailliet and Goldman 2004). The birth mark (age zero) was evident in both species as a change in the angle on the corpus calcareum. The opportunistic nature of the sampling precluded verification of band pair deposition periodicity and as there were no previous age studies of *D. polyommata* or *M. walkeri*, it was assumed that band pairs formed annually. This assumption was made for *D. polyommata* as another Australian deepwater *Dipturus* species and other deepwater rajids have been verified as having annual band pair deposition (Zeiner and Wolf 1993; Sulikowski *et al.*

2005; Matta and Gunderson 2007; Natanson *et al.* 2007; Treloar 2008; Aversa *et al.* 2011). It was made for *M. walkeri* as annual band pair deposition has been verified for three closely related Australian and Indo-West Pacific *Mustelus* species (Moulton *et al.* 1992; Yamaguchi *et al.* 1998; Francis and Maolagáin 2000).

The sections were read three times by a single reader without prior knowledge of L_T , L_{ST} , sex or previous counts. A subjective readability score was noted for each centrum section with '1' indicative of very high readability and '5' low readability (Chapter 5, Table 5.1). To accept a band count for age estimation, the counts of at least two of the three readings had to be identical and the readability score ≤ 3 (Officer *et al.* 1996). Within-reader precision was assessed by average percentage error (APE; Beamish and Fournier 1981). A second reader read a random subsample of 42 *D. polyommata* and 17 *M. walkeri* to evaluate between-reader precision and bias, calculated by APE and age bias plots (Campana *et al.* 1995). If the second reader count was >3 years different to the first reader, the second reader did another count with both second reader counts included in the evaluation of between-reader precision. To determine whether vertebral growth was proportional to somatic growth, the radius of each sectioned centrum was measured to the nearest 0.1 mm from the focus to the distal margin of the corpus calcareum and plotted with L_T (*D. polyommata*) and L_{ST} (*M. walkeri*).

4.2.4 Growth estimation

To determine the most appropriate growth model for each species, a multi-model approach was used as is recommended for modelling elasmobranch growth (Cailliet *et al.* 2006; Thorson and Simpfendorfer 2009). Three *a priori* candidate growth models were fitted to the length at age data for the separate sexes and the combined sexes of each species; the three parameter version of the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), the logistic function (Ricker 1979) and the Gompertz function (Gompertz 1825; Ricker 1975) (Table 4.1). Each model represented an alternative hypothesis for growth and has frequently been used to model elasmobranch growth. The three models were fitted using a length at birth parameter (L_0) rather than age at zero length (t_0) as L_0 has greater biological meaning (Cailliet *et al.* 2006; Goldman *et al.* 2012) and can be directly compared between models. The asymptotic length (L_∞) was also common between models, but the three growth completion parameters, that is k (VBGF), g (logistic) and G and g (Gompertz) cannot be directly compared. The L_∞ was not a fitted parameter of the Gompertz function and was calculated from the other parameters after they were estimated:

$$L_\infty = L_0 e^G$$

where L_∞ is asymptotic length, L_0 is length at birth and G is instantaneous growth rate at L_0 (Ricker 1979; Smart *et al.* 2015).

Models were fitted using the method of nonlinear least squares regression using the statistical package ‘R’ (R Development Core Team 2014). Model performance was evaluated using bias corrected Akaike’s Information Criteria (AIC_c) (Katsanevakis 2006; Zhu *et al.* 2009) calculated as:

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

Where $AIC = n \log(\sigma^2) + 2k$, k is the total number of parameters +1 for variance (σ^2) and n is the sample size. The most appropriate model was that with the lowest AIC_c value (AIC_{min}). The two remaining models were ranked by the AIC difference (Δ) relative to the best model ($i = 1 - 3$), calculated for each model as:

$$\Delta_i = AIC_{c,i} - AIC_{min}$$

Models with Δ of 0–2 had substantial support, those with Δ of 4–7 had considerably less support and models with Δ of >10 had virtually no support (Burnham and Anderson 2001). Akaike weights (w_i) were also calculated as they represent the probability that the chosen model is the best model from the candidates (Burnham and Anderson 2001). The w_i were calculated as:

$$w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{j=1}^3 \exp(-\frac{\Delta_j}{2})}$$

Where j is an individual candidate model. To ascertain if models for separate or combined sexes were more appropriate for each species, the growth curves of males and females were compared using likelihood ratio tests (Kimura 1980) as implemented by Haddon (2001).

Table 4.1 The three a priori growth model candidate equations where L_t is length at age t , L_0 is length at birth, L_∞ is asymptotic length. VBGF k is the Brody growth coefficient, Logistic g is the instantaneous growth rate and Gompertz G is the instantaneous growth rate at time zero with g the exponential rate of decrease of G .

Model	Growth function equation
Von Bertalanffy growth function (VBGF)	$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt})$
Logistic function	$L_t = \frac{L_\infty L_0 e^{gt}}{L_\infty + L_0(e^{gt} - 1)}$
Gompertz function	$L_t = L_0(e^{G(1-e^{-gt})})$

4.2.5 Reproductive biology

All *D. polyommata* and *M. walkeri* were dissected to investigate their reproductive biology. Reproductive staging of both species was adapted from Ebert (2005) and Walker (2007). For both species males were classed as: immature when claspers were pliable and shorter than pelvic fins; adolescent when claspers extended past the pelvic fins but were still pliable; and mature if the claspers extended past the pelvic fins and were rigid and fully calcified. For both species females were considered: immature when follicles, uteri and oviducal glands were undeveloped; adolescent when follicles were developed but not yolked and uteri and oviducal glands were enlarged; and mature when yolked follicles and/or a fully formed oviducal gland were present. Estimates of population length (L_{T50}) and age at maturity (A_{50}) with 95% confidence intervals were determined for males and females separately using a generalised linear model with a binomial error structure and logit-link function within the statistical package ‘R’ (R Development Core Team 2014).

Differences in mature male and female reproductive condition between the three sampling times were investigated for *D. polyommata* (October 2010, June–July 2011 and March–April 2012). This was not possible for *M. walkeri*, as only one mature male and two mature females were collected. For *D. polyommata* males, the presence or absence of seminal fluid was noted, however the volumes were too small to be accurately measured. The testes and ovaries (W_G), stomach (W_S) and liver (W_L) were weighed (± 0.1 g). For mature individuals, two indices were calculated for each sampling time: Gonadosomatic Index ($I_G = 100 * W_G / \text{Total weight}$) and hepato-somatic index ($I_H = 100 * W_L / \text{total weight}$) where Total weight = $W_{BT} - W_S$ (Hamlett 1999). The differences in I_G and I_H between sampling times were tested by analysis of variance (ANOVA).

To describe the female reproductive cycle, the maximum width of the left uteri (± 1 mm), the weight of each ovary, the number of yolked follicles in each ovary and the maximum follicle diameter (D_{Fmax}) (± 1 mm) were recorded. In mature females, differences between the left and right ovary weight and number of yolked follicles were tested by a paired *t*-test. Relationships between the total length and total ovary weight (W_G), number of yolked follicles, and D_{Fmax} were examined by linear regression. Differences in D_{Fmax} and the number of yolked follicles between the three sampling times were tested by ANOVA. When present in *D. polyommata*, the number of egg cases and uterus (left or right) were noted, and the egg case length (L_{EC}) was taken following Ebert and Davis (2007). For *M. walkeri*, the number of embryos and the sex, presence of internal or external yolk, uterus (left or right), and total length (± 1 mm) of each embryo were noted.

4.3 Results

4.3.1 Specimen collection and length equations

A total of 768 *D. polyommata* was collected: 366 males (95–369 mm L_T) and 402 females (89–371 mm L_T). The sex ratio across all the trawls was not significantly different from parity ($\chi^2 = 1.60$, d.f. = 1, $p = 0.21$). From across the full size range, 253 males and 306 females were measured and dissected (Figure 4.2), with four males and three females lodged as voucher specimens at the Australian National Fish Collection (CSIRO). The relationship between L_T and W_D was significantly different between the sexes (ANCOVA, $n = 532$, $p < 0.001$) and was described for males and females by the equations: $L_T = 1.62 W_D - 13.54$ ($R^2 = 0.99$, d.f. = 243, $p < 0.001$) and $L_T = 1.51 W_D + 1.07$ ($R^2 = 0.99$, d.f. = 287, $p < 0.001$), respectively.

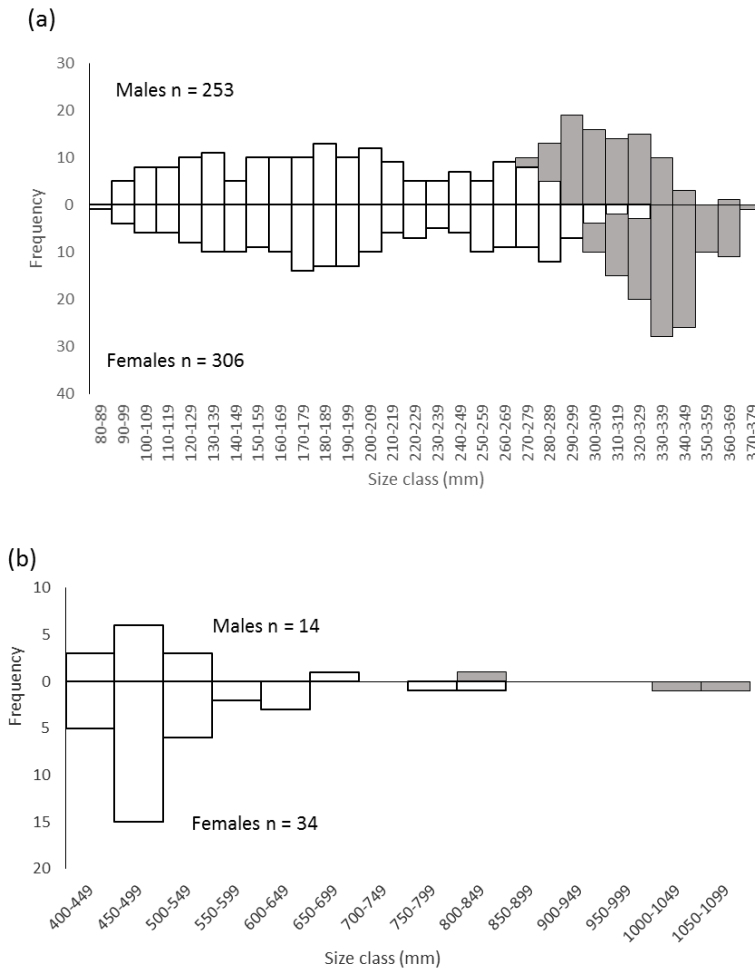


Figure 4.2 Size-frequency of immature (white) and mature (grey) (a) *Dipturus polyommata* and (b) *Mustelus walkeri* individuals.

A total of 48 *M. walkeri* was collected: 14 males (410–805 mm L_{ST}) and 34 females (410–1050 mm L_{ST}). The sex ratio across all trawls was significantly biased towards females (1:2.43, $\chi^2 = 7.52$, d.f. = 1, $p = 0.006$). Four males and five females were lodged as voucher specimens at the Australian National Fish Collection (CSIRO). The relationship between L_{ST} and L_F was not significantly different between sexes (ANCOVA, $n = 47$, $p = 0.80$) and for combined sexes was described by $L_{ST} = 1.15 L_F + 1.50$ ($R^2 = 0.99$, d.f. = 47, $p < 0.001$). The majority of the animals were immature with one mature male and two mature pregnant females collected (Figure 4.2). The mature male was captured in June 2011 at 132 m while the two pregnant females were both captured on the same night in April 2012, south of the main fishing grounds in deeper waters than most other *M. walkeri* at 214–262 m.

4.3.2 Age estimation

There was a positive linear relationship between centrum diameter and body length (sexes combined) for *D. polyommata* ($R^2 = 0.98$) and *M. walkeri* ($R^2 = 0.98$) (Figure 4.3), indicating the vertebrae of both species grew in proportion to the length of the animal.

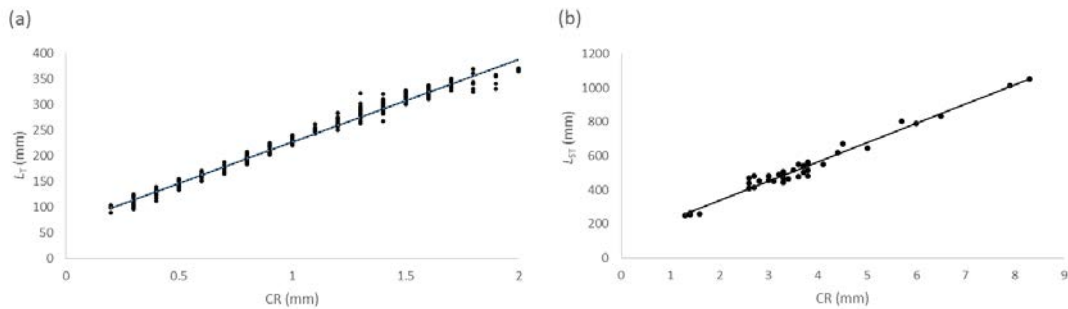


Figure 4.3 Relationship between centrum radius (CR) and (a) total length (L_T) for *Dipturus polyommata* ($L_T = 161.15CR + 65.94$, $R^2 = 0.98$, d.f = 210, $p < 0.001$) and (b) stretched total length (L_{ST}) for *Mustelus walkeri* ($L_{ST} = 113.61CR + 109.92$, $R^2 = 0.98$, d.f = 43, $p < 0.001$).

Dipturus polyommata

A subsample of 110 males and 110 females from across the full respective size ranges was used for age reading. Most centra had a readability score of 2 (51.4%). Within-reader precision of the three age estimates of each centrum was good with an APE of 5.6%. There was no systematic age estimation bias between readers (Figure 4.4) and between-reader precision was good with an APE of 4.8%. Nine centra age reads were discarded due to poor readability and lack of concordance of counts (5 males and 4 females), consequently the estimated age from 211 animals was used in the growth models: 105 males ranged from 0–10 years and 99–369 mm L_T and 106 females ranged from 0–10 years and 89–371 mm L_T .

Mustelus walkeri

In all, 39 animals and 5 near term pups (3 males and 2 females) were used for age reading. This was a subsample of the total 48 collected as 9 animals were lodged as voucher specimens. Within-reader precision of the three age estimates of the centra was good with an APE of 3.0%. There was no systematic age estimation bias between readers (Figure 4.4) and between-reader precision was good with an APE of 4.5%. The majority of centra (61%) had a good readability of 2 and there was concordance between counts, therefore the estimated age from all 44 specimens was used in the growth models: 13 males ranged from 0–9 years and 254–805 mm L_{ST} and 31 females ranged from 0–16 years and 250–1050 mm L_{ST} .

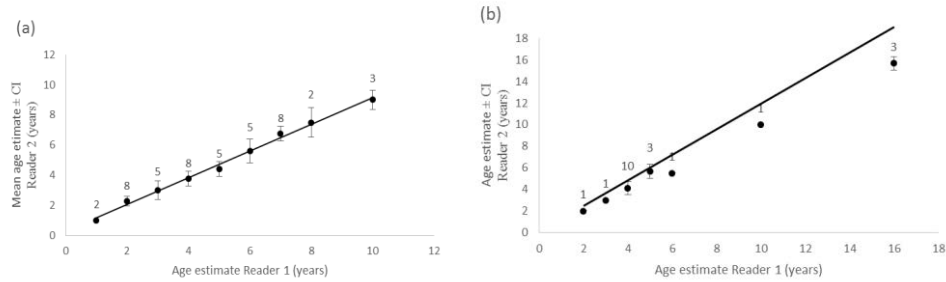


Figure 4.4 Age bias plots for the comparison of age estimates between readers for (a) *Dipturus polyommata* and (b) *Mustelus walkeri*. The solid line is the 1:1 relationship. Numbers above data points are sample sizes.

4.3.3 Growth estimation

Dipturus polyommata

The growth completion rates of males and females for each model were similar with no significant difference between the sexes ($\chi^2 = 6.92$, d.f. = 3, $p = 0.07$) (Table 4.2). For the combined sexes, the growth curves of the three models were very similar with the Gompertz model the most appropriate at the lowest AIC_C and $w_i = 97\%$ (Figure 4.5, Table 4.2). The VBGF was the least supported model, however since the growth curve was similar to the other models reference to the growth completion parameter of $k = 0.208 \text{ year}^{-1}$ (Table 4.2) was made for comparison to other *Dipturus* species age and growth studies. The estimated length at birth of all models (108–115 mm L_T) was similar and biologically realistic, as was the asymptotic length of $L_\infty = 358\text{--}412 \text{ mm } L_T$ (Table 4.2).

Mustelus walkeri

Length at age data from both sexes were combined due to the small sample size of males. All three growth models produced similar growth curves with the VBGF model as the most appropriate and best model with the lowest AIC_C , and $w_i = 72\%$ (Figure 4.5, Table 4.2). The VBGF growth completion parameter indicated relatively slow growth at $k = 0.033 \text{ year}^{-1}$ (Table 4.2) and had a biologically realistic length at birth of 273 mm L_{ST} . The VBGF asymptotic length was considerably larger than the maximums observed (1050 mm L_{ST}) and reported (1116 mm L_{ST}), respectively (White and Last 2008). While not statistically supported as the best fits for the data by the AIC_C and w_i , the Gompertz and Logistic models still had some support ($\Delta_i = 2.15$ and 5.76) and had biologically reasonable estimates of asymptotic length at $L_\infty = 1335 \text{ mm}$ and $L_\infty = 1165 \text{ mm}$, respectively (Table 4.2).

Table 4.2 Summary of model parameters and AIC_C results for the observed length at age data for *Dipturus polyommata* and *Mustelus walkeri*. n = sample size, AIC_C = small-sample bias adjusted form of Akaike's Information Criteria, Δ_i = difference in AIC_C values between models, w_i (%) = AIC_C weights, RSE = residual standard error, L_∞ = asymptotic length parameter in mm, L_0 = length at birth parameter in mm, k = growth rate parameter in year⁻¹ for the VBGF, g = growth rate parameter for Logistic model, G and g = growth coefficients of the Gompertz model. Only L_0 and L_∞ are comparable between the three models.

Sex	Model	n	AIC_C	Δ_i	w_i (%)	RSE	L_∞	L_0	k	G	g
<i>D. polyommata</i>											
Sexes combined	VGBF	211	1114.28	12.62	0.5	13.92	412	108	0.208	-	-
	Logistic	211	1108.78	7.12	2.5	13.74	358	115	-	-	0.528
	Gompertz	211	1101.66	0	97	13.51	375	112	-	1.212	0.365
Male	VGBF	105	560.64	8.67	1		416	115	0.204	-	-
	Logistic	105	551.97	0	66		354	120	-	-	0.531
	Gompertz	105	553.30	1.33	33		373	118	-	1.153	0.364
Female	VGBF	106	538.50	4.97	7.5		413	102	0.206	-	-
	Logistic	106	543.68	10.14	0.5		361	110	-	-	0.531
	Gompertz	106	533.53	0	92		376	106	-	1.269	0.366
<i>M. walkeri</i>											
Sexes combined	VGBF	44	293.35	0	72	26.62	2245	273	0.033	-	-
	Logistic	44	299.11	5.76	4	28.22	1165	295	-	-	0.205
	Gompertz	44	295.51	2.15	24	27.19	1335	284	-	1.547	0.119

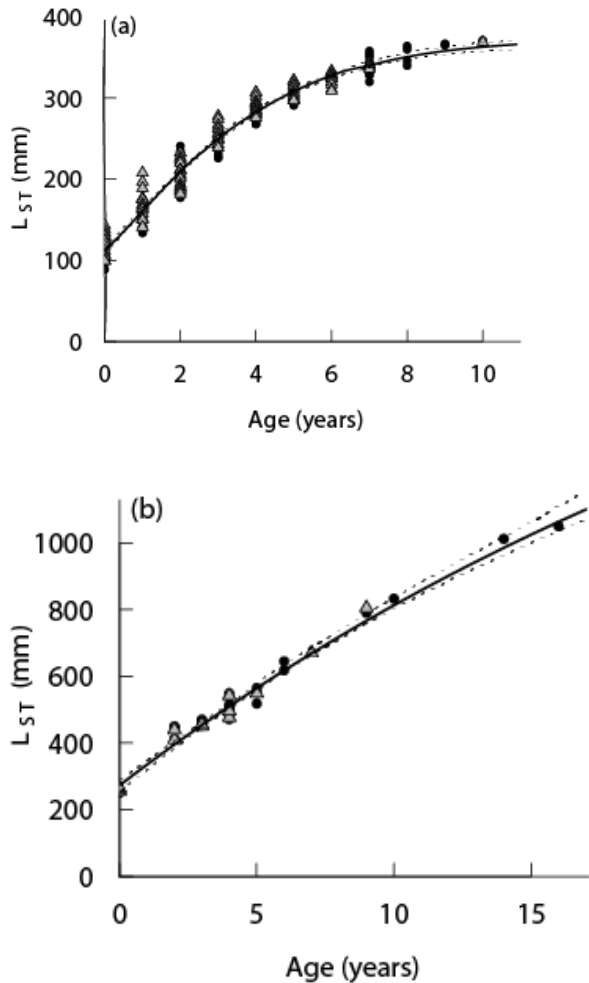


Figure 4.5 Growth models fitted to length at age data for combined sexes (male triangle, female circle) for (a) *Dipturus polyommata* Gompertz and (b) *Mustelus walkeri* VBGF. Dashed lines are 95% confidence intervals.

4.3.4 Maturity analyses

Dipturus polyommata

Length at maturity data were available for 253 males (95–369 mm L_T) and age at maturity data available for 105 males (0–10 years). The smallest and youngest mature male was 276 mm L_T and 4 yrs old. The largest and oldest immature male was 289 mm L_T and 4 yrs. Estimates of L_{T50} and A_{50} (with 95% CI) were 278.1 ± 6.9 mm and 4.0 ± 0.0 years, respectively (Figure 4.6).

Length at maturity data were available for 306 females (89–371 mm L_{ST}) and age at maturity data available for 106 females (0–10 years). The smallest and youngest mature female was 301 mm L_T and 4 years. The smallest gravid female was 307 mm L_{ST} . The largest and oldest immature female was 323 mm L_T and 6 yrs. Estimates of L_{T50} and A_{50} were 304.8 ± 7.0 mm and 5.1 ± 0.7 years, respectively (Figure 4.6).

Mustelus walkeri

It was not possible to determine estimates of L_{T50} and A_{50} for *M. walkeri* due to the limited number of mature males (1) and females (2). Males matured between 670–805 mm L_{ST} and 7–10 years old and reached adolescence between 549–670 mm L_{ST} and 5–7 years. Females matured between 833–1012 mm L_{ST} and 10–14 years old and reached adolescence between 645–790 mm L_{ST} and 6–9 years.

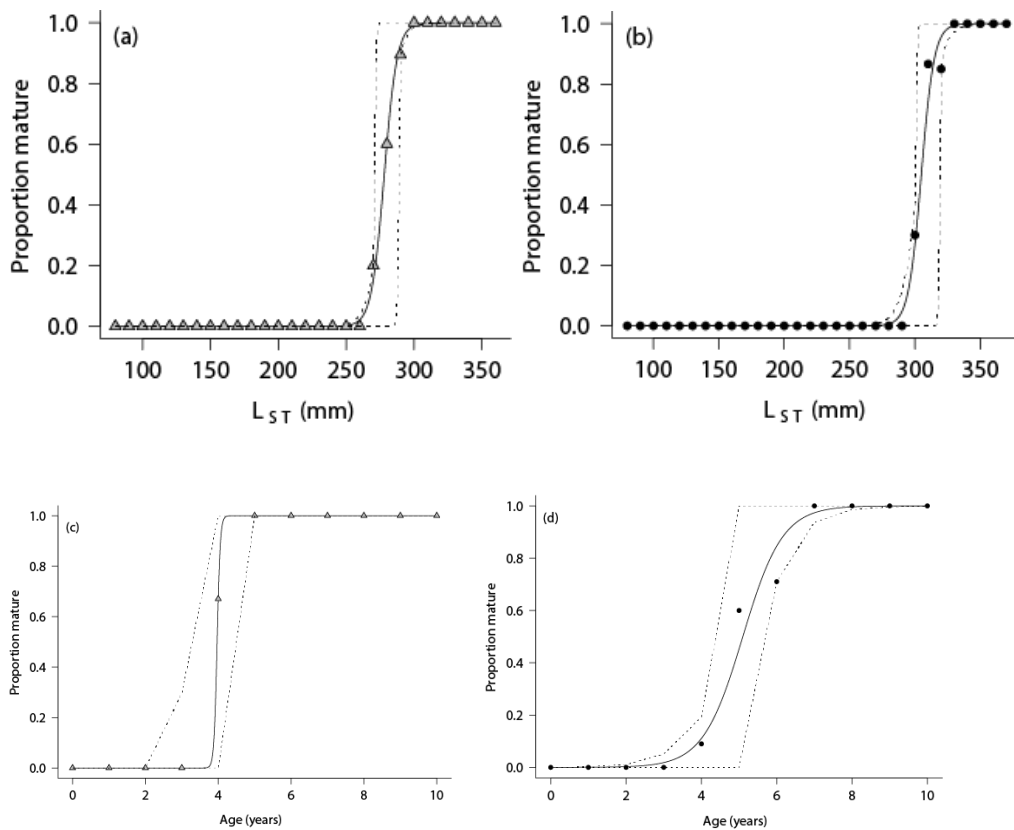


Figure 4.6 Length- and age-based maturity ogives for *Dipturus polyommata*: length at maturity (a) male and (b) female; and age at maturity (c) male and (d) female. Dashed lines are 95% confidence intervals.

4.3.5 Reproductive cycle and length at birth

Dipturus polyommata

Indices of reproductive condition tended to be lowest in October and highest in March–April among both mature males ($n = 84$) and females ($n = 112$). In June–July 2011 and March–April 2012, 50% of the mature males had seminal fluid present, but in October 2010 no mature males had seminal fluid present. For males, the I_G varied significantly between the three times being lowest in October and highest in March–April (ANOVA, $F_{2,81} = 3.11$, $p < 0.001$). The I_H was significantly lower in October than in June–July and March–April which were not significantly different (ANOVA, $F_{2,81} = 3.10$, $p < 0.001$). For females, the I_G in October and June–July was

not significantly different but was significantly lower than the I_G in March–April (ANOVA, $F_{2,109} = 3.08$, $p < 0.001$). The I_H varied significantly between the three times being lowest in October and highest in March–April (ANOVA, $F_{2,109} = 3.07$, $p < 0.001$). There was no significant difference in the MOD or number of yolked follicles between the three sampling times (ANOVA, $F_{2,105} = 3.08$, $p = 0.69$) and (ANOVA, $F_{2,105} = 3.08$, $p = 0.21$), respectively.

Both ovaries were functional and in mature females there was no significant difference between the left and right ovary in weight (paired t -test, d.f. = 105, $p = 0.21$) or number of yolked follicles (paired t -test, d.f. = 105, $p = 0.32$). The mean \pm s.e. total number of yolked follicles in both ovaries was 7.6 ± 0.2 (range 2–14). The left ovary contained an average of 3.9 ± 0.2 yolked follicles (range 1–10) and the right ovary 3.7 ± 0.2 yolked follicles (range 1–8). The ovary weight (M_G) and D_{Fmax} increased rapidly after maturity (Figure 4.7). In mature females there were significant relationships between M_G and L_T : $M_G = 0.19L_T - 53.24$ ($R^2 = 0.40$, d.f. = 111 $p < 0.001$); number of yolked follicles and L_T : no. yolked follicles = $0.07L_T - 16.36$ ($R^2 = 0.21$, d.f. = 105, $p < 0.001$); and D_{Fmax} and L_T : $D_{Fmax} = 0.17L_T - 36.63$ ($R^2 = 0.23$, d.f. = 111, $p < 0.001$).

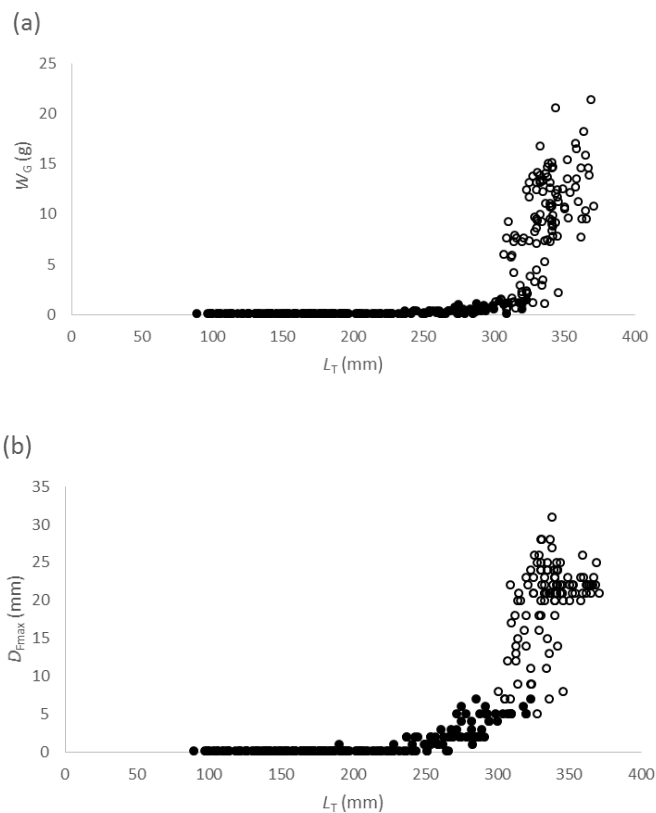


Figure 4.7 The relationship between total length (L_T) and (a) total ovary weight (M_G) and (b) maximum follicle diameter (D_{Fmax}) for immature (closed circle) and mature (open circle) females.

Females with egg cases *in utero* were collected on all sampling trips with a total of 11 collected. All gravid females had yolked follicles in their ovaries and had an egg case in each uterus, except for two specimens that only had an egg case in the left uterus. In the latter case, it is possible the egg case from the right uterus was aborted during capture. The egg cases were golden brown (Figure 4.8) and ranged in length from 41.5–58.8 mm L_{EC} and weight 3.5–8.3 g. There were no visible embryos within any of the egg cases and it was assumed there was one embryo per egg case, as is the case for all skates (except two *Raja* species) (Ebert and Davis 2007).

Length at hatching was deduced as 89–111 mm L_T from twelve specimens which were considered newly hatched as they had internal yolk sacs but no prey items in their stomachs. The smallest animals with food present were 98 mm L_T (with internal yolk sac) and 100 mm L_T (no internal yolk sac). Hence, size at first feeding was 98–100 mm L_T .

Mustelus walkeri

Only the right ovary was functional and yolked follicles were present in the only two mature females recorded, both of which were pregnant: 13 follicles with a D_{Fmax} of 11 mm in the 1012 mm L_{ST} female and 10 yolked follicles of D_{Fmax} 14 mm in the 1050 mm L_{ST} female. The smaller 14 year old individual had 7 uterine eggs in the uteri without macroscopically visible embryos, 4 in the left uterus and 3 in the right uterus. Each egg was contained in a golden brown, oval, transparent egg envelope (Figure 4.8) which measured 30.6–32.9 mm in length and weighed 5.8–7.1 g. The larger female (16 years) had 5 near term pups which all had umbilical scars and no external or internal yolk sac. There were 3 in the left uterus and 2 in the right uterus. They were 250–265 mm L_{ST} and were three males and two females.

(a)



(b)



Figure 4.8 (a) Egg case from a 352 mm L_T *Dipturus polyommata*. Anterior end at left of image (52.2 mm L_{EC}). (b) Uterine egg (32.1 mm in length) from the 1012 mm L_{ST} *Mustelus walkeri*.

4.4 Discussion

This study demonstrated that the sympatric *D. polyommata* and *M. walkeri* had different age and growth life history traits. *Dipturus polyommata* was relatively fast growing with a moderate observed longevity of 10 years and age at maturity of 4–5 years, traits typical of small-medium bodied skates from both shelf and deepwater habitats (Gallagher *et al.* 2005; Frisk and Miller 2006; Sulikowski *et al.* 2007b). *Mustelus walkeri* grew slowly with an observed longevity of 16 years and a likely age at maturity of 7–10 years. Some traits were not typical of *Mustelus* species, with the slower growth rates and later age at maturity a reflection of the greater depth of occurrence than most *Mustelus* and characteristic of deepwater habitats (Walker *et al.* 1998; Francis and Maolagáin 2000; Chapter 2). Slower growth, later age at maturity and higher longevity are associated with a reduced capacity to recover from exploitation (García *et al.* 2008; Simpfendorfer and Kyne 2009) and based on life history it is likely that *M. walkeri* is less resilient to fishing pressure than *D. polyommata* assuming that fishing mortality was the same between species.

Growth

For both species the length at age data fitted well to all three growth models with good quality age data that was precise with no systematic bias apparent in the age reading and low values of APE within and between readers (Beamish and Fournier 1981; Campana *et al.* 1995; Goldman *et al.* 2012). The Gompertz model provided the best statistical fit for *D. polyommata* which concurs with other batoid studies that found the Gompertz model characterizes the growth of skates and rays better than the von Bertalanffy growth function (Moura *et al.* 2007; Ainsley *et al.* 2011; Dale and Holland 2012). The Gompertz model estimated parameters were realistic with the size at birth of 112 mm similar to that observed and the L_{∞} of 375 mm likely as the maximum size of this species is reported at about 380 mm (Last and Stevens 2009). The lack of significant difference in growth rates between the sexes of *D. polyommata* was apparent in some, but not all other small skates species and there is no general trend for growth rates between the sexes of small–medium skates; where there are differences females typically grow more slowly than males (Treloar 2008; Cicia *et al.* 2009; Frisk 2010; Joung *et al.* 2011).

Dipturus polyommata is the smallest skate for which there are age and growth parameters and the growth rate, age at maturity and longevity aligned most closely with two other small–medium sized skates that inhabit deep water, the whitespotted skate *Dipturus cervia* (Whitely, 1939) and cuckoo ray *Leucoraja naevus* (Müller & Henle 1841). Both the von Bertalanffy and the Gompertz growth parameters were very similar to those for *D. cervia* (Treloar 2008).

Dipturus cervia is also endemic to Australia but from southern temperate waters where it is considered the most abundant skate in the Great Australian Bight (Last and Stevens 2009). Smaller skates and rays typically have faster growth rates, earlier age at maturity and shorter life spans than larger skates and are likely to sustain higher levels of exploitation (Frisk *et al.* 2002; Chapter 2). The age and growth parameters of *D. polyommata* were also similar to some small-medium shelf-dwelling rajids: longnose skate *D. confusus* Last 2008 (Australian endemic), little skate *L. erinacea* (Mitchell 1825), spotted ray *Raja montagui* Fowler 1910 and roundel skate *R. texana* Chandler 1921 (Gallagher *et al.* 2005; Frisk and Miller 2006; Sulikowski *et al.* 2007b; Treloar 2008). This suggests that the age and growth traits of the deepwater *D. polyommata* include some shelf habitat traits which is not surprising given their distribution encompasses shelf and upper slope waters.

Mustelus walkeri also occurs across shelf and slope waters, though it ranges deeper than *D. polyommata*. The growth was best represented by the VBGF model and while the *M. walkeri* sample size was small, there was a good representation of juvenile size classes and close to the

maximum reported size for this species was sampled, and back calculation techniques were not required (Smart *et al.* 2013). The Turtle Excluder Devices may have excluded the slightly larger animals and led to an under-estimate of the maximum age of *M. walkeri*. The model estimated parameters were realistic with the size of birth of 273–295 mm L_{ST} estimated for this species, as it was only slightly larger than the near term embryos and similar to that of another small white spotted species, narrownose smooth-hound *Mustelus schmitti* Springer 1939 (Massa *et al.* 2006). This size of birth is smaller than that of the congener *M. antarcticus*. There were insufficient male or female *M. walkeri* samples to fit separate growth models and maintain adequate size class representation. However, sexually dimorphic growth rates are usual among the *Mustelus* species with females generally growing more slowly than males particularly among older, mature sharks (Moulton *et al.* 1992; Goosen and Smale 1997; Yamaguchi *et al.* 1998). The combined sexes *M. walkeri* growth rate was slower than that of the male or female *M. antarcticus* and the *M. walkeri* male and female age at maturity greater and size at maturity smaller than those of *M. antarcticus* (Moulton *et al.* 1992; Walker *et al.* 1998; Walker 2007). Compared to all other reported *Mustelus* species, the *M. walkeri* growth rate was the slowest and the age at maturity greatest, except for the smooth-hound *Mustelus mustelus* (Lineaus 1758) that had an older female age of maturity (Yudin and Cailliet 1990; Goosen and Smale 1997; Walker *et al.* 1998; Francis and Maolagáin 2000; Conrath *et al.* 2002; Farrell *et al.* 2010a). Although the *M. walkeri* estimated age of maturity of 7–10 years was based on a limited number of mature animals it appears reasonable given elasmobranchs typically mature at 45–54% of their observed maximum age (Cortes, 2000; Chapter 2).

The longevity of *M. walkeri* was similar to the larger congener species *M. antarcticus*, *M. manazo* and *M. lenticulatus* (Yamaguchi *et al.* 1998; Francis and Maolagáin 2000; Pribac *et al.* 2005). Longevity among *Mustelus* is thought to generally increase with size (Francis and Maolagáin 2000), but the smaller *M. walkeri* defies this tendency. As size of carcharhiniform sharks typically decreases with increasing depth and *M. walkeri* had slower growth rates and later age at maturity that are aligned with deepwater habitat traits, *M. walkeri* probably spends the majority of its life cycle deeper than most other *Mustelus* species. The other *Mustelus* spend the greater part of their life cycle in shelf waters, even the three closely related species of similar longevity that are reported from depths greater than 200 m (Compagno *et al.* 2005; Kyne and Simpfendorfer 2010).

Reproduction

Sexually dimorphic size and age at maturity, where the females were larger and older than males at maturity, was common to both *D. polyommata* and *M. walkeri*. This is a characteristic

feature of elasmobranchs whereby females are considered to delay maturation to reach the larger size required to better support the production of offspring (Cortés 2000; Frisk 2010). Sexual dimorphism has been reported for many of the *Mustelus* species (Goosen and Smale 1997; Francis and Maolagáin 2000; Walker 2007; Segura and Milesi 2009; Farrell *et al.* 2010b). Among skates, sexual dimorphism in size at maturity (and maximum size) is quite variable and some suggest there may be no advantage for oviparous females to attain a larger size to produce larger young (Ebert *et al.* 2008a). However, there is a general trend for dimorphic maturity and maximum size to be more prevalent among the larger bodied skates (>1500 mm TL) and to be less common among the smaller skates (Mabragaña and Cousseau 2004; Ebert 2005; Ebert *et al.* 2008a; Treloar 2008). In contradiction of this trend, and similar to *D. polyommata*, some other small-medium bodied rajiids also exhibited sexually dimorphic maturity, including *D. cerva*, *D. confusus*, *L. erinacea* and *R. montagui* (Gallagher *et al.* 2005; Frisk and Miller 2006; Treloar 2008). One of these species, the small deepwater Australian endemic *D. cerva*, also lacked the dimorphism in maximum size and longevity that was apparent in *D. polyommata*. Among sharks, differences in maximum size and longevity between the sexes are much more usual for both small and large species and, similar to other *Mustelus* species (Smale and Compagno 1997; Francis and Maolagáin 2000; Conrath *et al.* 2002), it was evident in *M. walkeri*. Female *M. walkeri* attained a larger size and lived longer than males, which is considered an adaptive response for reproduction where the females partition more energy for reproduction than growth (Cortés 2000; Hussey *et al.* 2010).

Dipturus polyommata and *M. walkeri* both appear to have continuous reproductive cycles as yolked follicles were present in gravid and pregnant animals of both species. All gravid *D. polyommata* had mature follicles which indicated they may ovulate soon after oviposition. This has also been reported for the closely related *D. endeavouri* from southern Queensland waters and *D. cerva* and *D. confusus* from temperate Australia (Kyne *et al.* 2008; Treloar 2008). These temperate skates were reproductively active all year and it is common for many skates to display year-round egg production and deposition (Ruocco *et al.* 2006). This is likely the case for *D. polyommata* as gravid animals with fully developed egg cases were collected at all three sampling times, although there was also a suggestion of a peak in the reproductive cycle in March–April. The livers were larger and total ovary mass greater at that time. This indicated the potential for greater egg production during that time as the maternal liver produces yolk protein precursors that are taken up by the new developing follicles for the next reproductive cycle (Hamlett 1999). Further sampling across the year is needed for *D. polyommata* to substantiate the suggested peak. A reproductive cycle peak usually presents as greater egg production and has been reported for a number of skate species including the small bodied *L. erinacea*,

sandpaper skate *Bathyraja kincaidii* (Garman 1908) and zipper sand skate *Psammobatis extenta* (Garman 1913) (Rasmussen *et al.* 1999; Braccini and Chiaramonte 2002; Perez-Brazen *et al.* 2014). The strategy of an annual cycle with peaks has been proposed to be more limited to shelf species where environmental variability is greater than in deeper waters, however *B. kincaidii* is a deepwater species and more studies are required to confirm this habitat association (Ruocco *et al.* 2006; Ebert *et al.* 2008a).

Studies to date have found synchronicity between female and male skate reproductive cycles (Sulikowski *et al.* 2007a) and similar to the females, there was a peak in the reproductive cycle of male *D. polyommata* in March–April. Many skate males are able to mate year round (Treloar 2008) and as gravid females were present in October, the lack of reproductively active males in October may have been related to the limited samples and we suggest that male *D. polyommata* can likely mate all year. *Dipturus polyommata* was the least fecund of the *Dipturus* species for which ovarian fecundity could be compared. It had an average ovarian fecundity of 8 follicles compared to *D. endeavouri* (20), *D. cerva* (14) and *D. confusus* (16) (Kyne *et al.* 2008; Treloar 2008). *Dipturus polyommata* was smaller than the two southern Australian species which could account for the lower fecundity but it was of similar size to *D. endeavouri* and the reason for the difference in fecundity is not known. Two other small skates from the south-west Atlantic had very similar ovarian fecundity to *D. polyommata* with a fecundity of six for shortfin sand skate *Psammobatis normani* McEachran, 1983 and seven for smallthorn sand skate *Psammobatis rudis* Günther 1870 (Mabragaña and Cousseau 2004). The larger *D. polyommata* females potentially had higher fecundity as the number of yolked follicles increased with female size, which has also been found in *D. cerva* and some other skates (Ebert *et al.* 2008b; Treloar 2008). Size at birth in *D. polyommata* was similar to that of *D. endeavouri*, *D. cerva* and other small skates (Frisk and Miller 2006; Natanson *et al.* 2007; Kyne *et al.* 2008; Treloar 2008).

Reproductive mode among *Mustelus* species is divided into two groups: those without white spots that exhibit placental viviparity and those with small white spots that have aplacental viviparity with limited histotrophy (Walker 2007; Boomer *et al.* 2012). The near term pups in the pregnant *M. walkeri* had no internal or external yolk sacs and no umbilical cord which confirms *M. walkeri* as aplacental with limited histotrophy. With only two pregnant females we are cautious about comparisons of litter sizes but with litters of 5 and 7 from females near maximum known size for the species, the litter sizes are smaller than those of the closely related *M. antarcticus* and all other aplacental *Mustelus* species (Smale and Compagno 1997; Yamaguchi *et al.* 2000b; Francis 2003; Romero *et al.* 2007; Walker 2007; Segura and Milessi 2009; Farrell *et al.* 2010b). The *M. walkeri* continuous reproductive cycle is usual among

Mustelus which mostly breed annually, though in the closely related *M. antarcticus* this varies regionally with a biennial cycle in some areas (Walker 2007).

Resilience to fishing

Both *D. polyommata* and *M. walkeri* were captured in the deepwater EKP fishery at Swain Reefs yet their occurrence in the catch was markedly different with much larger numbers of *D. polyommata* captured than *M. walkeri*. Across the two sampling trips, *D. polyommata* was the most commonly caught elasmobranch at 46% of the total elasmobranch bycatch whereas *M. walkeri* was infrequently caught, accounting for 3% of the catch (Chapter 3). Skates are susceptible to capture by trawl gear (Ebert and Sulikowski 2007) and the closely related skate, *D. endeavouri* was also the most dominant species in the bycatch of the deepwater EKP fishery in an area further south in Queensland (Courtney *et al.* 2007). All size classes of these smaller skates are prone to capture by trawl gear and at Swain Reefs the entire size range of *D. polyommata* from newly hatched juveniles to mature and gravid adults were taken across the trawl grounds. No sexual, maturity or size segregation was evident in the sampled population with this lack of spatial segregation reported for the temperate Australian *Dipturus* species and common among other Rajiformes (Ebert 2005; Ebert *et al.* 2008a; Treloar 2008). It may be associated with the limited seasonal movement of most skate species (Dulvy and Reynolds 2002), however there are few studies to date in this area of skate life history. Spatial segregation and distinct nursery areas have been found for some other skate species with the segregation and movement linked to seasonal reproduction (Hoff 2008; Frisk 2010).

The small number of *M. walkeri* collected in this study preclude any definitive conclusion about their size and sex distribution. Sexual segregation and seasonal migrations are prevalent among the *Mustelus* that occur in coastal waters and also in the closely related *M. lenticulatus* that likely migrates to deeper water at times (Francis and Mace 1980; Francis 1989; Lenanton *et al.* 1990; Conrath and Musick 2012). No size segregation was apparent among *M. walkeri* at Swain Reefs as the only three mature individuals collected were all caught with immature animals but sexual segregation may occur at maturity; the mature male was in a different location from the two pregnant females that were both taken in an area deeper and to the south of where most *M. walkeri* were collected.

In the Swain Reefs area, the deepwater EKP fishery is limited in spatial extent and generally concentrated on the edge of the shelf, albeit there is some fishing on the upper slope habitat. The fishery interacts with all life stages of both *D. polyommata* and *M. walkeri* and though *D. polyommata* is likely more resilient to fishing pressure than *M. walkeri* as it grows faster,

matures younger and is shorter lived, it was much more frequently caught. However, the impact of the fishery on *D. polyommata* may be limited as the species has refuge in deeper waters and to the north of Swain Reefs as the fishery is at the southern edge of the species' range and probably the only fishery that currently captures *D. polyommata*. Consequently, *D. polyommata* is not likely currently at risk from fishing but with lower fecundity than the similar *D. cerva* in temperate Australia this could alter if fishing areas expanded. *Dipturus cerva* is also abundant though there are concerns for its sustainability as it is considered to have low productivity and its entire distributional range is exposed to demersal fishing pressure (Treloar 2008; Treloar 2009).

Mustelus walkeri was infrequently caught but the life history traits indicated it is less resilient to fishing pressure and with slower growth, later age at maturity and smaller litters it is probably less productive than both the closely related *M. antarcticus*, that is considered highly productive (Walker 1998). It is also likely to be less productive than other *Mustelus* species for which life history data are available, including the starry smooth-hound *M. asterias* Cloquet 1819, gray smooth-hound *M. californicus* Gill 1864, dusky smooth-hound *M. canis* (Mitchill 1815), spot-less smooth-hound *M. griseus* Pietschmann 1908, brown smooth-hound *M. henlei* (Gill 1863), *M. lenticulatus* and *M. manazo* (Francis and Mace 1980; Francis 1981; Yudin and Cailliet 1990; Yamaguchi *et al.* 1998; Cortés 2000; Francis and Maolagáin 2000; Yamaguchi *et al.* 2000a; Conrath *et al.* 2002; Conrath and Musick 2002; Frisk *et al.* 2005; Farrell *et al.* 2010b; Farrell *et al.* 2010a). When *Mustelus* species have been captured in unmanaged fisheries and all parts of their range fished, severe population declines have occurred, for example, as apparent for *M. schmitti* (Massa *et al.* 2006). However, under well managed fisheries some *Mustelus* species have been shown to support sustainable fishing and recovery after depletion, such as *M. antarcticus* and *M. lenticulatus* (Walker 1998; Francis 2003). While the current impacts of the deepwater EKP fishery to both *D. polyommata* and *M. walkeri* appear to be limited, any change in fishing practices in the Swain Reefs area that lead to an increase in catch susceptibility, such as expansion in area fished, could place both species at risk of depletion.

This study provides the first life history information for two sympatric elasmobranch species caught in a deepwater trawl fishery. The life history traits of *D. polyommata* were aligned with small deepwater skates and those of *M. walkeri* typical of deepwater sharks, but somewhat different to other *Mustelus* species. *Dipturus polyommata* was faster growing and shorter lived than *M. walkeri* and likely more resilient to exploitation, yet they both had low fecundity which could limit their potential for recovery if overfished. Both species are currently considered at low risk from the EKP fishery as *D. polyommata* is not exposed to fishing pressure across its

entire distributional range and *M. walkeri* is infrequently encountered, though more information is needed on *M. walkeri* capture in line fisheries to ensure its sustainability.

Chapter 5 Comparison of life histories of two deepwater sharks from eastern Australia: the piked spurdog and the Philippine spurdog



Piked spurdog *Squalus megalops* and Philippine spurdog *Squalus montalbani*

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5.1 Introduction

Dogfishes (Squaliformes) account for 46% of the deepwater chondrichthyan fauna (Kyne and Simpfendorfer 2010), are frequently targeted for their liver oil and taken as bycatch, and are among those species most affected by fishing (Compagno *et al.* 2005). This includes many *Squalus* species (squalids), and given that this group is one of the most taxonomically problematic (Last *et al.* 2007b) with regional variability evident in their age and growth parameters (Braccini *et al.* 2007), their effective management requires an understanding of the species-specific life histories at a regional scale.

Squalus megalops (Macleay, 1881) is a small squalid that is wide-ranging across the Atlantic and Indo-West Pacific and inhabits the shelf and upper continental slope in tropical and temperate waters to at least 732 m (Compagno *et al.* 2005). The wide-spread distribution and variability in morphometrics have raised the question whether there are different populations of *S. megalops* or whether it is a complex of similar species (Last and Stevens 2009), and until this is resolved, it is considered a single species. The medium-sized Philippine spurdog *S. montalbani* Whitley, 1931 occurs solely in the Indo-West Pacific and is restricted to the upper continental slope from 295–670 m in mainly tropical and subtropical latitudes (Last and Stevens 2009) of Australia, Indonesia and the Philippines. It was resurrected as a valid species in 2007, prior to which it was considered part of the *Squalus* ‘mitsukurii group’ (Last *et al.* 2007a). Hence, little is known of the life history of *S. montalbani*.

Studies of *S. megalops* life history to date indicate considerable regional variability in size, age and maturity. The populations from the Atlantic have a larger maximum size and size at maturity and are longer lived than populations from the Indo-West Pacific. However, across these oceans, populations from temperate regions have a similar age at maturity which is younger than that of the population from the subtropical Canary Islands (Table C.1 in Appendix C) (Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). Other life history parameters are common across regions including low growth rates, small litters and a 2-year reproductive cycle. The studies concur that *S. megalops* has low biological productivity and is a species vulnerable to the effects of fishing.

The demersal habit of both *S. megalops* and *S. montalbani* exposes them to capture by a variety of commercial fishing gear including trawl, Danish seine nets, gillnets, longlines and droplines (Graham *et al.* 2001; Braccini *et al.* 2007). *Squalus megalops* is a major bycatch in the Indian Ocean and the South Atlantic (Oliver *et al.* 2015). In Australia it is a significant bycatch in the Southern and Eastern Scalefish and Shark Fishery (SESSF) and a small bycatch component of

line and gillnet fisheries in the Coral Sea, Queensland and Western Australia (Graham *et al.* 2001; Furlani *et al.* 2007; Georgeson *et al.* 2014). It is also captured in the Queensland East Coast Otter Trawl Fishery (ECOTF) where the lack of information on squalids and other bycatch taken in the deepwater eastern king prawn sector of the ECOTF led to a precautionary assessment that trawling in that sector could pose a high risk to bycatch species and the habitat. (Pears *et al.* 2012). The sector operates within a poorly known upper slope habitat of the southern Great Barrier Reef Marine Park and there is need for further biological information to facilitate a more confident assessment of the fishery risks. *Squalus montalbani* is now rarely reported from Australian fisheries having suffered marked declines in the SESSF, although it may be taken in some Australian Commonwealth trawl fisheries and in relatively unmanaged deepwater demersal longline fisheries off Indonesia and the Philippines (Graham *et al.* 2001; White 2009; Sembiring *et al.* 2015).

Life history information is required for the tropical *S. megalops* population and *S. montalbani* to improve their regional management. To address this need, the aims of the present study were to: (1) describe and compare the life histories of the two squalids; (2) compare life history parameters of the tropical *S. megalops* population with temperate Australian and global populations; (3) consider the extent that differences in life history of the two species and regional differences within *S. megalops* were linked to depth and latitude; and (4) relate the life histories of the two species to the potential effects of fishing.

5.2 Materials and Methods

5.2.1 Sampling

Specimens of *S. megalops* were obtained from the bycatch of commercial prawn trawlers operating at Swain Reefs in the deepwater eastern king prawn sector (EKP) of the ECOTF (Figure 5.1, Chapter 3). All *S. megalops* landed during the two 5-week trawl trips (June–July 2011 and March–April 2012) were retained and frozen whole. They were collected over the depth range 187–280 m. The *S. montalbani* specimens were provided from a CSIRO research survey of gulper sharks along the upper slopes of New South Wales (NSW) onboard the F.V. Diana in September 2009. A subsample of the *S. montalbani* captured was retained and frozen whole from depths of 440–590 m (Figure 5.1). The fishing gear was auto-longline (1500 x 12/0 Mustad hooks per set) baited with squid and mostly set at approximately 0430 hours for a soak time of 2–4 hours (Williams *et al.* 2012).

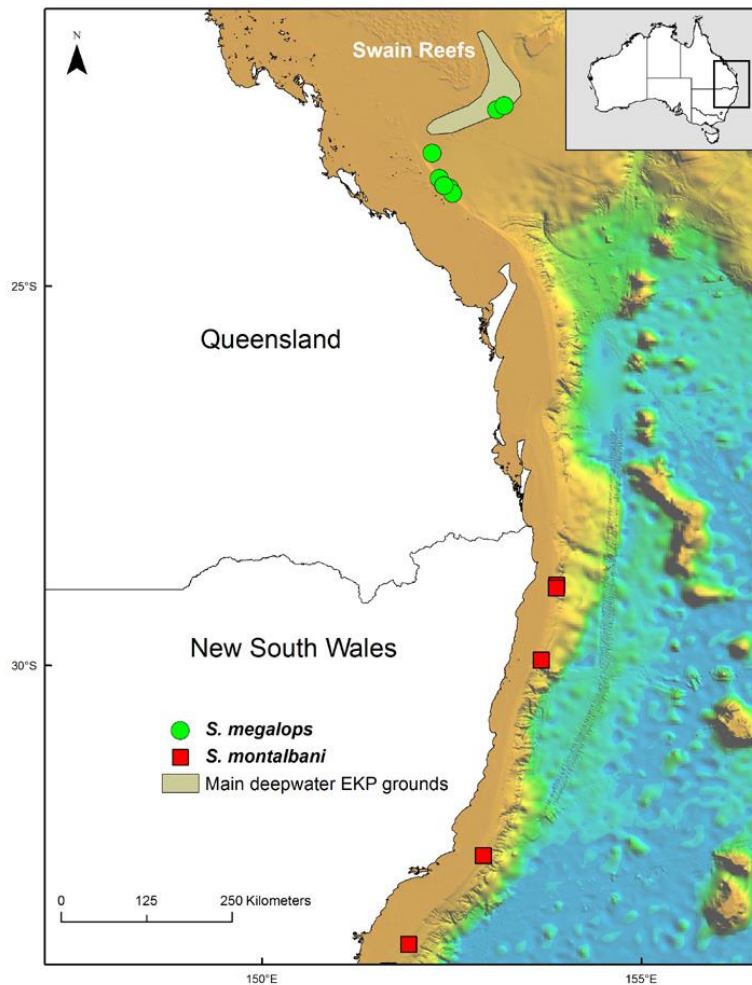


Figure 5.1 Sampling locations for *Squalus megalops* and *Squalus montalbani*. EKP, eastern king prawn sector.

Specimen Identification

Identification of *S. megalops* was confirmed by taxonomists at the Australian National Fish Collection, CSIRO Hobart (Tasmania, Australia) and by molecular techniques based on the structure of the NADH2 gene of two specimens (Naylor *et al.* 2012). To confirm the identification of *S. montalbani*, the denticles on a dorsal skin sample from each specimen were examined under a dissecting microscope to distinguish it from the morphologically similar greeneye spurdog *S. chloroculus* Last, White & Motomura 2007 (Last *et al.* 2007a) (K. Graham, Australian Museum, pers. comm., 2015).

5.2.2 Sample preparation

All *S. megalops* and *S. montalbani* were sexed, thawed, weighed (W_{BT}) (± 0.1 g) and measured for stretched total length (L_{ST}) and fork length (L_F) (± 1 mm) following Francis (2006b).

Differences in the sex ratio were tested by a Chi-square test with Yates' correction.

Relationships between L_{ST} and L_F were examined using linear regression with differences in the slopes of the relationships between the sexes tested by analysis of covariance ANCOVA. The entire first and second dorsal fin spines (DFS) were removed from each individual by making a horizontal cut just above the vertebral column to ensure the spine base and stem were intact (Beamish and McFarlane 1985; Irvine *et al.* 2006a). A segment of five vertebrae was excised from under the first dorsal fin of each individual and the neural and haemal arches removed. The retained centra and both DFS were cleaned by trimming off cartilage and tissue after immersion in hot water for 1 minute. The centra were then soaked in 4% sodium hypochlorite for 10–20 minutes to remove any remaining tissue and rinsed thoroughly in tap water. Both centra and DFS were air dried and stored in vials.

5.2.3 Age estimation

Many squalids have DFS with visible growth bands and these are generally the structure used to estimate age because the vertebrae tend to be poorly calcified and lack visible growth bands (Holden and Meadows 1962; Irvine *et al.* 2006b; Goldman *et al.* 2012). An enamel cap with visible growth bands covered a large portion of the DFS of both species. To ensure optimum readability and reliability of age estimation we investigated the other two growth band areas of DFS: the stem base and internal sections (Clarke and Irvine 2006). Base bands apparent on the DFS stem of *S. megalops* (but not *S. montalbani*), were enhanced by Alizarin Red S stain and appeared to match the number of bands on the enamel cap but they were not used for age estimation because, unlike the enamel cap bands, their annual deposition has not been verified. Braccini *et al.* (2007) found agreement between *S. megalops* internal DFS sections and external enamel cap band counts, and internal band counts have proved useful for other dogfishes (McFarlane and Beamish 1987; Tanaka 1990; Clarke *et al.* 2002a). Three *S. megalops* and three *S. montalbani* DFS were embedded in polyester resin and serial transverse sections (~ 300 μm) taken with a low speed diamond blade saw, rinsed in tap water, air-dried, resin mounted on glass slides and examined under a compound microscope (100 and 200x). Bands on the internal dentine layer of both species were clearest but were more difficult to read than the external enamel bands and so the age estimation of both species was done using the external enamel cap.

The bands were counted using reflected light and a dissecting microscope (x10), with a band defined as an alternating translucent and opaque zone or ridge, or both (Holden and Meadows 1962; Beamish and McFarlane 1985; Clarke and Irvine 2006; Braccini *et al.* 2007). The bands

and ridges on the enamel cap of *S. megalops* DFS were not as marked as those of the temperate Australian *S. megalops* population (M. Braccini, Western Australian Fisheries, pers. comm., 2014), although they became more distinctive after the enamel was rubbed with fine wet sandpaper and polished, as reported in other dogfishes studies (Watson and Smale 1999; Irvine *et al.* 2006b; Braccini *et al.* 2007). Sanding and polishing also highlighted the DFS bands and ridges of *S. montalbani*. Annual band pair deposition had been previously verified for temperate Australian *S. megalops* by enamel edge analysis of whole spines collected throughout the year, and comparison of internal and external band counts over the age range 1–28 years (Braccini *et al.* 2007). Because there were no previous age studies of *S. montalbani*, it was assumed that the enamel bands or ridges formed annually. This assumption was made because other squaloids have been validated or verified as having annual band deposition (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987; Campana *et al.* 2006; Coelho and Erzini 2007; Coelho and Erzini 2008). A subjective readability score was noted for each DFS, following Braccini *et al.* (2007) (Table 5.1).

Table 5.1 Readability scores for dorsal fin spine band counts (from Braccini *et al.* 2007).

Readability score	Definition
1	Band count unambiguous with clear bands
2	Band count unambiguous with bands of diminished clarity
3	Two band counts possible but indicated count most likely
4	More than two interpretations possible; count is best estimate
5	No band count possible; unreadable

The first and second DFS of two *S. megalops* full-term embryos were examined for pre-birth bands (no full term embryos of *S. montalbani* were collected) but none were observed. Thus, it was assumed that the first band was laid down just prior to or after birth, which has been reported previously for *S. megalops* (Braccini *et al.* 2007) and other dogfishes (Holden and Meadows 1962; Irvine *et al.* 2006a). Hence, the estimated age for both species was calculated as the total number of band counts minus one. To assess whether the first or second DFS was better for age estimation, a random subsample of first and second DFS from 68 *S. megalops* was read three times. Similar to Braccini *et al.* (2007), the first DFS of *S. megalops* had better readability scores and higher precision between readings (based on the index of average percentage error APE; (Beamish and Fournier 1981). Therefore, the first DFS was used for age estimation. *Squalus montalbani* had a high proportion of damaged first DFS, so the second DFS was used for age estimation.

The first DFS of *S. megalops* and second DFS of *S. montalbani* were read three times by a single reader without prior knowledge of L_{ST} , sex or previous counts. To accept a band count for age estimation, the counts of at least two of the three readings had to be identical and the readability score ≤ 3 (Braccini *et al.* 2007; Coelho and Erzini 2007). Within-reader precision was assessed by APE. A second reader read a random subsample of 40 *S. megalops* first DFS and 15 *S. montalbani* 2nd DFS to evaluate between-reader precision and bias, calculated by APE and age bias plots (Campana *et al.* 1995).

5.2.4 Growth estimation

To determine the most appropriate growth model for each species, a multi-model approach was used as is recommended for modelling chondrichthyan growth (Cailliet *et al.* 2006; Thorson and Simpfendorfer 2009). Three *a priori* candidate growth models were fitted to the length at age data for the separate sexes and the combined sexes of each species: (1) the three parameter version of the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938); (2) the logistic function (Ricker 1979); and (3) the Gompertz function (Gompertz 1825; Ricker 1975) (Table 5.2). Each model represented an alternative hypothesis for growth and has frequently been used to model elasmobranch growth. The three models were fitted using a length at birth parameter (L_0) rather than age at zero length (t_0) because L_0 has greater biological meaning (Cailliet *et al.* 2006; Goldman *et al.* 2012) and can be directly compared between models. The asymptotic length (L_∞) was also common between models, but the growth completion parameters, that is k (VBGF), g (logistic) and G, g (Gompertz) cannot be compared directly. The L_∞ was not a fitted parameter of the Gompertz function and was calculated from the other parameters after they were estimated as follows:

$$L_\infty = L_0 e^G$$

where L_∞ is asymptotic length, L_0 is length at birth and G is instantaneous growth rate at L_0 (Ricker 1979).

Models were fitted using the method of nonlinear least squares regression in the statistical package ‘R’ (R Development Core Team 2014). Model performance was evaluated using Akaike’s Information Criteria corrected for small sample size (AIC_c) (Katsanevakis 2006; Zhu *et al.* 2009) calculated as:

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

where $AIC = n \log(\sigma^2) + 2k$, k is the total number of parameters +1 for variance (σ^2) and n is the sample size. The most appropriate model was that with the lowest AIC_c value (AIC_{min}). The two

remaining models were ranked by the AIC difference (Δ) relative to the best model ($i = 1 - 3$), calculated for each model as:

$$\Delta_i = AIC_{c,i} - AIC_{min}$$

Models with a Δ of 0–2 had substantial support, those with a Δ of 4–7 had considerably less support and models with a Δ of >10 had virtually no support (Burnham and Anderson 2001). Akaike weights (w_i) were also calculated because they represent the probability that the chosen model is the best model from the candidates (Burnham and Anderson 2001). The w_i were calculated as:

$$w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{j=1}^3 \exp(-\frac{\Delta_j}{2})}$$

Where j is an individual candidate model. To ascertain whether models for separate or combined sexes were more appropriate for each species, the growth curves of males and females were compared using likelihood ratio tests (Kimura 1980) as implemented by Haddon (2001).

Table 5.2 Three a priori growth model candidate equations L_t , length at age t ; L_0 , length at birth; L_∞ , asymptotic length; VBGF, von Bertalanffy growth function; k , Brody growth coefficient; Logistic g , instantaneous growth rate; Gompertz G , instantaneous growth rate at time zero with g the exponential rate of decrease of G .

Model	Growth function equation
VBGF	$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt})$
Logistic function	$L_t = \frac{L_\infty L_0 e^{gt}}{L_\infty + L_0(e^{gt} - 1)}$
Gompertz function	$L_t = L_0(e^{G(1-e^{-gt})})$

5.2.5 Reproductive biology

All *S. megalops* and *S. montalbani* were dissected to investigate their reproductive biology. The reproductive staging of both species was determined using Braccini *et al.* (2007) modified indices of Walker (2005). Estimates of population length (L_{ST50}) and age (A_{50}) at maturity with 95% confidence intervals (CI) were determined for males and females separately using a generalised linear model with a binomial error structure and logit-link function within the statistical package ‘R’ (R Development Core Team 2014). These were used to determine the

life history invariant ratios of relative size (L_{ST50}/L_{STmax}) and age (A_{50}/A_{max}) at maturity (Dulvy and Forrest 2010; Chapter 2). Male maturity was based on clasper staging, because the claspers were the simplest to examine and Braccini *et al.* (2007) had found agreement for *S. megalops* between maturity ogives based on indices for claspers, vas deferens and gonad. For both species, males were classed as mature if the claspers were rigid and fully calcified with evident hooks. For females, Braccini *et al.* (2007) found *S. megalops* maturity ogives differed slightly between indices, although the criteria of large yolked follicles was preferred as an index of maturity because vitellogenesis was advanced and the ogive agreed with those of the other criteria. Hence, for the present study, females of both species were considered mature when large yolked follicles were present.

Because there were two sampling trips for *S. megalops*, differences in mature male reproductive condition between the two sampling trips was investigated. The presence or absence of seminal fluid was noted and the seminal vesicles weighed prior (W_{SV1}) and after (W_{SV2}) expression of spermatozoa. The testes (W_T), stomach (W_S) and liver (W_L) were also weighed (± 0.1 g). For individuals with seminal fluid present, three indices were calculated for each sampling trip, namely the: Gonadosomatic Index ($GSI = 100 * W_T / \text{Total weight}$), Hepatosomatic Index ($HSI = 100 * W_L / \text{Total weight}$) and proportion of spermatozoa within the seminal vesicle ($PS = 100 * (W_{SV1} - W_{SV2}) / W_{SV1}$) where total weight = $W_{BT} - (W_T + W_S + W_L)$ (Hamlett 1999; Awruch 2007; Awruch *et al.* 2009). The significance of differences in GSI, HSI and PS between trips were determined by ANOVA. The PS was also calculated for mature *S. montalbani*. To describe the female reproductive cycle, the maximum width of the left uteri (± 1 mm) was measured, the number of yolked follicles in each ovary counted and the maximum follicle diameter (D_{Fmax}) (± 1 mm) recorded. When present, the number of embryos and the sex, uterus (left or right), presence of internal or external yolk and total length (± 1 mm) of each embryo were noted.

5.3 Results

5.3.1 Specimen collection and length equations

In all, 422 *S. megalops* were collected: 117 males (253–407 mm L_{ST}), 304 females (261–505 L_{ST}) and one hermaphrodite (internal male, external female) (370 mm L_{ST}). One male and one female were lodged as voucher specimens at the Australian National Fish Collection (CSIRO). Most *S. megalops* were immature (Figure 5.2) and collected when the fisher was trialling the gear in three consecutive trawl shots at depths of 203–280 m south of the main EKP grounds (Figure 5.1). One of these shots captured 84 males (19 mature) and 225 females (18 mature, 4 of which were pregnant). Only 31 animals (15 males and 16 females, all immature) were

collected within the main EKP grounds. The sex ratio across all the trawls was significantly biased towards females (1: 2.6, $\chi^2 = 83.06$, d.f. = 1, $p < 0.0001$), however in the main EKP grounds, the sex ratio did not differ significantly from 1:1 ($\chi^2 = 0.06$, d.f. = 1, $p = 0.86$). The relationship between L_{ST} and L_F was significantly different between the sexes ($n = 420$, $p = 0.030$, ANCOVA) and was described for males by $L_{ST} = 1.129 L_F + 2.49$ ($R^2 = 0.99$, $p < 0.001$, d.f. = 117) and females by $L_{ST} = 1.128 L_F + 3.40$ ($R^2 = 0.99$, $p < 0.001$, d.f. = 301).

Ninety-eight *S. montalbani* were provided to this study: 58 males (370–920 L_{ST}) and 40 females (351–934 L_{ST}). The length-frequency was representative of the 465 *S. montalbani* captured in the CSIRO 2009 gulper survey where males ranged from 300–930 mm L_{ST} and females were 310–1110 mm L_{ST} (K. Graham, Australian Museum, pers. comm., 2015). The sex ratio did not differ significantly from 1:1 (1.4:1, $\chi^2 = 2.93$, d.f. = 1, $p < 0.08$) and the individuals were predominantly immature (Figure 5.2). The relationship between L_{ST} and L_F was significantly different between the sexes ($n = 97$, $p = 0.021$, ANCOVA) and was described by; $L_{ST} = 1.146 L_F - 0.512$ ($R^2 = 0.99$, $p < 0.001$, d.f. = 57) for males and by $L_{ST} = 1.138 L_F + 8.66$ ($R^2 = 0.99$, $p < 0.001$, d.f. = 39) for females.

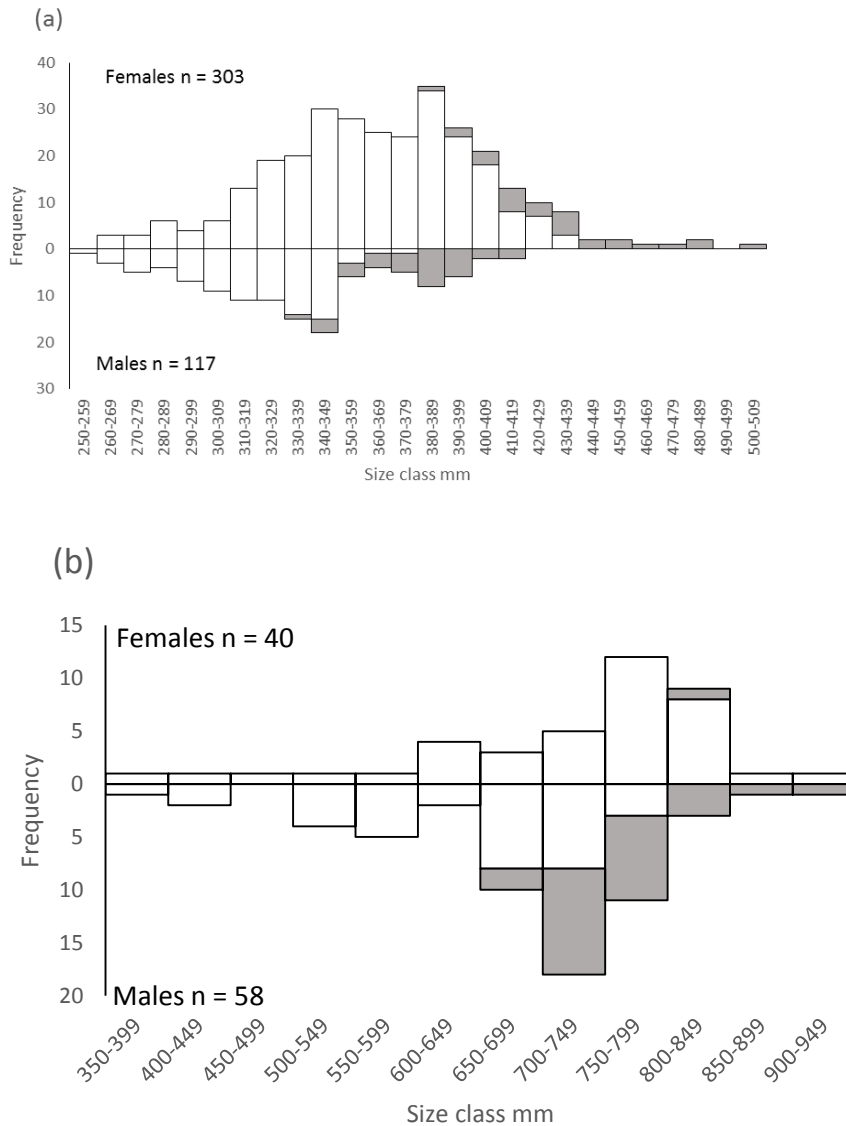


Figure 5.2 Size frequency of immature (white) and mature (grey) *Squalus megalops* (a) and *Squalus montalbani* (b) individuals.

5.3.2 Age estimation

Squalus megalops

Most first DFS had readability scores of 2 (33.8%) or 3 (60.3%) whereas the majority of the second DFS had poorer readability with scores of 3 (53.0%) or 4 (42.7%). The APE among readings was 4.00% for the first DFS and 5.32% for the second DFS. Of the 117 males, 17 had damaged first DFS and were not used for age reading. A subsample of the 304 female *S. megalops* from across the full size range was used for age reading with only whole spines used (no damaged, broken or worn spines). In all, 202 (100 male and 102 female) first DFS were read three times. Within-reader precision of the three age estimates was high with an APE of 3.66%. There was no systematic age estimation bias between readers (Figure 5.3) and between-

reader precision was good with an APE of 5.11%. Ten DFS were discarded because of poor readability and lack of concordance of counts (five males and five females); consequently, the estimated age from 192 animals was used in the growth models: 95 males ranged from 4 to 18 years and from 253 to 407 mm L_{ST} ; 97 females ranged from 5 to 25 years and from 262 to 505 mm L_{ST} .

Squalus montalbani

The second DFS was damaged in 14 animals. Unfortunately, this included the largest male of 920 mm L_{ST} and largest female of 934 mm L_{ST} . The second DFS of two animals had very worn enamel and these were also excluded from age reading. A few of the second DFS had slightly worn enamel on the top of the spines but the bands could still be read down the sides of the spines and were included in the age reading. In all, 82 (46 male and 36 Female) second DFS were read three times. The within-reader precision of the three age estimates was high with an APE of 4.60%. There was no systematic age estimation bias between readers (Figure 5.3) and between-reader precision was good with an APE of 5.43%. Five DFS (6.0 %) were discarded because of poor readability (readability ≥ 4) (four males, one female), therefore, 77 animals were used in the growth models: 42 males (5–28 years, 370–866 mm L_{ST}) and 35 females (3–27 years, 351–852 mm L_{ST}).

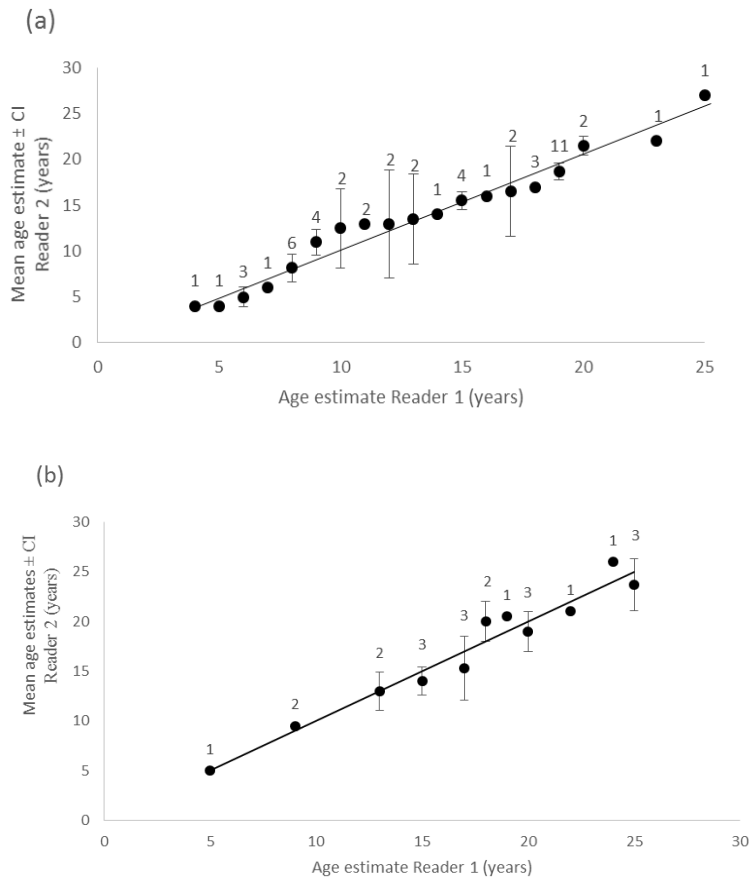


Figure 5.3 Age bias plots for the comparison of age estimates between readers for (a) *Squalus megalops* and (b) *Squalus montalbani*. The solid line is the 1:1 relationship. Numbers above the data points are sample sizes. Data show mean ($\pm 95\%$ confidence intervals) age estimates.

5.3.3 Growth estimation

Squalus megalops

The Gompertz growth model was the best fit for males and females with $w_i = 39\%$ for both sexes, although there was little difference in the performance of the three models for each sex and all models were well supported with $\Delta i < 1$ (Table 5.3). There was little variation in the estimates of length at birth and growth completion parameters between the models and two sexes, with only the estimates of L_∞ varying substantially for the males (Table 5.3). Likelihood ratio tests indicated no significant difference between the growth curves of the sexes (d.f. = 3, $\chi^2 = 2.26$, $p = 0.52$); hence the growth models for the sexes combined were considered the most appropriate. Of these, the VBGF was the best fit with the lowest AIC_c , though the Gompertz was also well supported ($\Delta i = 1.56$). The growth completion rate was very slow at $k = 0.003 \text{ year}^{-1}$ with almost linear growth which would account for the large value of L_∞ (3922 mm) that was biologically unrealistic (Table 5.3, Figure 5.3). There were no individuals less than 5 years of age collected, which may also have accounted for the larger estimate of L_0 (234 mm) (Table

5.3) than that observed from near term embryos (157 mm) (Table C.2 in Appendix C). Because the growth rate was close to linear, VBGF parameters should be used with caution when compared to other taxa.

Squalus montalbani

The male length at age data was best fitted by the logistic model at $w_i = 60\%$, and although there was little variation in the AIC_c performance of all three models, the Gompertz was more supported ($w_i = 30\%$ and $\Delta i = 1.33$) than the VBGF (Table 5.3). For females, the VBGF was the best fit, although all three models were well supported with comparable performance (Table 5.3). The L_∞ , L_0 and growth completion parameters between the respective male and female models were similar (Table 5.3) and the likelihood ratio tests indicated no significant difference between the growth curves of the sexes (d.f. = 3, $\chi^2 = 2.98$, $p = 0.39$). Consequently, the sexes combined model was used. All three growth models had similar performance, support and estimates of L_0 , although the Gompertz model had a marginally lower AIC_c value and was considered the best model at $w_i = 40\%$ (Table 5.3). The growth curve did not reach an asymptote (Figure 5.4), although the $L_\infty = 1285$ mm (Table 5.3) was biologically realistic compared to the observed maximums of 1010 mm (White and Dharmadi 2010) and 1110 mm from the CSIRO 2009 gulper survey (K. Graham, Australian Museum, pers. comm., 2015). L_0 (275 mm) (Table 5.3) was also biologically realistic because it was slightly higher than the size of near term pups reported from the CSIRO 2009 gulper survey of $L_0 = 234\text{--}235$ mm L_{ST} (Table C.2 in Appendix C).

Table 5.3 Summary of model parameters and Akaike's Information Criteria corrected for small sample size (AICC) results for the observed length at age data for *Squalus megalops* and *Squalus montalbani* n , sample size; Δ_i , difference in AICC values between models; w_i (%), AICC weights; RSE, residual standard error; L_∞ , asymptotic length parameter; L_0 , length at birth parameter; k , growth rate parameter for the von Bertalanffy growth function (VBGF); g , growth rate parameter for Logistic model; G and g , growth coefficients of the Gompertz model. Only L_0 and L_∞ are comparable between the three models.

Sex	Model	n	AICC	Δ_i	w_i (%)	RSE	L_∞ (mm)	L_0 (mm)	k (year ⁻¹)	G	g
<i>S. megalops</i>											
Sexes combined	VGBF	192	969.60	0	60	12.39	3922	234	0.003	–	–
	Logistic	192	972.75	3.15	12	12.50	855	243	–	–	0.046
	Gompertz	192	971.16	1.56	28	12.44	1249	241	–	1.646	0.021
Male	VGBF	95	445.80	0.28	34		3921	234	0.003	–	–
	Logistic	95	438.30	0.76	27		440	213	–	–	0.120
	Gompertz	95	437.25	0	39		455	207	–	0.788	0.093
Female	VGBF	97	518.45	0.28	34		3921	235	0.003	–	–
	Logistic	97	518.92	0.76	27		2202	252	–	–	0.031
	Gompertz	97	518.16	0	39		2323	247	–	2.240	0.014
<i>S. montalbani</i>											
Sexes combined	VGBF	77	478.78	1.15	22	21.89	3624	272	0.007	–	–
	Logistic	77	477.78	0.15	38	21.82	1079	287	–	–	0.082
	Gompertz	77	477.63	0	40	21.80	1285	275	–	1.54	0.046
Male	VGBF	42	274.48	3.57	10		3624	257	0.007	–	–
	Logistic	42	270.91	0	60		979	249	–	–	0.100
	Gompertz	42	271.04	1.33	30		1100	229	–	1.569	0.062
Female	VGBF	35	203.69	0	40		3628	285	0.007	–	–
	Logistic	35	204.58	0.89	25		1190	311	–	–	0.069
	Gompertz	35	203.94	0.25	35		1515	303	–	1.610	0.036

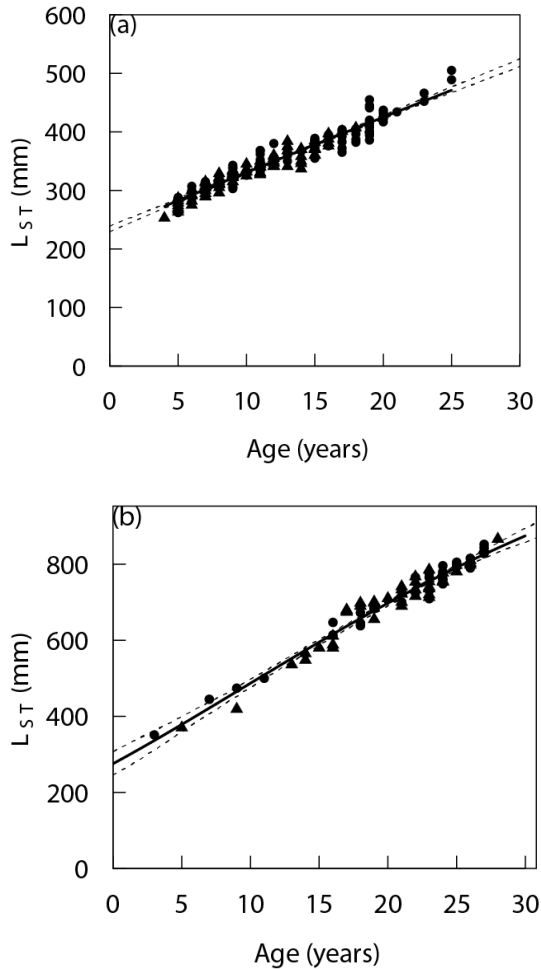


Figure 5.4 Growth models fitted to length at age data for combined sexes (triangles, males; circles, females) for (a) *Squalus megalops* von Bertalanffy growth function (VBGF) and (b) *Squalus montalbani* Gompertz. Dashed lines are 95% confidence intervals. L_{ST} , stretched total length.

5.3.4 Maturity analyses

Squalus megalops

Length and age at maturity data were available for 117 and 95 male *S. megalops*, respectively (253–407 mm L_{ST} and 4–18 years). The smallest mature male was 327 mm L_{ST} and the youngest mature male was 10 years old. The largest and oldest immature male was 370 mm L_{ST} and 14 years. Estimates of L_{ST50} and A_{50} (with 95% CI) were 352 (335, 370) mm and 12.4 (10.4, 14.5) years, respectively (Figure 5.5). Length and age at maturity data were available for 303 and 97 female *S. megalops*, respectively (261–505 mm L_{ST} and 5–25 years). The smallest mature female was 380 mm L_{ST} (not aged) and the youngest aged mature female was 18 years old (405 mm L_{ST}). The largest and oldest immature female was 436 mm L_{ST} and 20 yrs.

Estimates of L_{ST50} and A_{50} (95% CI) were 419 (400, 439) mm and 19.1 (17.5, 20.7) years, respectively (Figure 5.5).

Squalus montalbani

Length and age at maturity data were available for 58 and 42 male *S. montalbani* respectively (370–920 mm L_{ST} and 5–28 years). The smallest and youngest mature male was 674 mm L_{ST} and 17 years. The largest immature male was 785 mm L_{ST} and oldest immature 24 years.

Estimates of L_{ST50} and A_{50} (with 95% CI) were 700 (627, 783) mm and 21.8 (19.0, 24.0) years respectively (Figure 5.5). Although length and age data were available for 40 and 35 female *S. montalbani* respectively (351–934 mm L_{ST} and 3–27 years), this included only one pregnant female: 849 mm L_{ST} , not aged. Therefore, it was not possible to determine the female estimates of L_{ST50} and A_{50} . There were two females larger than the pregnant 849 mm L_{ST} , both of which were immature at 852 mm L_{ST} (27 years) and 934 mm L_{ST} (not aged).

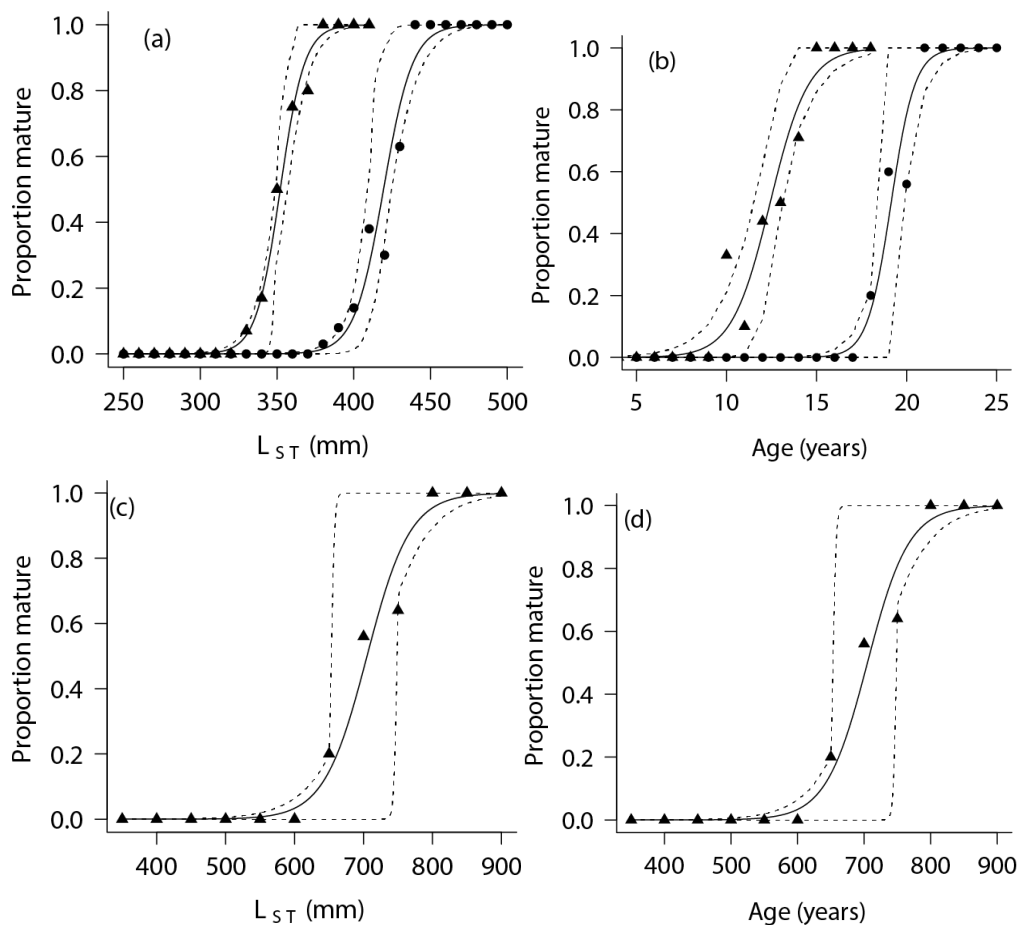


Figure 5.5 Length (a, c) and age at maturity (b, d) ogives for male (triangles) and female (circles). *Squalus megalops* (a, b) and *Squalus montalbani* males (c, d). Dashed lines are 95% confidence intervals.

Invariants

The invariants of relative size at maturity were similar for both male and female *S. megalops* (0.86 and 0.84 respectively) but larger than that of *S. montalbani* males (0.76). The relative age at maturity was high for both species at 0.70 and 0.76 for male and female *S. megalops* respectively and 0.87 for male *S. montalbani*.

5.3.5 Reproductive cycle and length at birth

Squalus megalops

Twenty seven of the 117 males collected had seminal fluid present (17 on the first trip and 10 on the second trip). There was no difference in the maturity condition of mature males between the two sampling trips, with similar values of mean GSI ($F_{1,25} = 4.24, p = 0.83$), HSI ($F_{1,25} = 4.24, p = 0.28$) and PS ($F_{1,25} = 4.24, p = 0.82$). Pregnant females were captured on both sampling trips with a total of 10 collected. The number of embryos ranged from two to three. One had near term embryos with umbilical scars and internal yolk sacs (Table C.2 in Appendix C). At 37.1% of the maternal L_{ST} it is likely they were close to length at birth, because Braccini *et al.* (2007) reported the temperate *S. megalops* mean length at birth as 38.5% (95% CI 35.6–42.4) of maternal total length. The remaining nine pregnant females all had candles with evident embryos and yolked follicles that at 12–14 mm in diameter, were smaller than the yolked follicles of maximum follicle diameter (D_{Fmax}) 32 mm in the female with near term pups (Table C.2 in Appendix C).

Although there were only limited data for mature and pregnant *S. megalops* females, a comparison of D_{Fmax} with uterus width for different phases of uterus development suggested a continuous reproductive cycle (Figure 5.6). The D_{Fmax} increased with uterus width for females ovulating for the first time (Uterus Index, UI = 1–3), with ovulation at a D_{Fmax} of ~ 35 mm. Pregnant animals had a smaller D_{Fmax} that increased with embryonic development (UI = 5a) to a size ready for ovulation when embryos were near term (UI = 5b) (Figure 5.6). The cycle is also likely asynchronous because not all mature females collected each trip were pregnant.

Squalus montalbani

Of the 58 males collected, 25 were mature and all but two had seminal fluid present with the proportion of seminal fluid at a mean (\pm se) of $50.5 \pm 2.7\%$. The one mature female was pregnant with a litter size of nine. Four other breeding *S. montalbani* have been recorded from

eastern Australian with litters of 6–16, with one of these litters near term at 234–245 mm and 29.3–30.6 % of maternal L_{ST} (Table C.2 in Appendix C).

The data were too limited to draw any definite conclusions about the female reproductive cycle. The D_{Fmax} increased with uterus width in immature females (UI = 1–2) and the pregnant female had developing yolked follicles (Table C.2 in Appendix C). Additional data for breeding females indicated one female of 800 mm L_{ST} with near term embryos and yolked follicles, whereas two larger pregnant females with less well developed embryos had no yolked follicles (Table C.2 in Appendix C).

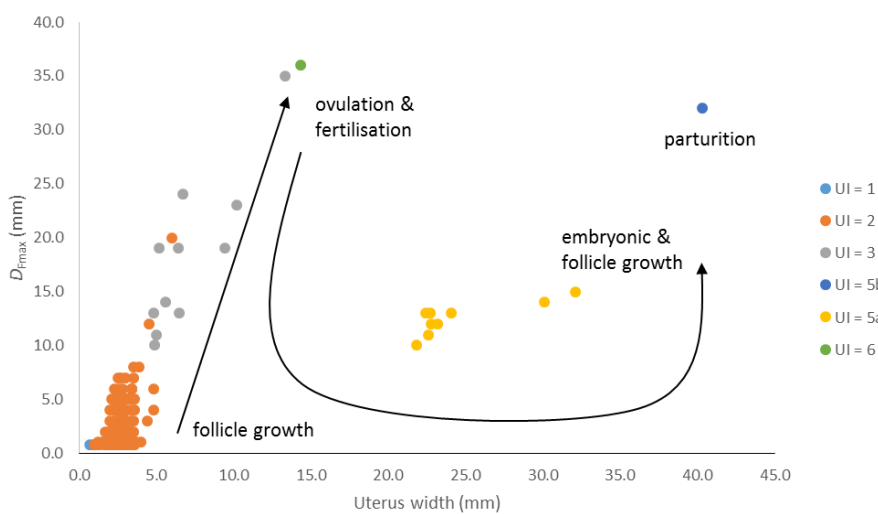


Figure 5.6 Relationship between maximum follicle diameter (D_{Fmax}) and uterus width for *Squalus megalops*. Uterus Index (UI) 1, 2 and 3, immature; UI 5a, developing embryo; UI 5b, near-term embryo; UI 6, *post partum*.

5.4 Discussion

The present study demonstrated that both *S. megalops* and *S. montalbani* are slow growing, long lived with a late age at maturity and mostly small litters. These conservative life history traits were similar to those reported in previous studies of *S. megalops* (Watson and Smale 1998; Watson and Smale 1999; Braccini *et al.* 2006a; Hazin *et al.* 2006; Braccini *et al.* 2007; Pajuelo *et al.* 2011), and are typical of deepwater squaloids (Compagno *et al.* 2005; Kyne and Simpfendorfer 2007; Graham and Daley 2011; Irvine *et al.* 2012) and deepwater chondrichthyans in general (Garcia *et al.* 2008; Barnett *et al.* 2013; Chapter 2). This combination of traits is indicative of low productivity and poor resilience to exploitation (Walker 1998; Morato *et al.* 2006b) which is of concern for both species. The deeper dwelling *S. montalbani* may be more vulnerable to fishing pressure than *S. megalops* because it was

found to be longer lived and matured later, which are life history differences associated with increasing depth and a reduction in the capacity to recover from exploitation (Garcia *et al.* 2008; Simpfendorfer and Kyne 2009; Chapter 2).

Growth

Both species exhibited almost linear growth with no evidence of an asymptote and a very slow growth completion rate. All three models examined fit the data well and produced very similar growth curves, for both males and females and sexes combined. The lack of difference in growth curves between the sexes is contrary to previous studies of *S. megalops* that have reported significant differences between growth of the sexes, although only for their later years (Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). Growth rates diverged between sexes at 10 years in temperate southeast Australian waters (Braccini *et al.* 2007) and 16 years in the Canary Islands subtropical waters (Pajuelo *et al.* 2011) when male growth slowed, whereas female growth increased steadily. It is possible that this divergence in growth rates does occur in the tropical population of *S. megalops* at a later age than sampled in the present study.

The lack of an asymptote in the growth curves of both species has occurred with other dogfishes, although usually only for females (Wilson and Seki 1994; Taniuchi and Tachikawa 1999; Cotton *et al.* 2011; Irvine *et al.* 2012), and, in one case, in both sexes (Cannizzaro *et al.* 1995). All previous growth studies of *S. megalops* also found fairly linear growth for females, but not for males (Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). The lack of an asymptote may be due to a paucity of older animals in the samples, which was the most commonly suggested reason by previous authors (Wilson and Seki 1994; Watson and Smale 1999; Braccini *et al.* 2007; Cotton *et al.* 2011). The lack of older *S. megalops* may have resulted from some degree of maturity segregation. Although there was some mixing of immature, mature and pregnant animals in the Swain Reefs area the majority of the samples were of immature animals. In addition, the commercial demersal otter trawl gear used to collect *S. megalops* possibly influenced the sizes collected and caused length selective sampling bias. The Turtle Excluder and Bycatch Reduction Devices, mandatory for trawl nets in the Australian tropics (Griffiths *et al.* 2006; Courtney *et al.* 2014), may have had an additional effect and excluded the larger *S. megalops*, although these devices generally only exclude larger sharks > 1000 mm in length (Brewer *et al.* 2006; Courtney *et al.* 2014).

Reproduction

The maximum age of *S. megalops* in the present study was 25 years which is less than that in temperate Australian waters, South Africa and the Canary Islands (Table 1) (Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). Comparisons with the Atlantic populations are treated with caution because the regional differences may be due to different populations or the possibility that *S. megalops* is a species complex (Compagno *et al.* 2005; Graham 2005; Last and Stevens 2009; Pajuelo *et al.* 2011).

The invariants of relative age at maturity also suggested that the oldest animals of *S. megalops* and *S. montalbani* were not aged, because the invariants were much higher than the average of 0.53 for deepwater chondrichthyans (Chapter 2), and invariants are known to be consistent across chondrichthyan taxa (Dulvy and Forrest 2010). Although specimens close to the maximum size of *S. montalbani* were provided to this study, the largest animals could not be aged because of their damaged dorsal fin spines. The 934 mm L_{ST} *S. montalbani* in the present study and the 1110 mm L_{ST} female captured in the CSIRO 2009 gulper survey were larger than the previously reported maximum of 910 mm for this species within Australia (Last and Stevens 2009) and 1010 mm for Indonesia (White and Dharmadi 2010). It was unlikely the maximum size of *S. megalops* was sampled; at 505 mm L_{ST} , the largest animal in the present study was considerably smaller than the 635 mm recorded from temperate Australia (Braccini *et al.* 2007) and the Atlantic maximum of 890 mm (Hazin *et al.* 2006). The invariant of relative size at maturity corroborates this, because the 0.84 was greater than the average relative size of maturity of 0.76 for deepwater chondrichthyans (Chapter 2).

Regional differences in the Australian *S. megalops* size and age at maturity were evident, with the tropical animals smaller and older at maturity than those of temperate waters. The regional differences were greater for females than males. The Swain Reefs population L_{ST50} values for females and males, at 422 and 352 mm respectively, were markedly less than those from two studies of temperate Australian *S. megalops* (Table 1) (Graham 2005; Braccini *et al.* 2006a). It is possible that the sizes and ages at maturity estimates from the present study may be biased because the majority of the samples were of immature animals. This could only be determined from further sampling in a wider area of the tropics to collect more mature animals. Regional size variations in shark population parameters have been linked to latitudinal differences in distribution correlated with water temperature (Yamaguchi *et al.* 2000a; Lombardi-Carlson *et al.* 2003; Colonello *et al.* 2007; Gutteridge *et al.* 2013), with the increased size at maturity hypothesised to enable higher latitude animals to store more energy (Blackburn *et al.* 1999).

This may explain the regional size differences because the temperate waters were on average 5°C cooler than those of the tropics, even in the shallower waters of the 21–238 metres depth range across which animals were collected in the temperate region (IMOS 2015).

The *S. megalops* males and females in the present study were mature at 12.6 and 19.1 years, respectively, which is older than previous estimates for temperate Australian waters (Table 1) (Braccini *et al.* 2006a; Braccini *et al.* 2007). Although there may be a bias because of a smaller proportion of mature animals sampled, there is still a regional difference in age at maturity, particularly for females. This difference could also be the result of the latitudinal separation, although logically it would be expected the *S. megalops* from higher latitudes would mature later because of slower growth in cooler waters. Although comparisons with Atlantic studies were treated with caution, the ages at maturity of the present study were more similar to those in the subtropical Canary Islands than in temperate South Africa (Table 1) (Watson and Smale 1999; Pajuelo *et al.* 2011). It seems plausible that the sampling of a smaller proportion of mature animals in temperate studies may have affected the estimates of age at maturity. The temperate studies included shallow shelf waters and the studies reported strong sexual segregation and the possibility that parturition and the majority of the larger females occurred outside the areas sampled (Watson and Smale 1999; Braccini *et al.* 2007). Pajuelo *et al.* (2011) and the present study did not sample depths <190 m and sexual segregation was not as strong as for the temperate studies. Pajuelo *et al.* (2011) found populations were not sex or size segregated at all and although the present study found some segregation, there was still some mixing, with immature and mature animals and pregnant females co-occurring in samples. In the Canary Islands, the lack of segregation was attributed to a narrow range of available habitat, but this was not a limiting factor in the Swain Reefs area. *Squalus megalops* is an opportunistic predator (Burrage *et al.* 1996; Braccini *et al.* 2005) and the mixed schools in the present study may have been due to the presence of a large mesoscale eddy, the ‘Capricorn Eddy’, which increases the availability of nutrients and food (Weeks *et al.* 2010; Jaine *et al.* 2014; Weeks *et al.* 2015).

Sexual dimorphism is typical of deepwater squaloids and many chondrichthyans (Cailliet and Goldman 2004; Cortés 2004; Kyne and Simpfendorfer 2007) and was apparent in the *S. megalops* in the present study, whereby the females were of a larger size and size at maturity, matured later and were older than the males. This was also the case, but to a lesser degree, for *S.*

montalbani, where the females were larger and older than males at maturity. This dimorphism, previously found for *S. megalops* (Watson and Smale 1999; Graham 2005; Hazin *et al.* 2006; Braccini *et al.* 2007; Pajuelo *et al.* 2011; Marouani *et al.* 2014), has been attributed to the need for females to partition more time and energy into growth before reproductive age is reached to be of sufficient size to support the production of large young (Cailliet *et al.* 1990; Frisk *et al.* 2001; Chapter 2) .

The *S. megalops* reproductive information suggested a continuous and asynchronous breeding cycle for females with males able to mate at both sampling times. This is a strategy common among outer shelf and upper slope deepwater dogfishes (Cotton *et al.* 2011; Graham and Daley 2011; Rochowski *et al.* 2015) and concurs with other *S. megalops* studies which found a 2-year ovulation and gestation period, and that males were able to breed throughout the year (Watson and Smale 1998; Graham 2005; Braccini *et al.* 2006a; Hazin *et al.* 2006; Pajuelo *et al.* 2011). It seems reasonable to assume that the Swain Reefs *S. megalops* have a biennial cycle, the same as for other regions ((Braccini *et al.* 2006a; Pajuelo *et al.* 2011). If this is the case, then combined with the low fecundity and late age at maturity, the Swain Reefs population has a low biological productivity similar to other populations of *S. megalops*.

The reproductive cycle of the deeper dwelling *S. montalbani* was difficult to discern from the one pregnant female in the present study and the four reported from the Australian east coast. Although two females had developing follicles during gestation, there were no such follicles in other pregnant animals and there were two very large but immature females with immature uteri, oviducal glands and ovaries. These limited data provide some evidence of a non-continuous breeding cycle with a resting phase that is common among the mid slope (>650 m) dogfishes (Kyne and Simpfendorfer 2010; Irvine *et al.* 2012). The larger litter sizes of nine to 16 were also more typical of mid slope than upper slope dogfishes (Daley *et al.* 2002). Litter sizes increased with increasing maternal size and were comparable for maternal size to those of four to 16 reported from Indonesia for 12 females of 830–952 mm L_T (White *et al.* 2006; White and Dharmadi 2010). The largest embryos were near term at 234–245 mm, which is similar to the largest embryo observed in Indonesia of 240 mm (referred to as *Squalus* sp. 1) (White *et al.* 2006). This extends the known size of birth range to 207–245 mm (Last *et al.* 2007a). Female size at maturity in Indonesia (White *et al.* 2006) and the CSIRO 2009 gulper survey was 800–820 mm (K. Graham, Australian Museum, pers. comm. 2009) which, from the growth curve in the present study, was estimated to be 26 years. Although the pregnant 849 mm L_{ST} specimen of the present study could not be aged because of damaged DFS, from the growth curve it was estimated to be 27–28 years old.

The size of maturity of male *S. montalbani* in the present study was similar to that for Indonesia (600–700 mm) (White and Dharmadi 2010) and to that for all males captured in the CSIRO 2009 gulper survey (650–700 mm) (K. Graham, Australian Museum, pers. comm., 2009). It was not possible to elucidate the synchronicity or length of the reproductive cycle, although an asynchronous breeding cycle was suggested for the Indonesian *S. montalbani* females (White and Dharmadi 2010). Although *S. montalbani* inhabits the upper slope, it has a reproductive cycle more typical of mid slope dogfishes, with larger litters and a potential resting period that may enable it to recover between pregnancies, particularly during times of low food supply (Daley *et al.* 2002; Irvine *et al.* 2012). This suggests it may have a long reproductive cycle because the length of the deepwater chondrichthyan cycle increases with depth (Chapter 2). Even though it has a larger litter size, *S. montalbani* is probably less productive than *S. megalops*, based on later age at maturity, greater longevity and a potentially longer and non-continuous reproductive cycle.

Resilience to fishing

The differences in reproductive cycles and life history traits between the two squalids are typically associated with their different distribution within the deepwater habitat (Chapter 2). *Squalus megalops* inhabits both the shelf and upper slope, whereas *S. montalbani* lives deeper, is more restricted to the upper slope and likely has a more conservative life history. An increase in depth is known to coincide with an increase in vulnerability to exploitation (García *et al.* 2008; Simpfendorfer and Kyne 2009). This was evident off the east Australian coast where trawling over two decades caused significant declines of > 90% in the relative abundance of a suite of dogfishes, including *S. montalbani* off Southern NSW, yet an increase by 18% in the relative abundance of *S. megalops* (Graham *et al.* 2001; Kyne and Simpfendorfer 2010). These highly disparate fishery impacts between the two species were mostly attributed to their different depth distributions, although the more conservative life history traits of *S. montalbani* identified in the present study would have also contributed to the differences. The distribution of *S. montalbani* on the upper slope exposed the entire population to fishing impacts whereas *S. megalops* was abundant in a relatively unfished outer shelf area that was thought to enable recruitment onto the fished upper slope area and help maintain their overall biomass (Graham *et al.* 2001; Walker and Gason 2007). Further south, where the outer shelf areas were much more

intensely trawled there were noticeable effects on *S. megalops* with some declines evident in their relative abundance (Graham *et al.* 2001).

The management arrangements for the east coast Australian trawl fishery have changed significantly since the surveys that highlighted the declines in upper slope dogfishes. Catch limits and spatial and depth closures were implemented to provide protection to the vulnerable dogfishes and to aid recovery of overfished populations (AFMA 2012b). Estimates of recovery times were multiple decades for two upper slope species with ages at maturity similar to *S. montalbani* (AFMA 2012b). The life history traits elucidated from the present study of *S. montalbani* of slow growth, late age at maturity, high longevity, and a possibly non-continuous breeding cycle indicate their recovery from overfishing off southern NSW in the east coast Australian trawl fishery is also anticipated to take decades.

Squalus megalops likely has a greater capacity to recover from fishery impacts than *S. montalbani*, although it still has low biological productivity that would hinder recovery. A risk assessment of temperate Australian *S. megalops* highlighted the potential vulnerability of this species to the effects of fishing (Braccini *et al.* 2006b). In the Swain Reefs area, the main deepwater EKP fishing grounds are limited in their spatial extent and are generally concentrated on the shelf, although there is some fishing on the upper slope habitat. The fishery appears to be interacting with only part of the *S. megalops* population with low catches within the main fishing grounds. Although the current effects of the fishery appear to be limited, any change in fishing practices in the Swain Reefs area that leads to an increase in catch susceptibility, such as a change in area fished, could place *S. megalops* at risk of depletion.

Both *S. megalops* and *S. montalbani* share life history traits aligned to other deepwater dogfishes that limit their ability to recover in the event of depletion. Their traits were associated with differences in their depth of occurrence, with the deeper dwelling *S. montalbani* more vulnerable to exploitation and expected to take decades to recover from overfishing. The tropical Great Barrier Reef population of *S. megalops* was smaller and older at maturity than the temperate Australian and global populations and may not be greatly affected by the deepwater trawl fishery in the Swain Reefs area, although to confirm this would require further temporal and spatial sampling.

Chapter 6 Novel method for shark age estimation using near infrared spectroscopy



Great hammerhead *Sphyrna mokarran* vertebra

Rigby, C.L., Wedding, B.B., Grauf, S., Simpfendorfer, C.A. (2015) A novel method for age estimation using near infrared spectroscopy. *Marine and Freshwater Research*. [doi: 10.1071/MF15104](https://doi.org/10.1071/MF15104)

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6.1 Introduction

Reliable age information is essential to accurately assess the status of shark populations and predict their ability to sustain exploitation (Goldman *et al.* 2012). The traditional approach to estimating age in sharks is the enumeration of periodic growth bands in their hard structures, mostly vertebrae or dorsal fin spines (Cailliet *et al.* 1983; Cailliet and Goldman 2004). As the animals age, calcified material accumulates in these structures and can produce visible band pairs that, once periodicity has been validated, enable determination of age (Cailliet *et al.* 1986; Cailliet and Goldman 2004; Cailliet *et al.* 2006).

The traditional age reading approach of band pair counts requires practice and experience to achieve accurate results and can require time-consuming sample preparation, such as sectioning and enhancement techniques that are often necessary on shark ageing structures to improve band resolution (Cailliet *et al.* 1983; Campana 2001; Irvine *et al.* 2006b). Band counts are highly subjective with quality control measures required to maintain consistency and precision to reduce the risk of reader bias (Goldman *et al.* 2012). The traditional approach also has its limitations, because many sharks do not have dorsal fin spines and may have vertebrae that are either too poorly calcified to provide age information, such as numerous deepwater species, or have reduced band resolution that creates difficulties in age interpretation (Cailliet 1990; Gallagher *et al.* 2006; Barnett *et al.* 2009b). Consequently, there is a need to investigate alternative approaches to the ageing of sharks that may be more cost-effective, and that have the potential to address shark age estimation limitations.

Near infrared spectroscopy (NIRS) is a technology that may provide an alternative approach to traditional age reading methods. It is a non-destructive technique (i.e. the original sample remains intact after ageing) that uses light data from the near infrared (NIR) region of the electromagnetic spectrum (12820–4000 cm^{-1}) in combination with chemometric methods (multivariate statistics) to analyse the chemical composition of a material (Murray and Williams 1987; Wold and Sjöström 1998; Williams 2008). All organic matter consists of atoms, mainly carbon, oxygen, hydrogen, nitrogen, phosphorus, and sulphur, with a minor amount of other elements. These atoms combine to form molecules that are constantly in motion and that vibrate (bend or stretch) at specific frequencies, referred to as wavelengths in NIRS terminology (Murray and Williams 1987). When an energy source such as NIR light is focussed onto a sample, it causes the molecules within the whole sample to increase their vibrational energy by absorbing specific wavelengths to a greater or lesser degree, depending on the atomic masses, bond strengths and molecular geometry of the material within the sample. The original NIR light energy is thus modified and reflected, and can be detected and analysed by a NIRS

instrument to produce a graph of the different amount of absorbance at each wavelength. This graph is an undulating pattern of peaks and troughs known as the spectrum and is characteristic of all the absorbing molecules in the sample; that is, it represents the molecular composition of the sample. Chemometric procedures are applied to analyse these spectra into the qualitative (identity) or quantitative chemical constituents of the sample (Murray and Williams 1987; Siesler *et al.* 2002; Reich 2005).

NIRS is widely used in agriculture, pharmaceutical and other industries, and was recently investigated as a method for teleost age estimation (McClure *et al.* 2002; Solberg *et al.* 2003; Wedding *et al.* 2014). The NIRS approach was demonstrated to rapidly and accurately estimate the age of saddletail snapper *Lutjanus malabaricus* (Bloch & Schneider 1801) using otoliths, which are the most commonly used structures to age fish (Campana and Thorrold 2001). NIRS is generally used as a secondary method of determination, which means the spectra must be calibrated against a primary reference method to develop a calibration model (Murray and Williams 1987). For instance, in the Wedding *et al.* (2014) otolith study, 100 whole otoliths were scanned using NIRS to produce 100 NIRS spectra and were then aged by traditional sectioning and increment counts. The 100 spectra were related to the age estimates from the increment counts (the primary reference method) using partial least squares regression to develop a calibration model. That calibration model could then be used to predict the age of a saddletail snapper otolith scanned by NIRS and not aged by traditional increment counts. In that study, the calibration model was shown to have a strong capacity to accurately predict the age of such an otolith (Wedding *et al.* 2014). This process required a sufficient number of samples to cover the variability in age among fish of similar length, which in this instance was only 100 otoliths. The scanning and analysis of each whole otolith took about 25 seconds; hence, once the initial 100 otoliths aged by traditional means were scanned and a calibration model developed, the NIRS method had the capacity to conduct up to 150–200 otolith age estimates per hour. This would provide substantial time and cost savings, not only in preparation time, as no sectioning was required, but also in age reading time because the NIRS scans were rapid (Dub *et al.* 2013; Wedding *et al.* 2014). This cost-efficiency and the non-destructive nature of the analyses are the major benefits of NIRS (Roggo *et al.* 2007; Williams 2008). The technique is considered non-destructive because whole otoliths can be scanned using NIRS once the calibration model is developed; they do not need to be destroyed by sectioning. Following on

from the otolith study, a more detailed assessment of using NIRS to age fish was undertaken (Robins *et al.* 2015).

The success of NIRS age estimation in teleost otoliths provided the impetus to investigate the potential ability of the NIRS method for age estimation in sharks. Although the chemistry of the otoliths differs from shark vertebrae and dorsal fin spines (Walker *et al.* 1995; Campana 1999; Hamlett 1999), visible band pair counts have been determined as useful for age estimation in both teleost and shark structures (Campana and Thorrold 2001; Goldman *et al.* 2012), so it is a feasible proposition that the NIRS approach may be viable with sharks. A current limitation of the NIRS approach is that it must be used in combination with traditional age reading, although only for potentially 100 structures (e.g. vertebrae), to develop the calibration model. The calibration model incorporates errors associated with the traditional age reading, so the more accurate and precise the growth band counts, the more accurate and precise the NIRS calibration model (Williams 2008; Wedding *et al.* 2014). NIRS could be used to scan the whole vertebrae and, after the 100 structures have been traditionally aged, the calibration model applied to estimate age. Because the NIRS age estimate can be performed on whole structures it would reduce the amount of time needed to prepare structures for age reading. The NIRS process is mechanised, rapid and precise (Siesler *et al.* 2002), and offers the potential of considerable cost savings associated with the conventional age reading. It also would remove age reading subjectivity and risk of reader bias for all vertebral ages predicted using NIRS after the calibration model has been developed (Williams and Norris 1987; Wedding *et al.* 2014). Because NIRS is a chemical assay approach, if the method is viable for shark age estimation, it has the potential to be used to address other limitations of shark ageing, such as poor calcification and reduced band resolution.

The purpose of the present study was to determine the feasibility of the use of NIRS for age estimation in sharks. Whole vertebrae from age-validated and -verified coastal and pelagic sharks were scanned. Their NIRS spectra were related to their age estimates derived from the traditional method of band pair counts to examine whether robust calibration models capable of predicting age could be developed. Finally, the NIRS estimated ages were used to fit growth models and these were compared to growth curves from vertebral ageing to determine whether there were differences.

6.2 Materials and methods

6.2.1 Study species

Samples of whole vertebral centra from great hammerhead *Sphyrna mokarran* (Rüppell 1837) and spot-tail shark *Carcharhinus sorrah* (Müller & Henle 1839) were provided from another research project on the life history of tropical sharks (Harry *et al.* 2011; Harry *et al.* 2013). Using these two species provided the opportunity to trial NIRS across habitats, body size and contrasting life histories. *Sphyrna mokarran* is a large, long-lived (up to 39 years), slow-growing, coastal-pelagic and semi-oceanic shark (von Bertalanffy (VB) growth constant $k = 0.079 \text{ year}^{-1}$) (Harry *et al.* 2011). *Carcharhinus sorrah* is a medium sized, faster-growing, coastal shark ($k \text{ female} = 0.34 \text{ year}^{-1}$) with a shorter life span (of up to 14 years) (Harry *et al.* 2013). The 80 *S. mokarran* (44 females, 32 males, 4 sex unknown) were collected from waters down to 110 m depth along the east coast of Australia from northern to southern Queensland between 2005 and 2010 (Harry *et al.* 2011). The 102 *C. sorrah* (all females) were collected from inshore waters less than 25 m depth in the Townsville region of Queensland between 2007 and 2012 (Harry *et al.* 2013).

In the tropical shark study, both species were aged by growth band counts of sectioned vertebral centra. A segment of five vertebrae was taken from each individual, the neural and haemal arches removed, the remaining centra bleached briefly, rinsed thoroughly and dried in an oven for 24 hours (Harry *et al.* 2011; Harry *et al.* 2013). One of the five vertebral centra was sectioned for age estimation by band counts and another was provided whole to the present study. The band counts of each individual were adjusted to partial ages in the tropical shark study using a mean population birth date for each species, based on their seasonal reproductive cycle (Harry *et al.* 2011; Harry *et al.* 2013). Those partial ages were used in the present study to represent the estimated age of each individual based on band counts and were called ‘vert-age’, with the term ‘NIRS-age’ used to represent age estimated by the NIRS calibration model.

The 80 *S. mokarran* ranged in size from 801 to 4391 mm stretched total length (L_{ST}) and in vert-age from 0.3 to 39.1 years. Ages were validated up to 9.5 vert-age years through calcein mark, tag and recapture. Five of the thirty-eight calcein-marked animals were recaptured, with vertebrae from two animals (7.1 and 9.5 vert-age years) used to validate annual band pair deposition (Harry *et al.* 2011). The 102 *C. sorrah* ranged in size from 634 to 1301 mm L_{ST} and in vert-age from 0.5 to 13.7 years. Age validation through calcein mark and recapture was unsuccessful because of low recapture rates and poor calcein uptake, although periodicity of annual growth band deposition had been verified previously in *C. sorrah* up to 2 years old

(Davenport and Stevens 1988). It was suggested by Harry *et al.* (2013) that this same periodicity may occur throughout life, because there was a recapture in a large northern Australian tagging program of an animal at liberty for 9.9 years estimated to be at least 12 years old (Stevens *et al.* 2000b; Harry *et al.* 2013). For clarity, in referring to ages that have been validated and verified, for both species known vert-age represents animals up to 10 years old and unknown vert-age represents those >10 years old. In addition, although ‘vert-age’ refers to the age of an individual, ‘vert-ages’ refers to all individuals (i.e. the entire age range).

6.2.2 Spectral acquisition and data analysis

To obtain a NIRS spectrum from each vertebral centrum, each centrum was scanned by a Bruker multipurpose analyser (MPA), Fourier transform (FT) NIR spectrophotometer (Bruker Optics, Ettlingen, Germany; operating software: OPUS version 6.5) in the 12 500–3600 cm^{-1} wavenumber range (corresponding to wavelengths of 800–2778 nm; wavenumbers are the inverse of wavelengths). Each individual centrum was hand positioned, with the centrum placed face down onto the sample window where the NIR light irradiates the centrum, and the diffusely reflected NIR light was detected and analysed. For each centrum, 16 individual scans at every 8 cm^{-1} of NIR wavenumber were taken and averaged (by the software) to produce a raw NIRS spectrum, which took about 16 seconds per centrum (Figure 6.1).

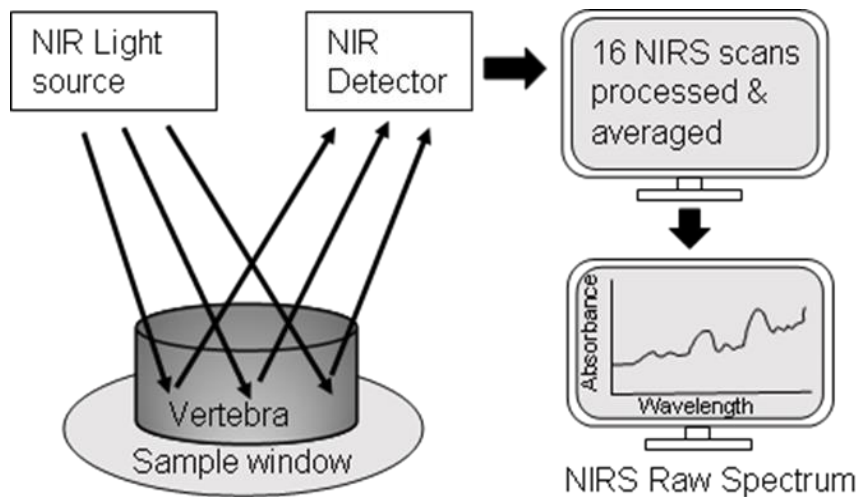


Figure 6.1 Schematic of the near infrared (NIR) spectroscopy (NIRS) scanning process.

For each species, the NIRS spectra of the centra and the vert-ages of the centra (reference age estimation by band counts) were compared to determine whether a robust calibration model could be developed. This was done by chemometric analyses methods, which included partial least squares (PLS) regression that attempted to build a calibration model (i.e. establish a regression relationship between all the NIRS spectra and all the vert-ages) that was represented

by a single plot. The plot defined the weights given to the different wavelengths in the linear PLS regression equation, with regression coefficients on the y-axis and wavelengths (expressed as wavenumbers) on the x-axis. If a calibration model could be developed, it was analysed further to identify the specific NIRS wavelengths within the plot that represented the molecular compounds in the centra most strongly related to the vert-ages. The final calibration model was presented as: (1) a calibration model plot; (2) calibration model statistics; and (3) a calibration model regression graph of the predicted NIRS-ages against vert-ages (Murray and Williams 1987; Foley *et al.* 1998; Wedding 2007). This chemometric process is explained in further detail below. All data analyses were undertaken using a multivariate software package The Unscrambler (version 9.8; Camo, Oslo, Norway).

As a first step in the analyses, prior to the PLS, raw NIRS spectral data often need to be mathematically transformed to both remove noise in the raw spectra (mostly caused by instrument effects) and to enhance the visual resolution of spectral peaks (Reich 2005; Wedding 2007). The raw NIRS spectra for all the scanned centra of *S. mokarran* and *C. sorrah* are shown in Figure 6.2. Several pre-treatments were investigated and, for all calibration models, all raw spectral data were transformed prior to model development using a 25-point Savitsky-Golay spectral smoothing and a first derivative transformation. During the PLS analysis, validation of the calibration model was undertaken to ensure the model accurately predicted the vert-ages. This was done by a process of segmented cross-validation, as recommended for small sample sets of less than 120 (Williams 2013). In the cross-validation process, a group of samples was withdrawn from the total set and the calibration model developed using the remaining samples. The resulting model was then used to predict the ages of the samples that had been withdrawn. This process was repeated using successive groups of randomly withdrawn samples until all the sample ages had been predicted, with none of them having been used in the development of the models used to predict them (Williams 2013).

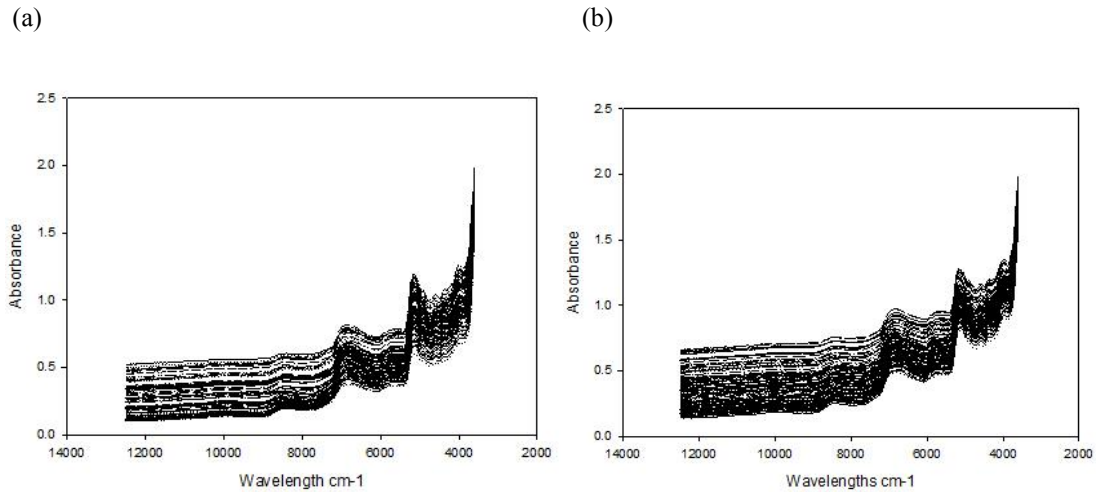


Figure 6.2 Raw near infrared spectroscopy (NIRS) spectra of centra of (a) 80 *Sphyrna mokarran* and (b) 102 *Carcharhinus sorrah*.

The PLS analysis initially used the full spectrum of the NIRS wavelengths of the scanned centra to develop the calibration model (Foley *et al.* 1998). This full spectrum contained an extensive amount of information on the chemical composition of the centra (Williams 2008). The next step was to develop an optimal calibration model. This included a process to identify the minimum subset of wavelengths in the initial calibration model plot that most closely related to the vert-ages. Spectral areas of the plot were serially removed and the PLS analysis run each time. If the removal of a spectral area improved the calibration model, that spectral area was considered as not closely correlated with age and was permanently removed; conversely, if the removal of a spectral area worsened the calibration model, that spectral area was considered as more strongly correlated with age and was retained. This was repeated until the optimal calibration model was obtained. The optimal calibration model was the model that best predicted age (NIRS-age), and was defined by a combination of several statistical criteria, namely, the combination of the highest possible coefficient of determination (R^2), the lowest root mean square error of cross-validation (RMSECV; the error in years of the predicted NIRS-age), the least number of terms, or factors, and the lowest bias (Wedding 2007; Williams 2008). Bias was the average difference between the vert-ages and the predicted ages (NIRS-ages) (Williams 2008). The standard deviation ratio (SDR = standard deviation of the vert-ages/RMSECV) was calculated to enable comparisons of model performance between the two species; the higher the SDR, the greater the relative predictive power of the model (Golic and Walsh 2006; Wedding 2007).

To provide further assessment of the accuracy of the predicted NIRS-ages, the predicted NIRS-ages for both species were used to fit a three parameter version of the von Bertalanffy growth models (von Bertalanffy 1938) given by:

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

where L_t is length at age t , L_0 is length at birth, L_∞ is asymptotic length and k is the Brody growth coefficient. These models were compared to the von Bertalanffy growth models of the known vert-ages using likelihood ratio tests (Kimura 1980), as implemented by Haddon (2001).

6.3 Results

There was a relationship between the vert-ages of both *S. mokarran* and *C. sorrah* and the spectral output of their vertebrae, evidenced by calibration models with R2 values of 0.83 and 0.78, respectively (Table 6.1). The older unknown vert-age animals were identified as outliers during the initial PLS regressions. In NIRS, an outlier was a sample that did not conform to the rest of the population and unduly influenced the calibration (Wedding 2007). Technically, it was a sample that differed from the rest of the population by three or more Mahalanobis distances (Williams 2008). The raw spectral data (Figure 6.2) did not indicate the spectra of these older vertebrae were anomalies; that is, there had been no uncharacteristic interferences, such as power supply fluctuations, which would require rescanning of the samples (Williams 2008). Most of the *S. mokarran* data (76 samples) were of animals up to 10 years of known vert-age with just four older animals of 14, 19, 35 and 39 unknown vert-age years. For the *C. sorrah*, most of the data (99 samples) were of animals up to 10 years of known vert-age with only three older animals of 11, 12 and 14 unknown vert-age years.

Table 6.1 Partial least-squares regression calibration model statistics for *Sphyrna mokarran* and *Carcharhinus sorrah*. The coefficient of determination (R^2), the root mean square error of cross validation (RMSECV), standard deviation ratio (SDR) and standard deviation ratio (SDR) and standard deviation (s.d.) are given for the vert-ages and known vert-ages, where the ages are based on band counts and the term ‘vert-ages’ represents the estimated ages of all individuals and ‘known vert-ages’ represents the ages that have been validated and verified.

Structure	Samples (n)	Age range (years)	s.d.	Terms	R^2	RMSECV (years)	Bias (years)	SDR
<i>S. mokarran</i> vert-ages	80	0.3–39.1	6.05	9	0.83	2.48	-0.146	2.44
<i>S. mokarran</i> known vert-ages	76	0.3–10.2	2.55	5	0.89	0.87	0.012	2.93
<i>C. sorrah</i> vert-ages	102	0.3–13.7	2.60	9	0.78	1.23	-0.007	2.11
<i>C. sorrah</i> known vert-ages	99	0.5–9.8	2.19	5	0.84	0.88	-0.005	2.50

Because no additional vertebrae from older unknown vert-age animals of these two species were available to increase the sample size for these older size classes, these older animals were removed from the data set and new calibration models developed. This improved the overall calibration model statistics for both species, with an improvement in R^2 values from 0.83 to 0.89 for *S. mokarran* and from 0.78 to 0.84 for *C. sorrah*, and a reduction in the error (RMSECV) for *S. mokarran* from 2.48 to 0.87 years and for *C. sorrah* from 1.23 to 0.88 years (Table 6.1, Figure 6.3). For the known vert-age models, *S. mokarran* had a marginally stronger predictive power with a SDR of 2.93, compared with a SDR of 2.50 for *C. sorrah* (Table 6.1). In summary, the NIRS spectra correlated well with vert-ages; however, this correlation was stronger when only the vertebrae of validated ages were used. The final NIRS calibration models could be used reliably to predict the ages of *S. mokarran* and *C. sorrah* from Queensland, up to the validated and verified ages of 10 years.

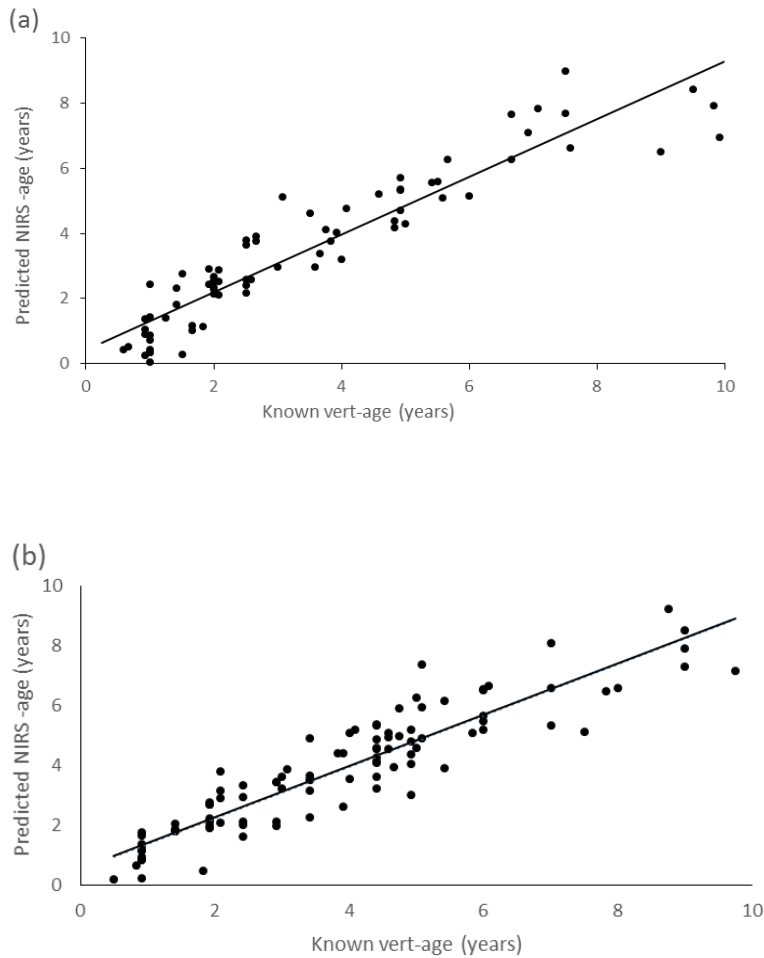


Figure 6.3 Partial least-squares regression calibration model of predicted near infrared spectroscopy (NIRS)-ages plotted against known vert-ages (based on band counts) for (a) *Sphyrna mokarran* ($R^2 = 0.89$) and (b) *Carcharhinus sorrah* ($R^2 = 0.84$).

The VB NIRS-age growth curves were not significantly different to the VB known vert-age growth curves for either species (Figure 6.4). Likelihood ratio tests indicated that, for both species, there was no significant difference between the two curves, with *S. mokarran* coincident curve $\chi^2 = 7.66$, $P = 0.0536$, and *C. sorrah* coincident curve $\chi^2 = 6.95$, $P = 0.0734$.

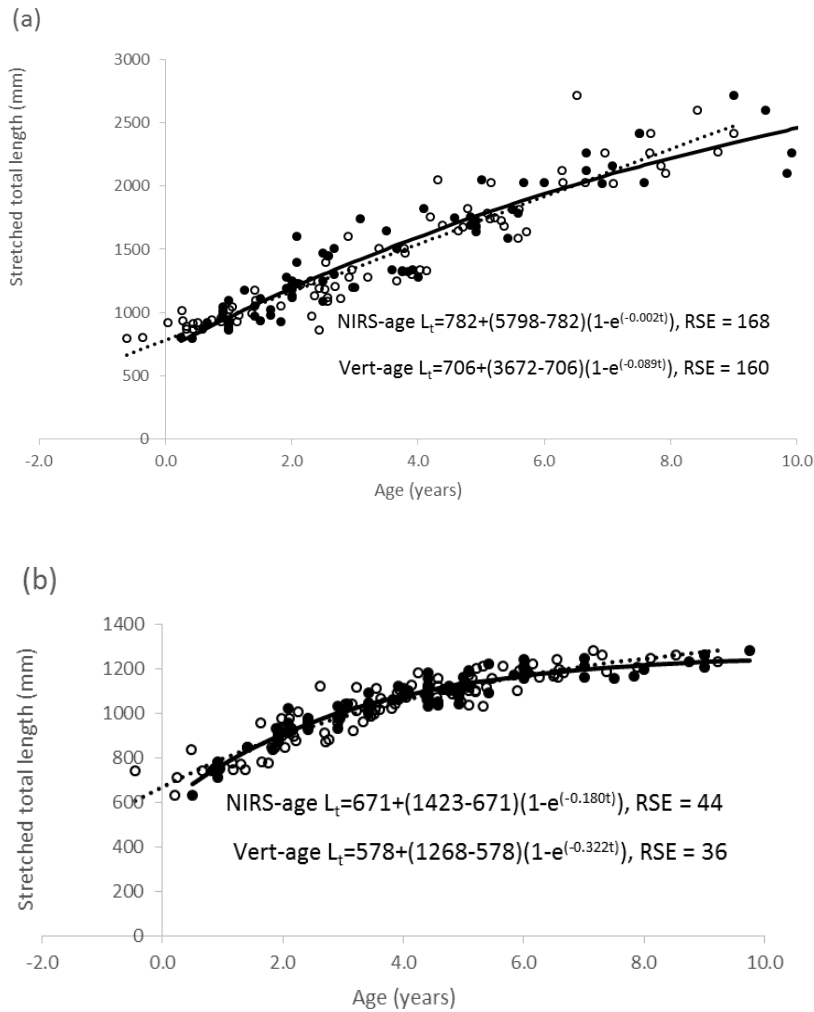


Figure 6.4 Length-at-age data for known vert-age (based on validated and verified band counts; solid circles) and near infrared spectroscopy (NIRS)-age (open circles) with the fitted von Bertalanffy growth models and residual standard error (RSE) for (a) *Sphyrna mokarran* and (b) *Carcharhinus sorrah* known vert-age (solid line) and predicted NIRS-age (dotted line). L_t , length at age t .

The spectral areas that correlated most strongly with the known vert-ages of the vertebral centra were very similar for both *S. mokarran* and *C. sorrah* (Figure 6.5). This suggested that similar molecular compounds correlated to known vert-age were being detected by the NIRS in the vertebrae of both species. There were three main spectral areas identified between 9200 and 4000 cm^{-1} (Figure 6.5). Without further NIRS research on the chemistry of the vertebrae, it is not possible to relate these spectral areas to a specific ageing chemical compound, such as calcium phosphate. At this stage, these main spectral areas can only be described in terms of the main molecular compounds to which they correspond, based on a table of group frequencies. This is a table of groups of wavelengths (frequencies) characteristic of molecules that are prominent absorbers in the NIR region, which is commonly found in NIRS textbooks

(Workman and Weyer 2008). The three main spectral areas corresponded to: Carbon-Carbon alkene, CH (aromatic), -CH₃ methyl, -CH₂ methylene all combination and second overtones; CH second overtone; -NH₂ primary amines combination and first overtone; -CONH₂ primary amides combination, first and second overtones; and -CONH-secondary amides combination and second overtone.

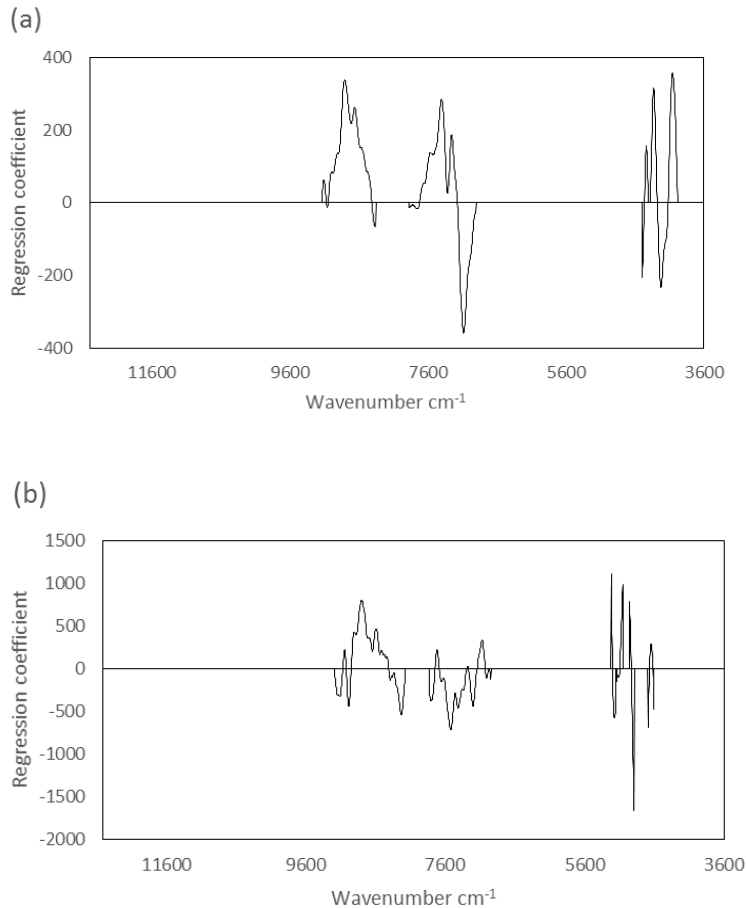


Figure 6.5 Spectral areas of the calibration model plot for (a) *Sphyrna mokarran* and (b) *Carcharhinus sorrah*.

6.4 Discussion

The results of this present study demonstrate that NIRS can be used to estimate the age of sharks. For both *S. mokarran* and *C. sorrah*, the NIRS method produced robust calibration models with a good ability to accurately predict the ages of vertebrae from these species; up to the validated and verified known vert-ages of 10 years. These predicted NIRS-ages also produced comparable VB growth curves to those of the traditional ageing method. We showed

that a robust age calibration model can be developed with 80–100 animals aged by the traditional method of growth band counts (Cailliet *et al.* 1986). Once the NIRS calibration model has been developed, further ageing of individuals of these species up to the validated and verified ages of 10 years included in the calibration model can be done rapidly and objectively. Their whole, dried vertebrae can be scanned with the NIRS instrument and the NIRS calibration model applied to predict their ages. Some random checks to monitor the age predictions would be required by occasionally using traditional ageing to verify the predicted age (Siesler *et al.* 2002). Although the NIRS method needs to be used in conjunction with traditional age reading methods and is not a validation method in itself, it does provide verification of the band counts and, most importantly, it can provide rapid age estimations of vertebrae that have not been traditionally aged up to the maximum age included in the calibration model.

The predicted age estimations can be done by NIRS very rapidly, which is one of the major benefits of the NIRS approach to ageing (Murray and Williams 1987; Roggo *et al.* 2007). Once the calibration model for a species has been developed, the predicted NIRS-age can be determined from a 16 second scan of a vertebra, without the need for sectioning or enhancement. An additional benefit of this NIRS approach to ageing is that because this predicted NIRS-age is mechanised, it is also objective and would maintain the precision of the age estimate of the calibration model and avoid further age reading subjectivity that would occur if all vertebrae needed to be aged by traditional visual band count estimates (Williams 2008). One aspect of age reading that cannot be avoided by NIRS is any errors associated with the traditional age reading of the reference samples. These errors would be incorporated into the calibration model and thus NIRS is reliant on accurate traditional age estimates to develop a calibration model that will be useful for prediction. NIRS instruments are widely available in industrial and research organisations, because NIRS is regularly used in the commercial and research sectors of agriculture, food, pharmaceuticals and medicine (Siesler *et al.* 2002; Ferrari *et al.* 2004). The availability of portable hand-held units is also increasing, because of improvements in their precision and accuracy in recent years, which has raised demand (Herberholz *et al.* 2010; Alcalà *et al.* 2013).

The NIRS ageing method offers the potential for major savings in time and cost over the traditional shark age estimation process. It would be particularly beneficial where large numbers of vertebrae need to be aged, such as for inclusion in stock and risk assessments for commercially captured sharks (Kritzer *et al.* 2001; Thorson and Simpfendorfer 2009). Ages could be reliably predicted up to the maximum validated age used in the calibration model, and the resources saved by negating the need to traditionally age all vertebrae could be invested to

increase the number of sharks aged. This would improve the reliability of age information for stock and risk assessments.

A limitation of the present study is that older age-validated material from the two species was not available and consequently it is yet to be determined whether the NIRS method would be viable for older animals of these two species. In the present NIRS investigation, the vertebral scans from individuals of both species >10 years of age were removed from the models because they were identified as outliers during calibration model development. This may have been because their ages were not well represented in the data set, with very few older individuals among a much larger population of younger animals. Ideally, the calibration samples would consist of an even representation of all age classes (Reich 2005; Williams 2008), although with sharks this can be logistically difficult. Alternatively, age underestimation of the older individuals that had not been age validated could have caused poor correlations between the vertebral ages and their corresponding spectra that led to the identification of these older animals as outliers. Age underestimation has been identified for older individuals of a number of species (Campana *et al.* 2002; Francis *et al.* 2007; Andrews *et al.* 2011). In the tropical shark study, a low recapture rate of larger *S. mokarran* precluded validation of animals > 10 years of age and for *C. sorrah*, although some calcein-marked larger animals were recaptured, the calcein failed to mark their vertebrae and it was suggested that somatic growth and calcification of their vertebrae had either slowed or ceased (Harry *et al.* 2011; Harry *et al.* 2013).

The issue of NIRS age predictions for older animals could not be resolved in the present study because no additional older individuals were available; however, it was addressed in subsequent work that extended the NIRS shark ageing research to deepwater shark species (Chapter 7). Two dogfish species (*S. megalops* and *S. montalbani*) were traditionally aged up to 25 and 31 years respectively using band counts on their dorsal fin spines (DFS) (Chapter 5). Vertebrae and fin clips were also removed from the same *S. megalops* animals aged by DFS because DFS annual band pair deposition had been verified for *S. megalops* (Braccini *et al.* 2007). Scans of the three structures from *S. megalops* (DFS, vertebrae and fin clips) and the DFS from *S. montalbani* all produced NIRS calibration models with a good ability to predict ages up to the maximum ages of 25 and 28 years (Chapter 7). In that study, the vertebrae themselves could not be aged by traditional age reading because growth bands were not visible, yet the DFS proxy ages from the same animals clearly indicated that chemical changes occurred in the vertebrae

correlated with age up to the maximum ages in the study. The older age classes were much better represented for *S. megalops* and *S. montalbani* than for *S. mokarran* and *C. sorrah*, which suggested that the older *S. mokarran* and *C. sorrah* were outliers in the NIRS models because of a lack of representation in the data set. However, possible age underestimation of the older animals by traditional age reading cannot be discounted, but was outside the capacity of the present study to resolve.

The NIR spectra of the vertebrae contained large amounts of information about the chemistry of the vertebrae, yet the spectral areas that correlated most strongly with age were very similar for both *S. mokarran* and *C. sorrah*. This suggested that chemical changes in the vertebrae associated with age were detected by the NIRS method. These chemical changes could have been related to hydroxyapatite $3(\text{Ca}_3\text{PO}_4)_2 \cdot \text{Ca}(\text{OH})_2$, the primary growth mineral in the calcified cartilage of vertebrae (Walker *et al.* 1995; Hamlett 1999). The deposition of hydroxyapatite within an organic matrix creates the growth bands used for vertebral ageing, with different ratios of the mineral and organic matrix producing the two optically distinct opaque and translucent bands (Casselmann 1974; Kerr and Campana 2014). However, the specific chemical compound in the vertebrae that correlated to the NIRS spectra is unknown at this stage. A limitation of NIRS is that the spectra are very complex (Murray and Williams 1987), and to determine the identity of the chemical compounds that could be related to the vertebral ages would require considerably more research into NIRS and the chemistry of shark ageing structures, which was beyond the scope of the present study.

Future work to investigate what the NIRS is detecting in the shark vertebrae is discussed in Chapter 8. Regional variability in the intraspecific age and growth of sharks is well documented (Cailliet and Goldman 2004; Cope 2006; Chapter 2) and should be considered in the development of future NIRS calibration models for age estimation. The models from the present study could be used to reliably predict ages up to 10 years for *S. mokarran* and *C. sorrah* from Queensland. To increase the regional scope of the model, additional samples from a wider geographic area could be added to the existing calibration model as they became available, providing they were from animals with the same age and growth parameters as the Queensland populations (Foley *et al.* 1998; Williams 2008). This would also then include the potentially different water bodies that can affect the microchemistry of the age structure and the corresponding spectral characteristics (Tillett *et al.* 2011; Kerr and Campana 2014; Wedding *et al.* 2014). For NIRS in general, it is recommended to include the entire range of biological and geographic variability in the NIRS calibration model to ensure acceptable accuracy in the predicted parameter (Siesler *et al.* 2002; Bobelyn *et al.* 2010). In the teleost otolith study

(Wedding *et al.* 2014), seasonal rather than regional differences were detected and separate calibration models developed. However, the accuracy of prediction improved when both seasons were included in one calibration model, because of the inclusion of greater biological variability. The shark NIRS age prediction models could possibly be improved by the development of separate models for males and females where sufficient data are available, which is done for traditional age and growth studies because sexually dimorphic growth is a general feature of shark populations (Cortés 2000; Cailliet and Goldman 2004). The present study was inconclusive on this matter because the NIRS model for *S. mokarran* was based on combined sexes and was stronger than that of *C. sorrah*, which used just females.

The present investigation of NIRS for ageing sharks clearly demonstrated it is feasible for age estimation of sharks. Although the NIRS approach needs to be first used in concert with accurate traditional age reading and validated ages to develop a robust calibration model, it then has the ability to rapidly estimate ages of vertebrae that have not been traditionally aged up to the maximum ages used in the calibration model. This offers the potential to cost-effectively age large numbers of sharks, which could improve the reliability of age information for stock and risk assessments and provide benefits to fisheries management. We consider the NIRS approach to ageing could be applicable to a wide range of shark taxa, because the two study species were of different habitats, body sizes and life histories.

Chapter 7 The utility of near infrared spectroscopy for age estimation of deepwater sharks



Piked spurdog *Squalus megalops* first dorsal fin spine

Rigby, C.L., Wedding, B.B., Grauf, S., and Simpfendorfer, C.A. (2014) The utility of near infrared spectroscopy for age estimation of deepwater sharks. *Deep Sea Research Part I: Oceanographic Research Papers* 94, 184-194. [doi: 10.1016/j.dsr.2014.09.004](https://doi.org/10.1016/j.dsr.2014.09.004)
Available online 2 October 2014.

7.1 Introduction

Many deepwater chondrichthyans have poorly calcified vertebrae that lack visible growth bands and most do not have dorsal fin spines that can be used for ageing (Cailliet 1990; Barnett *et al.* 2009b; Cotton *et al.* 2014). Consequently, alternative ageing methods are required for many deepwater chondrichthyans to provide age information essential for their management and conservation, particularly as this group of chondrichthyans are more vulnerable to exploitation than shelf and pelagic species (Koslow *et al.* 2000; García *et al.* 2008; Simpfendorfer and Kyne 2009; Norse *et al.* 2012) (Chapter 2).

Given the vulnerability of deepwater chondrichthyans there would also be considerable benefit from investigating non-lethal ageing methods. Current methods require the lethal removal of the vertebrae or dorsal fin spines to enumerate age. With mounting evidence of declines in many elasmobranch populations (Cortés *et al.* 2012), and one-quarter of the world's chondrichthyans estimated to be threatened (Dulvy *et al.* 2014), a non-lethal ageing method would also be beneficial more broadly than just for deepwater species, especially for those identified as rare or threatened (Heupel and Simpfendorfer 2010; Kerr and Campana 2014). A promising approach of using telomere length change with age was unsuccessful in sharks (Izzo 2010). Non-lethal removal of dorsal fin spines may be possible for some dogfish species that can be aged by band counts of internal sections from the exposed portion of the spine, and may also be viable for Port Jackson sharks, yet to date non-lethal removal has not been investigated (Tanaka 1990; Machado and Figueiredo 2000; Clarke *et al.* 2002a; Clarke *et al.* 2002b; Irvine *et al.* 2006b; Coelho and Erzini 2007; Tovar-Ávila *et al.* 2009). Caudal thorns could potentially be removed from live skates for age estimation (Gallagher *et al.*, 2006), though their reliability as an ageing structure varies among species (Goldman *et al.* 2012). Consequently, a different non-lethal ageing method applicable to a broad range of chondrichthyan taxa is required.

Near infrared spectroscopy (NIRS) is a technology that may provide an alternative ageing approach that is potentially non-lethal and applicable to deepwater chondrichthyans. The technique is described in the Introduction in Chapter 6. A current limitation of the NIRS approach is that it must be used in combination with traditional ageing by band counts, though only for potentially 100 structures, for example, dorsal fin spines, to develop the calibration model. The calibration model incorporates errors associated with the traditional age-reading, so the more accurate and precise the growth band counts, the more accurate and precise the NIRS

calibration model (Williams 2008; Wedding *et al.* 2014). Once the calibration model has been developed, NIRS could be used to scan dorsal fin spines not aged by traditional band counts, and the calibration model applied to estimate their age. The benefits of the NIRS approach to deepwater shark age estimation are that it can be performed on whole structures and is non-destructive (Luypaert *et al.* 2007; Roggo *et al.* 2007; Williams 2008), and that as a chemical assay approach it has the potential to address the issue of ageing deepwater sharks with poorly calcified structures.

The aims of this study were (1) to investigate whether NIRS can be used to estimate age in deepwater sharks, including those with poorly calcified vertebrae, and (2) assess the potential of NIRS for non-lethal ageing, by demonstrating the potential of ageing structures that could be measured in the field or which could be collected non-lethally.

7.2 Materials and methods

7.2.1 Study species

Two species of squaloid shark: *S. megalops* and *S. montalbani* were sampled for their first and second dorsal fin spines (DFS) (Figure 7.1, Chapter 5), with vertebrae and fin clips also sampled from *S. megalops*. Vertebrae and fin clips were also sampled from 100 female *A. pallidus*. This small deepwater catshark was collected in 174–280 m depths from the Swain Reefs, Queensland in 2011 and 2012 (Figure 7.1). It is endemic to Queensland, Australia, and occurs on the continental slope down to 400 m (Last and Stevens 2009). There is no information on its age and growth.

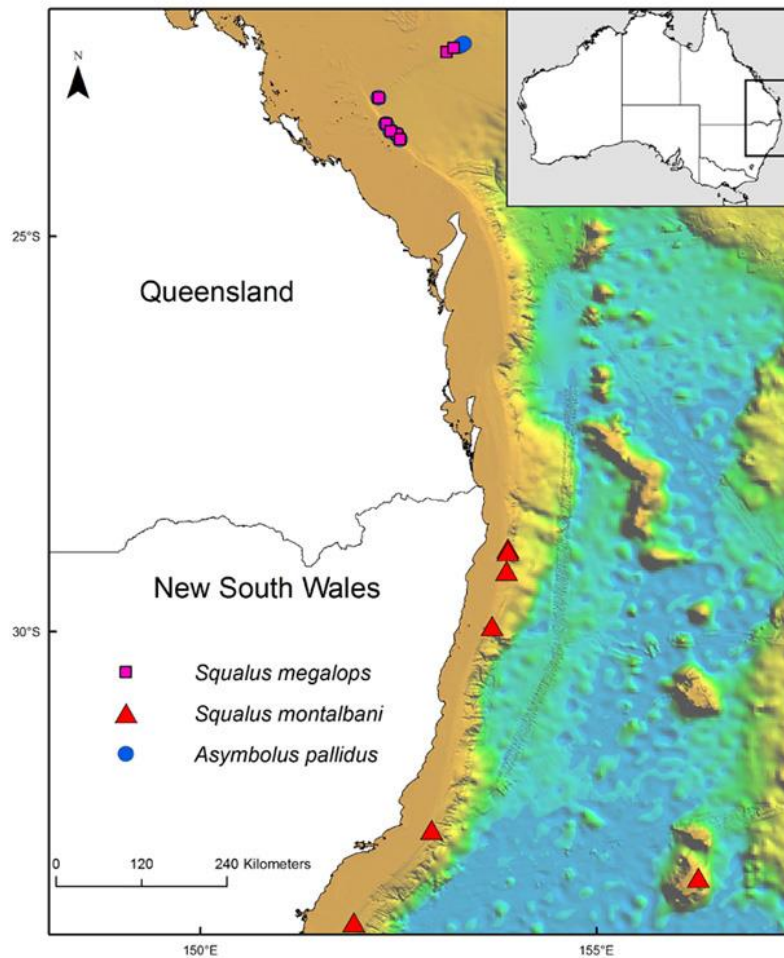


Figure 7.1 Sample locations of *Squalus megalops* and *Asymbolus pallidus* in Queensland, and *Squalus montalbani* in New South Wales

7.2.2 Structures

For both dogfish species, the stretched total length (L_{ST}) was measured and the entire first and second DFS were removed from each individual, cleaned of tissue and cartilage, and rubbed with fine wet sandpaper to highlight the bands on the enamelled cap that covered a large portion of the spines of both species. They were air dried and stored in vials. To determine the viability of NIRS to age deepwater sharks using their DFS, and to assess the potential of NIRS for non-lethal ageing, all first DFS of *S. megalops* and all second DFS of *S. montalbani* were traditionally aged by band counts (Chapter 5) (termed estimated-age in this Chapter 7) and also scanned by NIRS. To assess whether NIRS produced consistent results between the first and

second DFS, 39 *S. megalops* second DFS were also aged by band counts (Chapter 5) (estimated-age) and scanned by NIRS.

The vertebrae of deepwater *S. megalops* and *A. pallidus* have no visible banding (Braccini *et al.* 2007; Chapter 5). To ascertain whether NIRS could be used to determine age from vertebrae of these species, vertebrae were retained from all *S. megalops* and *A. pallidus*. The L_{ST} was measured for all *A. pallidus*. For both species, a segment of five vertebrae were removed from under the first dorsal fin of each individual, the neural and haemal arches removed, and the remaining centra cleaned, air dried and stored in vials. One of these centra were randomly chosen to be scanned using NIRS, with the vertebral diameter measured and plotted with L_{ST} to determine if vertebral growth was proportional to somatic growth.

The potential of a fin clip to be applicable for ageing deepwater chondrichthyans and for non-lethal ageing was investigated, as taking a fin clip is a non-lethal sampling method that is widely accepted, being commonly used for genetic samples (Heist 2004). As far as the authors are aware, fins have not been previously used in a chondrichthyan ageing study, consequently their utility as an ageing structure has not been investigated and it is unknown what part of the fin structure, if any, may be useful for ageing. Thus, practical reasons dictated the size of the piece of fin removed; to match the 2 cm diameter of the NIRS instrument sample window, a standard sized 2 cm square piece (termed fin clip), was cut from the trailing edge of the left pectoral fins of all *S. megalops* and *A. pallidus* (Figure 7.2). While the proportion of the pectoral fin sampled varied due to size differences among individuals, the left pectoral was used for all fin clips to maintain some consistency. For both species, the whole animals were stored frozen prior to pectoral fin samples being taken. The fin clips appeared to be very moist, possibly due to the high humidity at the time the fin clips were taken, and as water absorbs strongly in the NIR region and can mask the spectra of other materials (Wedding 2007), the whole fin clips were pinned to keep them flat and oven dried at 50°C for 4 hours to remove excess moisture, then stored in envelopes.

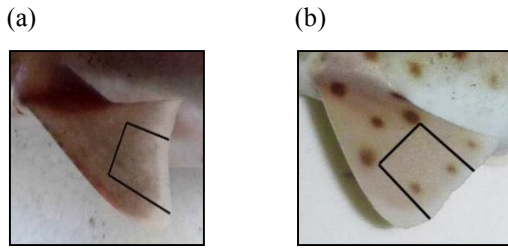


Figure 7.2 Fin clips taken from the left pectoral fin of (a) *S. megalops* and (b) *A. pallidus* indicated by the black square.

7.2.3 Age estimation

Squalus megalops and *S. montalbani* were aged by counting growth bands on their DFS (Chapter 5). As *A. pallidus* have no hard parts that can be used to visually estimate age, the L_{ST} was used as a proxy for age, for the sampled vertebrae and fin clips. We recognise that considerable variability in growth rates among individuals and the asymptotic slow growth rate of sharks (Cailliet *et al.* 1986) renders total length not ideally suited for age estimation, but in the absence of any other means of age estimation we decided to use L_{ST} as a rough proxy for age estimation. To fully demonstrate the utility of this NIRS method for catsharks, future work to provide validated reference ages will be required.

7.2.4 Spectral acquisition and data analysis

To obtain the NIRS spectra, each whole dried vertebral centrum, DFS and fin clip were scanned by a Bruker multipurpose analyser (MPA), Fourier Transform (FT) NIR spectrophotometer (Bruker Optics, Ettlingen, Germany; operating software : OPUS™ version 6.5) in the 12 500–3600 cm^{-1} wavenumber range (corresponding to wavelengths of 800–2778 nm; wavenumbers are the inverse of wavelengths). The reference calibration for the Bruker MPA was automatically provided by a gold plated internal standard. Each individual structure was hand positioned on the round integrating sphere sample window, with the centra placed face down and fin clips laid flat. The NIR light irradiated the structure, with the diffusely reflected NIR light detected and analysed. Sixteen individual scans at every of 8 cm^{-1} of wavenumber were taken and averaged (by the software) to produce a raw NIRS spectrum, which took about 16 seconds per structure.

The whole DFS were up to 5 cm in total length and as such, were mostly longer than the 2 cm diameter integrating sphere sample window on the Bruker MPA spectrophotometer. A different

unit was tried that provided a larger spectral scan diameter of approximately 5 cm, that is, the Bruker Matrix-F, FT-NIR spectrophotometer coupled with an external halogen light source. However, due to the intense heat produced by the light source, the DFS heated up substantially, which could potentially damage the DFS and change the NIRS spectral characteristics. Thus, the 2 cm diameter integrating sphere sample window on the Bruker MPA was used for all the DFS, resulting in just the anterior 2 cm part of the enamel cap being scanned on most DFS. All DFS were scanned in two positions, a lateral and plan orientation, as orientation may potentially affect the NIRS spectral output.

For the structure (DFS, vertebrae and fin clips) from each species, the NIRS spectra of the structure and the estimated-ages were compared to see if a calibration model could be developed, that is, for *S. megalops* DFS, *S. montalbani* DFS, *S. megalops* vertebrae, *A. pallidus* vertebrae, *S. megalops* fin clips, and *A. pallidus* fin clips. The *S. megalops* and *S. montalbani* DFS models used the estimated-ages from the DFS band counts. The *S. megalops* vertebrae and fin clips models used the estimated-ages of the DFS band counts, from the DFS sampled from the same animals from which vertebrae and fin clips were removed. The *A. pallidus* vertebrae and fin clips models used L_{ST} as the proxy for estimated-age.

Chemometric analyses methods were used to build each of the calibration models. These methods included partial least squares (PLS) regression, which for each model attempted to establish a regression relationship between all the NIRS spectra of the structure and all their estimated-ages. The regression relationship of the calibration model was represented by a single plot that defined the weights given to the different wavelengths in the linear PLS regression equation, with regression coefficients on the y-axis and wavelengths (expressed as wavenumbers) on the x-axis. If a calibration model could be developed, it was analysed further to identify the specific NIRS wavelengths within the plot that represented the molecular compounds in the structure most strongly related to their estimated-ages. The final calibration models were presented for each species's structure as 1) a calibration model plot, 2) calibration model statistics, and 3) a calibration model regression graph of the predicted NIRS-ages against the estimated-ages (Murray and Williams 1987; Foley *et al.* 1998; Wedding 2007). This chemometric process is explained in further detail below. All data analyses were undertaken using a multivariate software package 'The Unscrambler' version 9.8 (Camo, Oslo, Norway).

As a first step in the analyses, prior to the PLS, raw NIRS spectral data often needs to be mathematically transformed to both remove noise in the raw spectra mostly caused by instrument effects, and to enhance the visual resolution of spectral peaks (Reich 2005; Wedding

2007). The raw spectra for all the scanned first DFS of *S. megalops* provide an example of their appearance (Figure 7.3). The same pre-treatments and subsequent analyses applied in Chapter 6 were used.

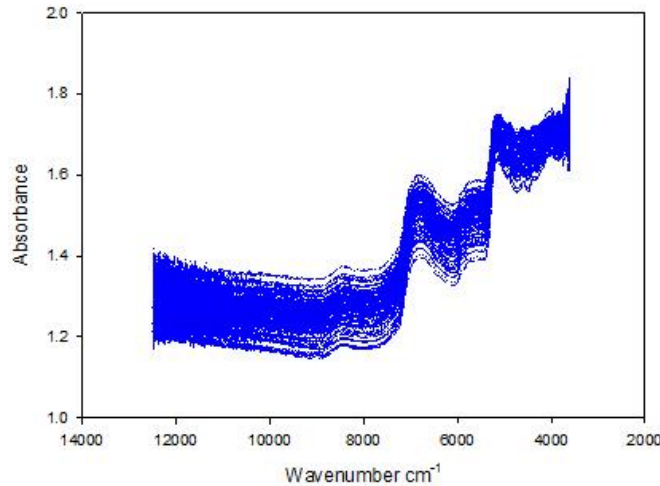


Figure 7.3 Raw NIRS spectra for all 97 first DFS of *Squalus megalops*.

The optimal calibration model was the model that best predicted age (NIRS-age), and was defined by a combination of several statistical criteria, that is, the combination of the highest possible coefficient of determination (R^2), the lowest root mean square error of cross-validation (RMSECV; the error in years of the predicted NIRS-age), the least number of terms, or factors, and the lowest bias (Wedding 2007; Williams 2008). Bias was the average difference between the estimated-ages and the predicted ages (NIRS-ages) (Williams 2008). The Standard Deviation Ratio (SDR = standard deviation of the estimated-ages/RMSECV) was calculated to enable comparisons of model performance among the species's structures; the higher the SDR, the greater the relative predictive power of the model (Golic and Walsh 2006; Wedding 2007). To investigate if size correlated with the NIRS spectra, calibration models were developed between the L_{ST} of the *S. megalops* and the NIRS scans of their dorsal fin spines, vertebrae and fin clips. These L_{ST} calibration models used the same spectral areas as each of corresponding structure's optimal estimated-age calibration models.

To determine whether NIRS scans produced consistent results between the first and second DFS, that is, could be used to develop calibration models that predicted the same age, a *S. megalops* calibration model was developed using the 39 first DFS estimated-ages and was used

to predict the ages of the second DFS from the same 39 *S. megalops*. A linear regression compared the predicted NIRS-ages of the second DFS against the estimated-ages of the second DFS. This method was also applied to assess if orientation of the DFS during scanning affected the age predictions.

7.3 Results

The estimated-ages of 97 *S. megalops* and 77 *S. montalbani*, from their DFS band counts, ranged from 5–25 years for *S. megalops* and 3–28 years for *S. montalbani*, with respective size ranges of L_{ST} 262–505 mm and 351–866 mm (Chapter 5). The *A. pallidus* included one neonate of 141 mm L_{ST} , with the remainder of the 99 animals ranged in size from 306–436 mm L_{ST} . There was a positive logarithmic relationship between L_{ST} and centrum diameter for both *S. megalops* ($R^2 = 0.89$) and *A. pallidus* ($R^2 = 0.84$) (Figure 7.4). This indicated that the vertebrae of both species grew in proportion to the length of the animal.

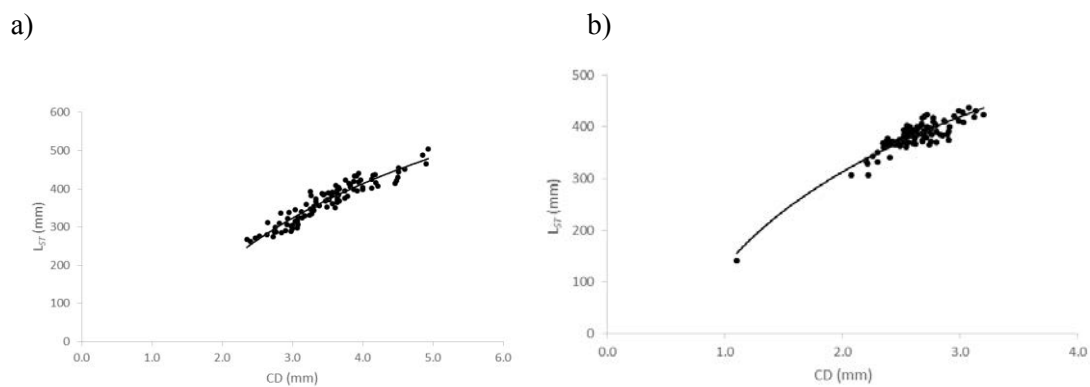


Figure 7.4 Relationship between centrum diameter (CD) and stretched total length (L_{ST}) for (a) *Squalus megalops* ($L_{ST} = 312.83\ln*CD - 20.26$; $R^2 = 0.89$) and (b) *Asymbolus pallidus* ($L_{ST} = 262.42\ln*CD + 130.91$; $R^2 = 0.84$).

7.3.1 NIRS Spectral Areas

The spectral areas that correlated most strongly to the estimated-ages of the shark structures were similar across all species and structures (Figure 7.5). This suggested that similar molecular compounds correlated to age (DFS and vertebrae) and size (fin clips) were being detected by the NIRS method. There were three main spectral areas identified: 9300–8200, 7800–6800, and 4600–4000 cm^{-1} (Figure 7.5). Without further NIRS research on the chemistry of the structures it is not possible to relate these spectral areas to a specific chemical compound, such as calcium phosphate. Nor is it possible to define the varying importance, if any, between these three areas in relation to the correlation with age and size. At this stage, these main spectral areas can be described in terms of the main molecular compounds to which they correspond, based on a table

of group frequencies. This is a table of groups of wavelengths (frequencies) characteristic of molecules that are prominent absorbers in the NIR region, which is commonly found in NIRS textbooks (Siesler *et al.* 2002). The three main spectral areas corresponded to Carbon-Carbon alkene, CH (aromatic), -CH₃ methyl, -CH₂ methylene all combination and second overtones; CH second overtone; -NH₂ primary amines combination and first overtone; -CONH₂ primary amides combination, first and second overtones; and -CONH-secondary amides combination and second overtone.

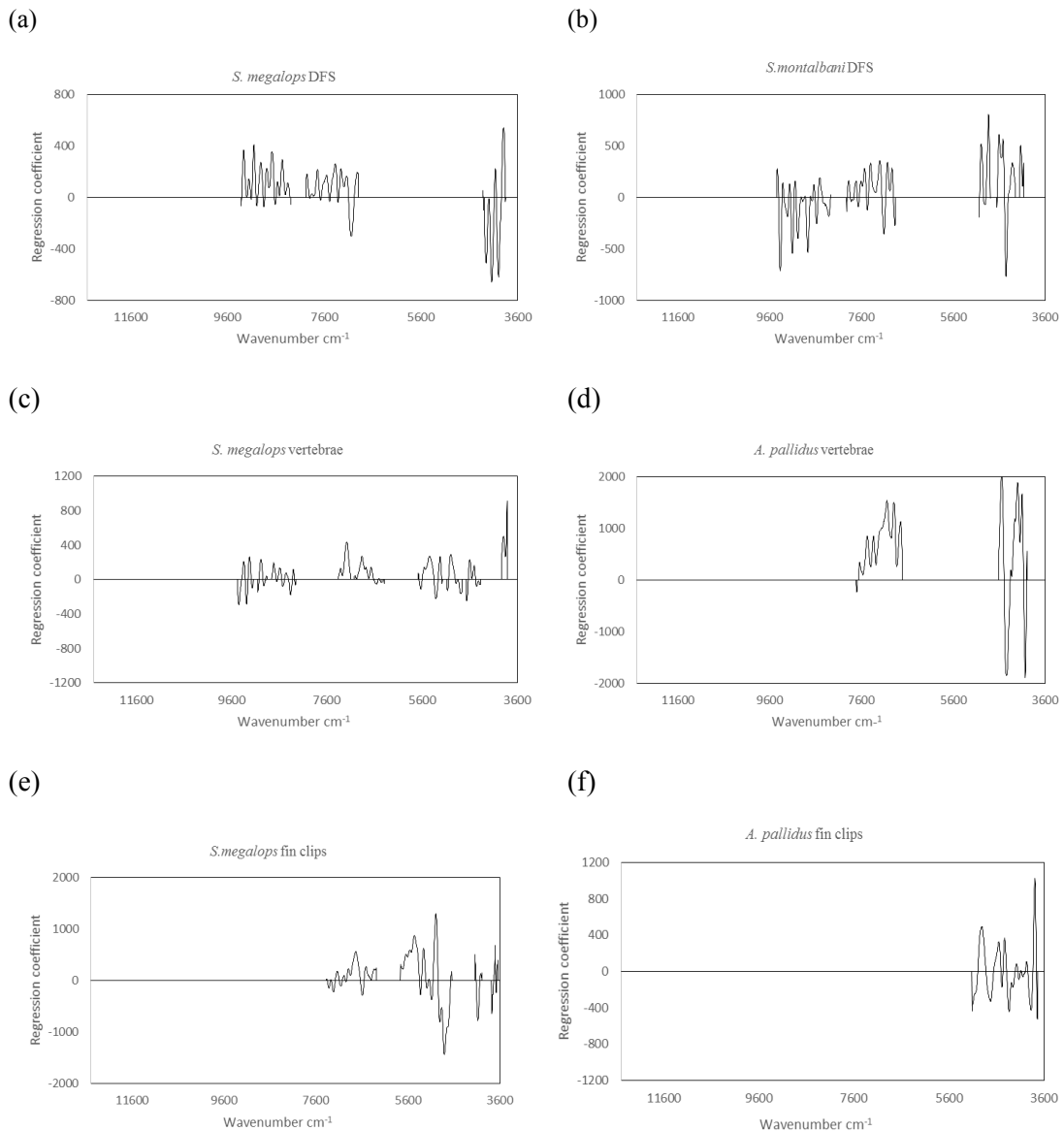


Figure 7.5 Calibration model plot for (a) *Squalus megalops* DFS, (b) *Squalus montalbani* DFS, (c) *Squalus megalops* vertebrae, (d) *Asymbolus pallidus* vertebrae, (e) *Squalus megalops* fin clips, and (f) *Asymbolus pallidus* fin clips.

7.3.2 Dorsal fin spines

The dorsal fin spines of both *S. megalops* and *S. montalbani* proved to be very useful structures for ageing using the NIRS method, as evidenced by the good relationship between their estimated-ages and the NIRS spectra, with $R^2 = 0.82$ and 0.73 , respectively (Table 7.1, Figure 7.6). The calibration model for *S. megalops* was stronger than that of *S. montalbani*, with the higher R^2 , lower error and bias, fewer terms and greater predictive power ($SDR = 2.32$ compared to 2.02) (Table 7.1).

Table 7.1 PLS regression calibration model statistics for each shark structure: coefficient of determination (R^2), the root mean square error of cross validation (RMSECV), standard deviation ratio (SDR); standard deviation (SD) is for the estimated-ages.

Structure	Samples (n)	Age & Length (yrs, mm)	SD	Terms	R^2	RMSECV (yrs, mm)	Bias (yrs, mm)	SDR
<i>S. megalops</i> DFS	97	5-25	5.59	3	0.82	2.41	-0.008	2.32
<i>S. montalbani</i> DFS	77	3-28	5.98	4	0.73	2.96	0.052	2.02
<i>S. megalops</i> Vertebrae	97	5-25	5.59	4	0.89	1.85	-0.004	3.02
<i>A. pallidus</i> Vertebrae	99	306-436*	24.5	3	0.81	10.96 [#]	0.004	2.24
<i>S. megalops</i> Fin clips	97	5-25	5.59	7	0.76	2.67	-0.058	2.10
<i>A. pallidus</i> Fin clips	100	141-436*	34.56	8	0.54	23.51 [#]	0.174	1.47

*Stretched total length (mm), # mm

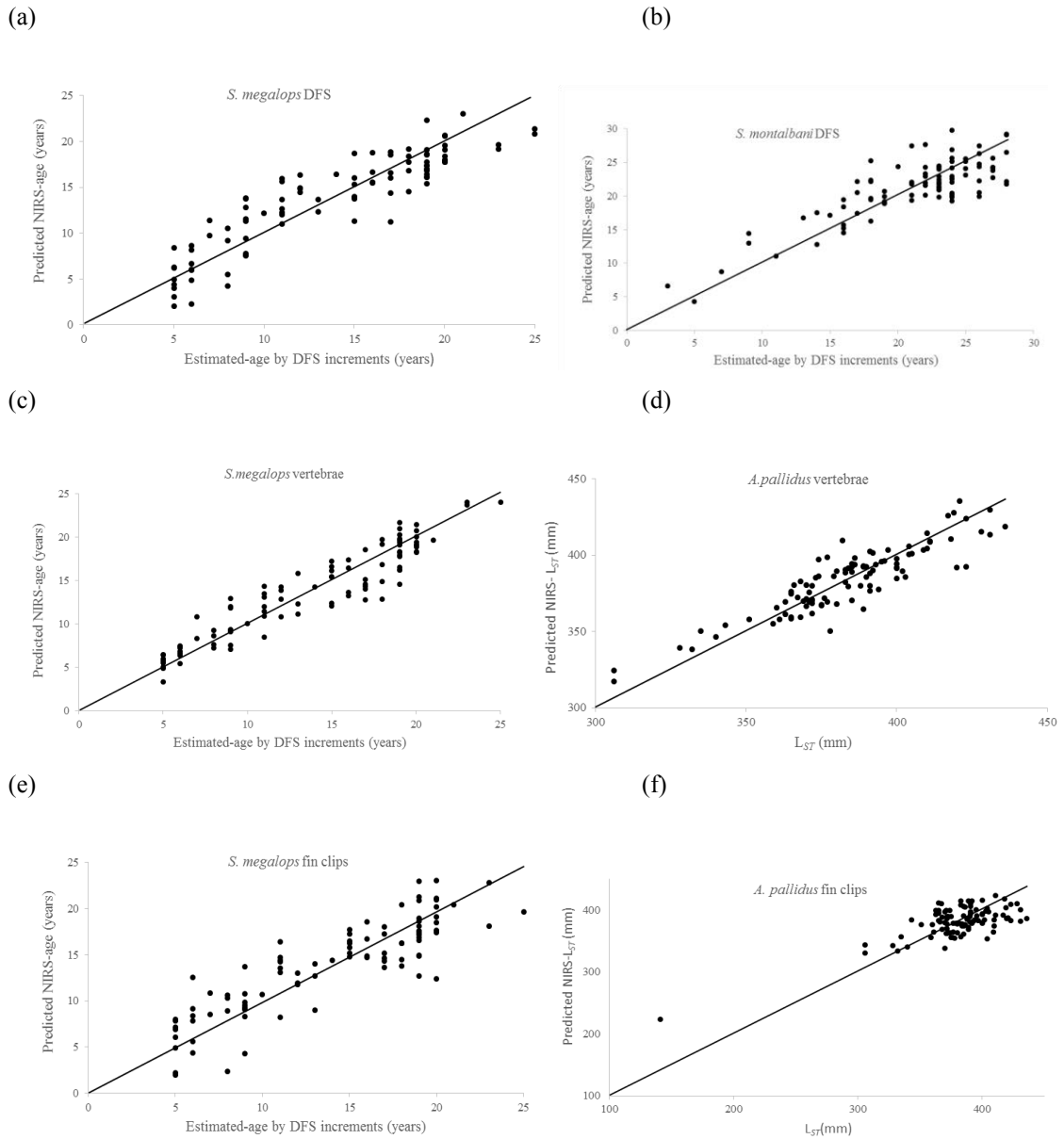


Figure 7.6 PLS Regression calibration models of predicted NIRS-age on estimated-age with a 1:1 trend line for (a) *Squalus megalops* DFS ($R^2 = 0.82$), (b) *Squalus montalbani* DFS ($R^2 = 0.73$), (c) *Squalus megalops* vertebrae ($R^2 = 0.89$), (d) *Asymbolus pallidus* vertebrae ($R^2 = 0.81$), (e) *Squalus megalops* fin clips ($R^2 = 0.76$) and (f) *Asymbolus pallidus* fin clips ($R^2 = 0.54$)

The comparison of the NIRS *S. megalops* 39 first and second DFS indicated that the NIRS calibration model of the first DFS consistently predicted the estimated-age of the second DFS as older than their actual ages, with a bias = 3.11 years (Figure 7.7); that is, the average difference between the NIRS-predicted age of the second DFS and the estimated-ages of the second DFS

was 3.11 years. The second DFS was consistently much larger than the first DFS, which is a diagnostic feature of this species (Last and Stevens 2009), and it is possible the bias was attributable to this size difference. Once the bias = 3.11 years was added to each of the estimated-ages of the 39 second DFS, the calibration model of the first DFS accurately predicted the ages of the second DFS, with a similar $R^2 = 0.82$ and error = 2.31 years, to the calibration model of all 97 *S. megalops* first DFS (Figure 7.7, Table 7.1). Similarly, orientation of the fin spine when scanned did affect the NIRS model, but in a consistent manner with a bias = 2.57 years. Once this bias correction was applied to all estimated-ages of the lateral orientation, the plan orientation NIRS calibration model accurately predicted the lateral orientation estimated-ages ($R^2 = 0.82$ and error = 2.40 years).

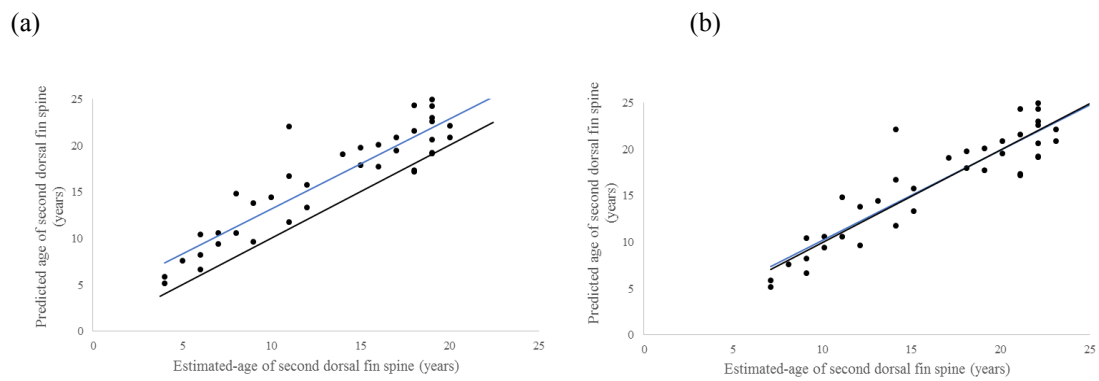


Figure 7.7 (a) Linear regression of *Squalus megalops* second DFS NIRS-predicted ages (using the first DFS calibration model) on the second DFS estimated-ages; $R^2 = 0.51$, Bias = 3.11 years; regression line and 1:1 trend line, and (b) Bias corrected linear regression of *Squalus megalops* second DFS NIRS-predicted ages (using the first DFS calibration model and bias corrected estimated-ages of second DFS) on the second DFS estimated-ages; $R^2 = 0.82$, Bias = 0.00 years; regression line and 1:1 trend line.

7.3.3 Vertebrae

The NIRS method detected changes in the *S. megalops* and *A. pallidus* vertebrae strongly related to estimated-age and size respectively, with an $R^2 = 0.89$ and 0.81 (Table 7.2, Figure 7.6). The optimal model for *A. pallidus* vertebrae excluded the neonate as it was identified as an outlier during the initial PLS regressions, most likely as it was much younger than all other samples (Table 7.1, Figure 7.6). The calibration models for the vertebrae were the strongest of all the structures. The *S. megalops* vertebrae model (based on their corresponding DFS estimated-ages) was stronger than that of the *S. megalops* DFS model with a higher R^2 , smaller age error, lower bias and higher SDR (Table 7.1). It was also stronger than the *S. megalops* fin clips model (Table 7.1). Similarly, the *A. pallidus* vertebrae model had a much stronger relationship with size ($R^2 = 0.81$) than the *A. pallidus* fin clips model ($R^2 = 0.54$) (Table 7.1).

7.3.4 Fin clips

The fin clips of *S. megalops* showed a good relationship between the estimated-ages of the animals and the corresponding NIR spectra, with an $R^2 = 0.76$ (Table 7.1, Figure 7.6). The relationship was slightly weaker than that of the *S. megalops* DFS model, evidenced by a lower R^2 and SDR and a higher bias (Table 7.1). The relationship of *A. pallidus* fin clips NIRS spectra and L_{ST} was weaker than that of the *S. megalops* fin clips model (Table 7.1, Figure 7.6). For both *S. megalops* and *A. pallidus*, the NIRS models of fin clips had the greatest number of terms, or principal components, compared to the DFS and vertebrae models (Table 7.1). This trial of fin clips for ageing using NIRS has demonstrated there was a relationship between the fin clips estimated-ages or lengths and their NIRS spectra, which indicated the NIRS detected changes in the chemistry of the fin clips that were related to age and size for *S. megalops* and *A. pallidus*, respectively.

7.3.5 NIRS calibration models of size

Size correlated with the NIRS spectra for all three *S. megalops* structures (Table 7.2). Compared to the estimated-age calibration models, the size model was stronger for vertebrae, but weaker for the DFS and fin clips (Table 7.1, Table 7.2). The L_{ST} vertebrae model had a higher $R^2 = 0.94$ and a higher SDR = 4.04, compared to $R^2 = 0.89$ and SDR = 3.02 for estimated-age (Table 7.1, Table 7.2). The DFS and fin clips L_{ST} calibration models statistics were all weaker compared to those of the corresponding estimated-age models, with lower R^2 s, SDRs and higher biases (Table 7.1, Table 7.2).

Table 7.2 PLS regression calibration model statistics for L_{ST} of *Squalus megalops* shark structures: coefficient of determination (R^2), the root mean square error of cross validation (RMSECV), standard deviation ratio (SDR); standard deviation (SD) is for the L_{ST} .

Structure	Samples (n)	L_{ST} . (mm)	SD	Terms	R^2	RMSECV (mm)	Bias (mm)	SDR
<i>S. megalops</i> DFS	97	262-505	54.27	3	0.79	25.00	-0.079	2.18
<i>S. megalops</i> Vertebrae	97	262-505	54.27	4	0.94	13.44	0.105	4.04
<i>S. megalops</i> Fin clips	97	262-505	54.27	7	0.74	27.32	-0.477	1.99

7.4 Discussion

This study demonstrated that the NIRS spectra correlated with ages for dorsal fin spines, vertebrae and fin clips, and that the technique has the potential for non-lethal ageing of two of the structures. Once a calibration model has been developed, NIRS can be used to predict the estimated-ages of deepwater sharks using their dorsal fin spines, and both fin clips and poorly calcified deepwater shark vertebrae where no banding is visible. In light of the successful NIRS ageing of saddletail snapper using whole otoliths, where the NIRS calibration model had $R^2 = 0.94$ and error = 1.35 years (Wedding *et al.* 2014), this technique may have application as an ageing tool for both cartilaginous and bony fishes.

For both deepwater squaloids, *S. megalops* and *S. montalbani*, the NIRS analyses of dorsal fin spines produced calibration models with a good ability to predict estimated-ages up to the maximum ages in this study of 25 and 28 years, respectively. Around 100 animals were sufficient to develop a NIRS calibration model, with further ageing able to be done objectively by scanning the fin spines with the NIRS instrument and applying the NIRS model to predict the estimated-ages of that species. The ageing would also be rapid, as the predicted NIRS-age was determined from a 16 second scan, without the need for sectioning or enhancement of the fin spines. Some random checks to monitor the age predictions would be required, by occasionally using traditional ageing of the fin spines to verify the predicted age estimation (Siesler *et al.* 2002). Calibration models are generally transferable between different spectrophotometer instruments, though the calibration model usually needs adjustments such as bias correction due to instrument differences, and random verification of predicted age estimates should be conducted (Fearn 2001; Feudale *et al.* 2002; Cao 2013). While the NIRS method needs to be used in conjunction with traditional ageing methods and is not a validation method in itself, it does provide verification of the band counts and most importantly, it can provide age estimations of fin spines that have not been traditionally aged. The advantage of the rapid age determinations offered by NIRS could assist to broaden sampling programs to encompass age estimations of the many squaloid species for which there are currently insufficient age and growth data (IUCN 2013) for fisheries and conservation management strategies.

The NIRS ageing method also clearly indicated that, despite not being visible as growth bands, chemical changes occurred in the vertebrae of *S. megalops* and *A. pallidus* strongly correlated with age and size. This has previously been reported for another squaloid, piked dogfish *Squalus acanthias* Linnaeus 1758, that ranges from inshore to deep waters (Last and Stevens 2009), and whose vertebrae have no observable banding (Jones and Geen 1977). X-ray

spectrometry indicated a cyclical pattern of the ageing materials calcium and phosphorous, which was considered to suggest seasonal changes in rates of deposition with an annual cycle (Jones and Geen 1977). X-ray spectrometry analysed individual elements by scanning across a vertebral section (Jones and Geen 1977), whereas NIRS detected the chemical composition of the entire vertebrae at a molecular bond level, though the resultant spectra were complex and difficult to relate directly to an element, which is a limitation of the NIRS method that is discussed further below (Murray and Williams 1987). While the elemental identification enabled by X-ray spectrometry was very useful, the method was extremely time consuming and expensive (Jones and Geen 1977; Cailliet and Radtke 1987), which may have been the reason it has not been explored further for shark age estimation.

Interestingly, NIRS detected changes in the chemistry of the fin clips that were also correlated with age and size. *Squalus megalops* fin clips estimated-ages were based on the band counts of the dorsal fin spines, which reinforced the indication that the NIRS is actually detecting changes in the fin clips associated with age. The *A. pallidus* fin clips NIRS model demonstrated there was a relationship between fin clips and size, however the plot spectral regions were the most limited, and it was the weakest model of all species and structures. The fin clips spectra may have not related well to L_{ST} as length may not be a particularly good proxy for age for this species. The surface of the fin clip is entirely covered in minute dermal denticles that have a similar chemical composition to dorsal fin spines and vertebrae (Hamlett 1999). However, dermal denticles have always been considered unsuitable for ageing, as they do not grow continuously throughout the life of the animal (Maisey 1979; Reif 1982). They can only grow to a definitive size, based on the size of the underlying dermal papilla, then they are discarded and replaced by larger dermal denticles, though this is not synchronous, with individual denticles replaced independently of their neighbours (Maisey 1979; Hamlett 1999). Perhaps at any given age, there are sufficient numbers of dermal denticles in a fin clip that represent the age of the animal, and that have not yet been discarded, to enable the age to be predicted with NIRS. Alternatively, either some or all of a fin's internal mineralised components, cartilaginous platelets, radials and ceratotrichia, may represent the age of the animal (Clement 1992; Hamlett 1999; Vannuccini 1999). The proportion of these components in each fin clip sample may have varied within and between the two species studied, as the fin clip samples were a consistent size but from different sized individuals, and there is variability in the relative size of these components among species (Compagno 1977; Grogan and Lund 2004). Based on available

evidence, it was not possible to determine which components of the fin clips would be reliable structures for age estimation (Campana 2001), and accordingly whether the NIRS age predictions were from dermal denticles, platelets, fin internal radials or ceratotrichia, or from a combination of the four.

NIRS spectra of the deepwater dorsal fin spines, vertebrae, and fin clips contained a large amount of information about the chemistry of each of the structures, yet the spectral areas that correlated most strongly with age were similar for all structures. This suggested that chemical changes in the structures associated with age were detected by the NIRS method. These chemical changes could have been related to hydroxyapatite $3(\text{Ca}_3\text{PO}_4)_2 \cdot \text{Ca}(\text{OH})_2$, the primary growth mineral in all chondrichthyan hard parts (Hamlett 1999). It forms the basis of all ageing structures examined in this study: calcified cartilage of vertebrae, fin clip radials, platelets and ceratotrichia (Walker *et al.* 1995; Hamlett 1999; Vannuccini 1999); and dentine and enamel of dorsal fin spines and fin clip dermal denticles (Ketchen 1975; Maisey 1979; Hamlett 1999). The deposition of hydroxyapatite within an organic matrix creates the growth bands used for ageing, with different ratios of the mineral and organic matrix producing two optically distinct opaque and translucent bands (Casselmann 1974; Kerr and Campana 2014). However, the specific chemical compound in the structures that correlated to the NIRS spectra is unknown at this stage. A limitation of NIRS is that the spectra are very complex and chemical elements in other components of the structures will also be present in the spectral information (Murray and Williams 1987; Siesler *et al.* 2002; Wedding *et al.* 2014). To determine the identity of the chemical compounds that could be related to the ages would require considerably more research into NIRS and the chemistry of shark ageing structures, which is beyond the scope of this study. The potential future work to determine this is described in Chapter 8.

The NIRS spectra also correlated with size for all three structures. NIRS is likely detecting changes in the structures' chemistry associated with both age and size, evidenced by correlations between the NIRS spectra of the structures and both of these parameters. Compared to the estimated-age calibration models, the strength of the size calibration models was variable, with the vertebrae model stronger but fin spine and fin clips models weaker. More accurate L_{ST} measurements compared to estimated-ages may be the reason the vertebral size model was stronger than that of vertebral estimated-ages, since with NIRS, the more accurate the reference information, the stronger the calibration model (Siesler *et al.* 2002; Williams 2008). Though it would then be expected that the DFS and fin clips size models would also be stronger than their corresponding estimated-age models, which was not the case. These findings are inconclusive, and while NIRS may be detecting changes in both size and age, further work is needed to both

clarify this, and to determine whether NIRS can be used to predict age in older animals that have reached their maximum size. The latter issue could not be examined in this study as the largest *S. megalops* specimen was 505 mm and 25 years, whereas they are reported to reach 640 mm and 28 years in southern Australia, and 825 mm and 32 years in the Atlantic Ocean (Braccini *et al.* 2007; Last and Stevens 2009; Pajuelo *et al.* 2011). To enable a robust comparison of older age and size calibration models, a good sample size would be required of individuals that have reached maximum length and continued to age.

The stronger estimated-age and L_{ST} calibration models of vertebrae compared to those of dorsal fin spines and fin clips, may have been due to chemical differences in structures that created more variability in the dorsal fin spine and fin clips spectral information. This was particularly evident in the fin clips NIRS models, where more terms were required to develop an optimal model, a possible indication of greater spectral variability (Murray and Williams 1987). This may also account for the inclusion of the *A. pallidus* neonate in the weaker fin clips model that was excluded from the stronger *A. pallidus* vertebrae model, where the NIRS spectra were less variable and better correlated to the small size differences among all the larger animals. The fin clips may have absorbed variable amounts of moisture after they were dried. This was a first investigation and methodological improvements in subsequent work, such as storing dried fin clips in a desiccator, may enable more accurate NIRS models to be developed using fin clips.

Squalus megalops vertebral estimated-ages were provided from the dorsal fin spines, not the vertebrae themselves, and the stronger vertebrae NIRS estimated-age calibration model implies that, in addition to the spectra of the vertebrae being less variable than those of fin spines, the estimated-ages from band counts of the fin spines were good estimates of all ages, including those of the older spines. This raises the possibility that dorsal fin spine age estimation with older animals may not be subject to the issue of age under-estimation that can occur with vertebral band counts of older animals, which is caused by either difficulties in discerning growth bands, or a decrease or cessation in band pair deposition (Francis *et al.*, 2007; Natanson *et al.*, 2013). The limited studies of older dorsal fin spines where they have been validated or verified, support this hypothesis (Campana *et al.* 2006; Braccini *et al.* 2007; Pajuelo *et al.* 2011). Dorsal fin spines growth bands counts of *S. acanthias* were validated for animals up to at least 45 years of age (Campana *et al.* 2006), and those of *S. megalops* verified as annual up to 32 (Pajuelo *et al.* 2011) and 28 years of age (Braccini *et al.* 2007).

Non-lethal ageing of sharks with dorsal fin spines and fin clips is potentially feasible using the NIRS approach. As most of the NIRS scans were of just the tip of the DFS, and with the precision and accuracy of hand-held NIRS units improving (Herberholz *et al.* 2010; Alcalà *et al.* 2013; O'Brien *et al.* 2013), ageing of squaloids could potentially be done in the field using a hand held NIRS unit to scan the DFS on a live animal. Either of the two spines could be scanned; the consistent difference in age prediction of the *S. megalops* NIRS calibration models of the first and second DFS was possibly attributable to the larger second DFS having a greater absolute amount, but same relative proportion, of ageing material than the first DFS. Beyond about the 100 animals required for a calibration model, further age determinations of squaloids could be non-lethal and enable provision of a larger sample size to improve reliability of assessments (Kritzer *et al.* 2001; Thorson and Simpfendorfer 2009). This would be beneficial for stock and risk assessments of commercially targeted dogfish, such as *S. acanthias* (Sulikowski *et al.* 2013), listed by the IUCN Red list as Vulnerable. Fin clips could be easily collected in the field, and while NIRS estimation of age would require manual ageing of another structure from the animal for the calibration model, such as dorsal fin spines or calcified vertebrae, it could have a wider applicability beyond just deepwater species. Large-scale chondrichthyan sampling programs may benefit by facilitating the ageing of large numbers of easily collected samples. For example, this could improve regional population assessments of sharks taken as bycatch in the tuna fisheries, which are currently hampered by the quality and quantity of data (Clarke *et al.* 2013).

Future studies of NIRS for shark ageing should consider the influence of sexually dimorphic growth rates common in sharks (Cortés 2000; Cailliet and Goldman 2004), and regional variability. The NIRS *S. montalbani* model may have been weaker than that of *S. megalops* DFS model as it included both sexes, compared to the single sex used for *S. megalops*. Further, the *S. montalbani* samples were from a large geographic range, while those of *S. megalops* were all from a relatively small area. This may have caused more variability in the spectral characteristics of the *S. montalbani* dorsal fin spines, as different water bodies can affect chemistry of the age structure (Tillett *et al.* 2011; Kerr and Campana 2014), and the corresponding spectral characteristics (Wedding *et al.* 2014).

The NIRS approach to ageing has a broad utility for deepwater sharks. While it needs to be used in concert with traditional ageing by band counts to develop a calibration model, it then has the ability to rapidly predict the estimated-ages of deepwater sharks using dorsal fin spines. It offers a method that would facilitate age estimations for many deepwater squaloids to improve their

conservation and fisheries management. NIRS also detected changes in the poorly calcified deepwater shark vertebrae correlated with ageing, which with further NIRS work, could enable ageing of deepwater chondrichthyans vulnerable to exploitation that cannot currently be aged by traditional band count methods. The NIRS method presents the potential for non-lethal ageing with dorsal fin spines and fin clips, which provides capacity to significantly reduce the numbers of sharks that need to be lethally sampled with a wider applicability beyond deepwater sharks. The NIRS approach was used on a range of shark structures and, based on similarity of age structures across chondrichthyans, it is likely to also be effective for batoids and chimaerids.

Chapter 8 General discussion



Sunset at sea

8.1 Conclusions and implications

Life history traits

Chondrichthyan life history traits are associated with the three distinctive marine habitats: shelf, pelagic and deepwater (Clarke *et al.* 2003; Garcia *et al.* 2008; Chapter 2). Species from deep habitats on average grow more slowly, mature later and live longer than those in shelf and pelagic habitats; an observation strengthened by this dissertation through a robust analyses of a larger data set of deepwater species than previously available (Chapter 2). These typical deepwater chondrichthyans traits were exhibited by the species taken as bycatch in the deepwater eastern king prawn fishery in the southern GBRMP. Although they were from a diverse range of chondrichthyan taxa, they had generally slow growth rates, relatively late ages and sizes at maturity, small litters, low ovarian fecundity and moderate to long life spans (Chapters 3, 4 and 5). This combination of traits suggests that these species captured within the EKP fishery generally have low biological productivity (i.e. low ability to sustain fishing pressure or recover from overfishing) (Simpfendorfer and Kyne 2009). However, variability was evident among the species' life history traits and their depth and spatial distribution that would likely result in varying degrees of resilience to fishing pressure, assuming that fishing mortality was the same among species. This highlights the need for species to be individually assessed to accurately determine their productivity and susceptibility to commercial fishing.

The differences in life history traits displayed by the four species for which age and growth was analysed are likely associated with their depth distribution. The skate, *D. polyommata*, which inhabits the shelf and upper slope at depths of 135–320 m had the fastest growth rate, shortest longevity of 10 years (Figure 8.1). It also had the earliest ages of maturity of 4–5 years. These traits were typical of small–medium bodied skates from both shelf and deepwater habitats (Gallagher *et al.* 2005; Frisk and Miller 2006; Treloar 2008), which is not surprising given *D. polyommata* distribution encompasses both shelf and upper slope waters. The gummy shark, *M. walkeri* which also inhabits shelf and upper slope waters but to deeper depths (403 m) than the skate, had a slower, moderate growth rate, greater longevity of 16 years and older ages at maturity of 7–10 years (Figure 8.1, Chapter 4). These traits were not typical of *Mustelus* species (Walker *et al.* 1998; Francis and Maolagáin 2000) and likely a reflection of the greater depth of occurrence than most *Mustelus* species. The two *Squalus* species, *S. megalops* and *S. montalbani* which are found at the deepest depths (732 and 670 m, respectively) had the slowest growth rates, were the longest lived at 25 and 28 years, respectively (Figure 8.1) with the latest

ages at maturity of 13–19 and 22–26 years, respectively (Chapter 5). These conservative life history traits were typical of deepwater squaloids (Kyne and Simpfendorfer 2010; Graham and Daley 2011; Irvine *et al.* 2012).

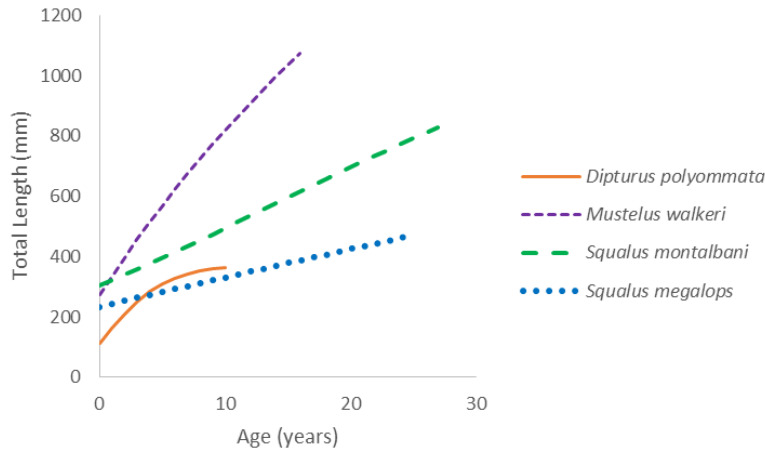


Figure 8.1 Best fit growth models fitted to length at age data for combined sexes of the four species; *Dipturus polyommata* Gompertz; *Mustelus walkeri* von Bertalanffy; *Squalus montalbani* Gompertz; and *Squalus megalops* von Bertalanffy.

This reinforces the finding in this dissertation that within the deep habitat, across all deepwater chondrichthyan taxa, there were differences in life history traits down the continental slope. With increasing depth, species matured at a later age and lived longer. They also had smaller litters and bred less frequently, a combination of traits that indicates a marked decline in productivity with depth (Chapter 2). Based on life history traits and the assumption that fishing mortality was the same, among the four species studied it is likely that *D. polyommata* is the most biologically productive, followed by *M. walkeri* and then the dogfish. The two dogfish both had very slow growth rates, and although *S. montalbani* grew slightly faster than *S. megalops* (Figure 8.1) it was longer lived, matured later and had a potentially longer reproductive cycle than *S. megalops* (Chapter 5). These trait differences may be due to their different depths of distribution. *Squalus megalops* occurs mainly on the shelf and shallower depths of the upper slope, only being recorded to depths of 580 and 732 m occasionally (Compagno *et al.* 2005; Last and Stevens 2009). In contrast, *S. montalbani* does not occur on the shelf and tends to remain deeper, being restricted to upper slope waters at 295–670 m (Last and Stevens 2009). The suite of *S. montalbani* traits would lead to lower productivity and greater vulnerability to exploitation, and in areas where it has been overfished, the population has shown dramatic population declines of > 90% in relative abundance (Graham *et al.* 2001; Kyne and Simpfendorfer 2010). Even with the management arrangements instituted after these

declines were observed to protect the vulnerable dogfish (AFMA 2012b), the life history traits elucidated from this study indicate these overfished *S. montalbani* populations may take decades to recover.

While both of these dogfish species have wider distributions beyond Australia, all other species taken in the EKP fishery were endemic to Australia with half of them only occurring in waters offshore from Queensland (Chapter 3). This supports the general concept of high levels of endemism and geographically restricted distribution among deepwater chondrichthyans that reduces their potential resilience to fishing pressure (Kyne and Simpfendorfer 2010). It also emphasises the need for information on the catch composition and frequency of capture of these species where they are exposed to fishing pressure (Pears *et al.* 2012).

This dissertation found despite their restricted geographic distributions, none of the species occurred only within the area of the deepwater eastern king prawn fishery at Swain Reefs. All species had refuge outside the fishery both spatially and at depth (Chapter 3). Their frequency of capture is also an important consideration when assessing their risk from the fishery (Pears *et al.* 2012). The likely most productive *D. polyommata* was caught the most frequently but it is probably not exposed to fishing pressure across other areas of its distributional range where there are no other active deepwater trawl fisheries (Chapter 4). The more vulnerable *M. walkeri* was infrequently captured in the deepwater EKP fishery, though it may experience fishing pressure from deepwater line fisheries in other parts of its range (Sumpton *et al.* 2013; Chapter 4). Of the two, more widely distributed dogfish, *S. megalops* was mostly caught outside the main fishing grounds and although *S. montalbani* occurs within the Great Barrier Reef Marine Park it has not been recorded from the deepwater EKP fishery, probably as its upper depth limit is at a depth fished very rarely in the deepwater EKP fishery. All other species were captured very infrequently, except the catshark *A. pallidus* which appeared to have a size segregated distribution as mostly adults were captured (Chapter 3).

In summary, the deepwater chondrichthyans bycatch species are currently considered likely at low risk from the deepwater EKP fishery, mostly as they have refuge outside the fishery. However, their life history traits engender vulnerability to exploitation and any change in fishing practices in the Swain Reefs area that lead to an increase in catch susceptibility, such as expansion in area fished, could place species at risk of depletion. In addition, the variability in

life history traits leads to varying resilience to fishing pressure and the species composition and catches should be monitored to ensure the sustainability of all the deepwater chondrichthyans bycatch species within the GBRMP.

Policy and management implications

The findings of this dissertation indicate that the most effective management and conservation of deepwater chondrichthyans would be achieved by a policy focussed solely on deepwater chondrichthyans. Such a policy should be conservative with a precautionary approach to all deepwater chondrichthyans but especially for the deeper occurring species. One of the most pressing findings from this dissertation is that the deeper the fishing, the less capacity the chondrichthyans have to recover. A policy could include triggers for more stringent protection for the deeper occurring species, particularly those that are exposed to fishing pressure. The very limiting life history of these deeper species makes them highly vulnerable to over-exploitation and consequently, the margin for error in their management is very small. Once they are overfished, recovery of populations' biomass to ensure their long term survival can take decades, even after management measures to promote recovery are enacted. This is evident in the trawl fishery off New South Wales where along with *S. montalbani*, a suite of dogfish species were overfished and it is considered some species will take decades for their populations to recover (AFMA 2012b; Williams *et al.* 2013; Georgeson *et al.* 2014).

A recent assessment of the threat of extinction risk of all chondrichthyans found that deepwater chondrichthyans are currently less threatened than their coastal relatives because they are comparatively less exposed to current fishing pressure and inaccessible to most fisheries (Dulvy *et al.* 2014). That may be the case at the moment but trend analyses indicate that with the decline of coastal fisheries resources, increasing demand and new technology, fishing effort is moving into deeper waters (Morato *et al.* 2006b; Watson and Morato 2013). As this trend continues, a greater proportion of deepwater chondrichthyans will be exposed to fishing pressure and implementation of a deepwater chondrichthyans policy would help facilitate more effective management of this group of chondrichthyans and ensure they are not placed at a high risk of extinction.

A deepwater chondrichthyans policy could include the capacity to explore the potential of both closing areas to fishing to avoid interactions with the deeper occurring species and employment of catch quotas for areas that remain open to fishing. A policy could guide these explorations for all fisheries rather than on individual fishery by fishery basis. Deepwater chondrichthyan management measures were effected off the east Australian coast where a series of spatial

closures were implemented and a multispecies quota applied on the take of all deepwater shark species combined (AFMA 2012, Georgeson et al. 2014). In addition, a ban on trawling below 700 m to protect orange roughy (*Hoplostethus atlanticus*) stocks also provided protection to the deepwater shark species (AFMA 2012, Georgeson et al. 2014). A depth limit to bottom trawling to manage deepwater fisheries is also currently being debated by the European Union, in recognition of the vulnerability of targeted and bycatch fish and deepwater shark species and consideration over whether deepwater fisheries can operate in an ecologically sustainable manner in deeper waters (Clarke *et al.* 2015).

A policy would need to include the ability to review and change any management measures regularly to enable incorporation of any new biological and distribution information on the species, and any changes to catch data that occur as a result of the measures. Flexibility would also be required to enable responses to alterations to fishing practices, such as effort creep and new fishing technologies. A research and monitoring component of the policy could prioritise the deepwater chondrichthyans with respect to those species being taken by a fishery, and promote support for better recording of such species through logbooks, onboard electronic monitoring techniques and observers.

A research component could also encourage taxonomic surveys in data poor areas, especially those regions exposed to deepwater fisheries or where fisheries may expand into deeper waters. This dissertation reinforced the knowledge that deepwater chondrichthyans have high levels of endemism and are often geographically restricted. It is important to clearly define the geographic and depth range of the deepwater chondrichthyan species to ascertain the percentage of the stock exposed to fisheries, and enable a more accurate assessment of the risk of the fishery to the species.

Further to a policy research component, is the implicit need for species-specific life history studies. Variability in life histories among deepwater chondrichthyan results in varying degrees of resilience to fishing pressure, as evident in this dissertation. The management measures off eastern Australia encompass a large number of deepwater dogfish species (Georgeson *et al.* 2014), yet the various species may be responding differently to the measures, depending on their individual life histories. The effectiveness of the measures could be better assessed if the life histories of each species were better understood. A policy could also support deployment of

the best available techniques to improve life history information, in consideration of the current recognised limitations in age and growth data for deepwater chondrichthyans. New approaches, such as near infrared spectroscopy, could enable progress towards addressing these limitations.

A policy could also include recognition of regional variability in the deepwater chondrichthyans life history traits. Such variability was indicated in the summary of life history traits in Appendix A and obvious in a couple of deepwater species collected from the EKP fishery; that is *S. megalops* and *U. bucculentus*. These regional differences in population traits have implications for management strategies used to maintain sustainable catches. This dissertation has provided information that has compounded the need for a distinct policy for deepwater chondrichthyans. It has also provided direction for such a policy that would enable more effective management and conservation of this inherently vulnerable group of chondrichthyans.

Age and growth data

Age information is important for management strategies under a deepwater chondrichthyans policy. Yet for many deepwater chondrichthyans age data cannot be provided because the species are unable to be aged using the current methods (Cailliet 1990; Cotton *et al.* 2014). This dissertation demonstrated that near infrared spectroscopy (NIRS) can be used to estimate the age of sharks. The NIRS method had a good ability to accurately predict the ages of a coastal and a coastal-pelagic species from their vertebrae that have visible banding (Chapter 6). This was an important step as the ages of these two species had been validated and were known to be accurate. This clearly demonstrated that NIRS was detecting and predicting the ages correctly and accurately. For deepwater dogfish, the NIRS method was also found to be able to predict estimated ages using the dorsal fin spines, as shown for two species, *S. megalops* and *S. montalbani* (Chapter 7). Thus, for chondrichthyan species that have age structures with visible banding, only 80-100 individuals from a species need to be aged traditionally, then this NIRS approach can be used to estimate ages of many more individuals of the species, rapidly and cost-effectively. It would be particularly beneficial where large numbers of vertebrae or dorsal fin spines need to be aged, such as for inclusion in stock assessments for commercially captured sharks and risk assessments for deepwater dogfish encountered as bycatch (Sulikowski *et al.* 2013; Oliver *et al.* 2015).

More relevant to the progression of ageing deepwater chondrichthyans that lack age structures with visible banding, was that NIRS also detected changes associated with age in the chemical composition of the vertebrae and fin clips where no growth bands are visible (Chapter 7). The NIRS spectra correlated very well with age for these structures and the region of the spectra

associated with age were similar for the dorsal fin spines, vertebrae and fin clips. This similarity compounds the evidence that the chemical changes were related to age and that the chemical compounds detected are possibly related to hydroxyapatite, the primary growth mineral in all three of these structures (Hamlett 1999). It was beyond the scope of this dissertation to determine this as considerably more research is required and detailed in future research below. However, this detection of ageing in the chemistry of a structure that cannot be aged by traditional band counts opens the way to a whole new approach to ageing that could enable ageing of deepwater chondrichthyans that currently cannot be aged.

The life history information gathered in this dissertation has improved understanding of deepwater chondrichthyans and is directly relevant to managers of fisheries that interact with deepwater chondrichthyans and on a local scale, the managers of the deepwater EKP fishery and the Great Barrier Reef Marine Park Authority. The information is also valuable for the IUCN Red List of Threatened Species to inform assessments of threatened status of the species captured in the southern Great Barrier Reef Marine Park. The novel approach to ageing offers the ability to cost-effectively age large numbers of sharks and provide benefits to fisheries management. It is also likely applicable to a wide range of chondrichthyan taxa.

8.2 Future research

The examination of patterns in life history traits (Chapter 2) raised the question of whether the effects of different degrees of regional fishing pressure are apparent in the deepwater chondrichthyans life history traits. Further investigation of expected deepwater trait changes that may result from the mechanism of differing fishing pressure is warranted, along with reanalyses of traits and habitat as more deepwater life history data becomes available across regions. The examination also highlighted the lack of theoretical understanding of the association of chondrichthyan life history traits with habitat. Further exploration of hypotheses and drivers for this association would be beneficial to our understanding of chondrichthyan life history.

The main area of further research identified from this dissertation is the progression of the novel approach to ageing deepwater chondrichthyans. Future work to investigate the age related compounds detected by NIRS could include NIRS scans of pure hydroxyapatite to create a reference spectrum for comparison with the spectra of dorsal fin spines, vertebrae and fin clips.

This could enable a quantitative measure of the ageing compounds and the potential for entirely non-lethal ageing through a direct measure of the chemical changes in vertebrae, dorsal fin spines or fin clips, rather than having to enumerate visible growth bands. Unlike previous chemical assay approaches that were time consuming and costly (Jones and Geen 1977; Cailliet and Radtke 1987), the NIRS method is rapid and cost-effective and consequently offers a realistic ability to investigate the ageing chemistry of chondrichthyan structures. Similar to the conventional age method of band enumeration (Goldman *et al.* 2012), validation of the quantitative chemical changes would be required, though this is particularly challenging in deepwater chondrichthyans (Cotton *et al.* 2014). Bomb radiocarbon validation may be the most suitable approach because it has proven effective with shark vertebrae and dorsal fin spines (Campana *et al.* 2006; Francis *et al.* 2007; Andrews *et al.* 2011; Passerotti *et al.* 2014).

The other promising aspect of the NIRS work in this dissertation was the potential for non-lethal ageing. It could significantly reduce the number of individuals that need to be sacrificed for traditional band count ageing. Future work could examine the accuracy and precision of age estimations from hand held NIRS units that can be used in the field to scan dorsal fin spines on live dogfish captured and released at sea. It could also explore the applicability of fin clip NIRS age estimations across a range of species. As part of that work, the component of the fin clip that is a reliable NIRS age structure could be investigated. It is unknown whether the NIRS age predictions were associated with the dermal denticles or internal fin components. If the age predictions involved the dermal denticles, consideration should be given to investigation of dermal denticle replacement with growth and the affect this may have on the predicted NIRS age. Such research of the potential for fin clip NIRS ageing would be beneficial to large scale chondrichthyan sampling programs because it would facilitate the ageing of large numbers of easily collected samples.

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Appendix A

Table A.1: Life history traits and habitat data for 226 female and male chondrichthyan populations. S_{max} = Maximum size, S_m = Size at maturity, T_m = Age at maturity, $^oT_{max}$ = Observed longevity, $^tT_{max}$ = Theoretical longevity, k = von Bertalanffy growth constant, S_{birth} = Size at birth, l = Litter size (for Rajidae this is annual fecundity), I_i = Interbirth interval (years) (¹empirical, ²estimated in the literature, ³assumed based on same species in different region, ⁴assumed based on congeneric species) for Rajidae with year-round spawning used $I_i = 1$, R_m = Reproductive mode (O - oviparous single - one egg case is deposited at a time from each oviduct, usually in pairs; Om - oviparous multiple (uncommon) - a number of egg cases are retained in the oviduct during most of the development before deposition; Va, Vh, VI, Vo, Vp refer to adelphophagic, histotrophic, lecithotrophic, oophagic and placental viviparity respectively). All ages are in years and all sizes are in millimetres and are Total Length unless specified (¹Disc Width, ²Fork Length, ³Standard Length, ⁴Pelvic Length, ⁵Pre-supra Caudal Fin Length). NA= no data available. When multiple studies were cited for a species or population, the median of the range of values for each life history parameter was used. For each species or population the FAO Fisheries Areas of the life history data is abbreviated in brackets, with the full names provided at the end of the table. Where no FAO Area is specified, the data is from the entire distributional range of the species. Numbers and text after the FAO abbreviation refer to different parts of the FAO Area and different studies in the same part of the FAO Area, respectively. The source of the life history data is provided in the attached reference list which includes studies to January 2012.

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^tT_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
Superorder: Squalomorpii																		
Order: Hexanchiformes																		
Family: Hexanchidae																		
<i>Notorynchus cepedianus</i>	Shelf	2960	2430	2210	1500	16.0	4.7	28.5	28.5	35	23	0.099	0.153	440	88.5	2 ²	VI	1-3
Order: Squaliformes																		
Family: Squalidae																		
<i>Squalus acanthias</i> (NWA)	Shelf	1100	900	799	595	12.1	6.0	40	35	33	23	0.106	0.148	270	5.8	2 ¹	VI	4-5
<i>S. acanthias</i> (NEA1)	Shelf	1100	900	715	600	11.0	5.0	21	19	32	17	0.110	0.210	270	8.5	2 ³	VI	6
<i>S. acanthias</i> (NEA2)	Shelf	1100	900	770	600	12.5	6.0	23	23	39	39	0.089	0.089	270	5.8	2 ¹	VI	4, 8-10
<i>S. acanthias</i> (SWP)	Shelf	1100	900	730	580	9.9	5.8	32	9	50	29	0.070	0.120	240	5.1	2 ¹	VI	6-7
<i>S. blainville</i> (MED)	Deep	920	735	601	480	5.1	3.3	15	13	34	26	0.102	0.135	215	4.0	2 ³	VI	11-12
<i>S. megalops</i> (SEA)	Deep	782	572	500	400	15.0	9.0	32	29	105	39	0.033	0.089	255	3.0	2 ²	VI	13-15
<i>S. megalops</i> (SWP/EI)	Deep	635	490	483	386	15.0	10.0	28	15	83	22	0.042	0.158	217	3.0	2 ¹	VI	16-19
<i>S. megalops</i> (ECA)	Deep	825	640	647	490	23.0	10.0	32	26	87	69	0.040	0.050	226	3.5	2 ¹	VI	20

Appendix A

Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
<i>S. mitsukurii</i> (NWP1)	Deep	910	820	980	700	9.0	10.5	21	20	89	53	0.039	0.066	235	8.8	2 ²	VI	21-23
<i>S. mitsukurii</i> (NWP2)	Deep	910	820	740	540	9.0	5.0	27	21	68	58	0.051	0.060	235	4.5	2 ²	VI	21-22
<i>S. mitsukurii</i> (NWP3Ta)	Deep	910	820	700	540	15.0	6.5	17	12	34	14	0.103	0.252	235	3.5	2 ²	VI	21-22
<i>S. mitsukurii</i> (NWP3Wi)	Deep	910	820	690	480	15.0	4.0	27	18	85	22	0.041	0.155	235	3.5	2 ¹	VI	15, 23
<i>S. mitsukurii</i> (ECP)	Deep	1010	670	640	470	15.0	8.5	26	23	43	43	0.080	0.080	233	6.5	2 ⁴	VI	24 10, 25-
<i>S. suckleyi</i>	Shelf	1300	1030	935	785	29.0	19.0	81	50	96	50	0.036	0.070	260	7.1	2 ¹	VI	26
Family: Centrophoridae																		
<i>Centrophorus acus</i> (NWP)	Deep	1608	1165	1572	1025	20.0	10.0	18	17	22	20	0.155	0.173	400	5.0	2 ⁴	VI	15, 27- 30
<i>C. granulosus</i> (MED)	Deep	950	825	794	724	16.5	8.5	39	25	36	32	0.096	0.107	337	1.0	2 ¹	VI	30-32
<i>C. squamosus</i> (NEA)	Deep	1450	1220	1263	1000	40.0	27.5	70	54	139	139	0.025	0.025	420	8.5	2.5 ²	VI	2, 33-37
<i>Deania calcea</i> (NEA)	Deep	1170	1090	1050	850	25.0	16.0	35	32	45	26	0.077	0.135	260	11.0	3 ⁴	VI	30, 38
<i>D. calcea</i> (SWP)	Deep	1150	910	950	740	21.5	13.5	37	33	68	71	0.051	0.049	310	8.0	3 ²	VI	39
Family: Etmopteridae																		
<i>Etmopterus baxteri</i> (SWP)	Deep	870	720	630	540	30.0	20.0	57	48	87	42	0.040	0.082	230	8.8	3 ²	VI	2, 39-40
<i>E. pusillus</i> (NEA)	Deep	502	479	436	380	9.9	7.1	17	13	27	20	0.130	0.170	128	3.5	2 ²	VI	41-43 41, 44-
<i>E. spinax</i> (NEA)	Deep	411	338	309	254	4.7	4.0	10	7	29	39	0.120	0.090	90	7.6	2.5 ²	VI	45 2, 44,
<i>E. spinax</i> (MED)	Deep	460	370	340	240	5.0	3.5	9	7	22	18	0.160	0.190	83	6.8	2.5 ⁴	VI	46-47
Family: Somniosidae																		
<i>Centroselachus crepidater</i> (SWP)	Deep	1010	880	840	640	20.0	9.0	54	34	48	25	0.072	0.141	310	6.0	2.5 ²	VI	39

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
Order: Squatiniformes																		
Family: Squatinidae																		
<i>Squatina californica</i>	Shelf	1520	1180	1070	950	10.5	10.5	22	22	21	23	0.162	0.152	235	6.0	1 ¹	VI	15, 48-50
<i>S. guggenheim</i>	Shelf	920	920	742	740	4.5	4.5	12	12	13	13	0.275	0.275	250	5.5	3 ¹	VI	2, 51-52
<i>S. occulta</i> (SWA)	Deep	1310	1310	1100	1100	10.0	10.0	21	21	27	27	0.129	0.129	330	6.0	2 ²	VI	2, 51
Order: Rajiformes																		
Family: Pristidae																		
<i>Pristis microdon</i> (WCP)	Shelf	6000	6000	3000	3000	9.0	9.0	44	44	50	50	0.070	0.070	850	7.0	2 ²	VI	19, 53-57
<i>P. pectinata</i>	Shelf	5500	5500	3600	2700	10.0	10.0	30	30	43	43	0.080	0.080	610	17.5	1 ²	VI	51, 55, 58-59
<i>P. perotteti</i> (WCA)	Shelf	4300	4300	3000	3000	10.0	10.0	30	30	39	39	0.089	0.089	760	7.3	2 ²	VI	51, 58
Family: Rhinobatidae																		
<i>Rhinobatos horkelii</i>	Shelf	1420	1420	1050	1050	8.0	5.5	28	28	23	23	0.150	0.150	290	8.0	1 ¹	VI	2, 51, 48, 60-62
<i>R. productus</i>	Shelf	1560	1140	825	865	7.0	8.1	11	11	36	36	0.016	0.095	195	9.0	1 ¹	VI	62
<i>R. rhinobatos</i> (MED)	Shelf	1470	1240	850	750	5.0	3.0	24	15	26	11	0.134	0.310	260	10.0	1 ¹	VI	63-64
Family: Narcinidae																		
<i>Narcine entemedor</i>	Shelf	930	670	630	450	4.0	4.0	15	11	11	33	0.302	0.104	137	12.0	1 ¹	VI	48
Family: Torpedinidae																		
<i>Torpedo californica</i>	Shelf	1370	920	731	645	9.0	6.0	16	14	47	25	0.073	0.137	206	17.0	2 ⁴	VI	48, 65
<i>T. marmorata</i> (MED/ECA)	Shelf	630	630	440	440	12.0	5.0	20	13	39	39	0.088	0.088	85	9.5	2 ²	VI	2, 66
<i>T. torpedo</i> (MED)	Shelf	410	390	220	180	4.0	4.0	10	10	13	13	0.275	0.275	73	7.2	1 ¹	VI	2, 66
Family: Arhynchobatidae																		
<i>Bathyraja albomaculata</i> (SWA)	Deep	762	732	653	628	10.0	11.0	17	17	39	50	0.090	0.070	102	9.5	1 ²	O	67-68
<i>B. aleutica</i> (NEP)	Deep	1534	1499	1241	1228	10.5	9.0	17	16	35	32	0.100	0.110	206	13.5	1 ⁴	O	30, 69

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Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>B. brachyurops</i> (SWA)	Deep	1250	1000	579	639	8.2	10.0	20	20	50	69	0.070	0.050	150	NA	1 ¹	O	70-71
<i>B. griseocauda</i> (SWA)	Deep	1600	1600	1082	945	17.8	14.0	28	23	173	173	0.020	0.020	200	NA	1 ¹	O	43, 70
<i>B. kincaidi</i>	Deep	610	635	480	490	6.8	7.3	17	18	15	19	0.237	0.185	140	NA	1 ¹	O	72-74
<i>B. minispinosa</i> (NWP)	Deep	895	837	674	701	23.5	23.1	37	35	128	147	0.027	0.024	152	8.0	1 ⁴	O	75-76
<i>B. parmifera</i> (NWP)	Deep	1190	1180	933	918	10.0	9.0	17	15	40	29	0.087	0.120	215	29.0	1 ¹	O	2, 30, 77-78
<i>B. scaphiops</i>	Deep	1110	1110	743	742	13.5	9.0	38	31	55	60	0.063	0.058	210	NA	1 ⁴	O	30, 79 30, 48, 73, 75,
<i>B. trachura</i>	Deep	865	910	740	750	9.0	10.0	17	20	43	39	0.080	0.090	125	7.5	1 ⁴	O	80 69, 75,
<i>Rhinoraja interrupta</i> (NEP)	Deep	820	825	700	694	7.5	7.0	13	12	50	39	0.070	0.090	160	10.3	1 ²	O	81
Family: Rajidae																		
<i>Amblyraja radiata</i> (NWA)	Deep	1005	1003	875	865	11.0	10.9	16	16	27	32	0.130	0.110	100	42.0	1 ¹	O	82-86
<i>A. radiata</i> (NEA)	Deep	865	915	564	633	10.7	14.7	28	28	58	39	0.060	0.090	100	27.5	1 ³	O	54, 86
<i>A. georgiana</i> (AP)	Deep	1000	1000	690 ⁴	640 ⁴	9.5	6.5	14	12	9	21	0.402	0.163	17	NA	1 ¹	O	87-88
<i>Dipturus batis</i> (NEA)	Deep	2850	2050	1500	1250	11.0	11.0	50	50	61	61	0.057	0.057	215	20.0	1 ¹	O	51, 89
<i>D. cerva</i>	Deep	658	620	487	470	5.0	4.8	9	9	15	14	0.160	0.140	110	NA	1 ¹	O	19, 91
<i>D. confusus</i>	Shelf	668	700	526	479	6.6	5.9	11	12	32	50	0.110	0.070	98	NA	1 ¹	O	19, 91
<i>D. innominatus</i>	Deep	1380 ⁴	1180 ⁴	1122 ⁴	933 ⁴	13.0	8.2	24	15	36	36	0.095	0.095	250	NA	1 ⁴	O	92 30, 51,
<i>D. laevis</i>	Deep	1335	1320	1163	1079	6.9	6.0	11	11	25	25	0.141	0.141	185	23.5	1 ⁴	O	93-97
<i>D. pullopunctatus</i>	Deep	1245 ¹	1130 ¹	927 ¹	890 ¹	9.0	9.0	14	18	69	35	0.050	0.100	120	NA	1 ⁴	O	98-99
<i>D. trachyderma</i> (SEP)	Deep	2530	2530	2150	1950	17.0	15.0	26	25	44	40	0.079	0.087	250	48.0	1 ⁴	O	100

Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>Leucoraja erinacea</i> (NWA)	Shelf	540	540	445	390	7.3	5.0	13	13	17	20	0.200	0.170	107	15.0	1 ¹	O	95, 101-105
<i>L. naevus</i> (NEA1)	Deep	700	710	562	569	4.3	4.2	8	6	18	12	0.197	0.294	NA	NA	1 ¹	O	2, 43, 89-90, 106
<i>L. naevus</i> (NEA2)	Deep	700	710	588	588	9.0	9.0	14	14	32	32	0.109	0.109	NA	55.3	1 ¹	O	2, 43, 89-90, 95-96, 102, 104,
<i>L. ocellata</i> (NWA)	Shelf	932	940	760	555	11.5	11.0	18	19	59	47	0.059	0.074	NA	17.5	1 ¹	O	107-109
<i>L. ocellata</i> (NEA)	Shelf	925	925	837	799	13.4	11.3	14	19	23	23	0.150	0.150	NA	NA	1 ³	O	54
<i>L. wallacei</i> (SEA)	Deep	963 ¹	870 ¹	737 ¹	715 ¹	7.0	7.0	15	12	13	13	0.260	0.270	NA	NA	1 ⁴	O	98-99, 102,
<i>Malacoraja senta</i> (NWA)	Deep	625	680	405	500	5.7	5.7	14	15	28	28	0.125	0.125	100	NA	1 ¹	O	110-111
<i>M. senta</i> (NEA)	Deep	510	560	454	491	10.1	11.7	15	15	35	23	0.100	0.150	100	NA	1 ³	O	54
<i>Okamejei acutispina</i>	Shelf	338	289	262 ¹	237 ¹	7.2	6.8	11	10	23	21	0.367	0.365	NA	NA	1 ¹	O	112
<i>Raja asterias</i> (MED)	Shelf	760	720	561	517	3.5	3.5	6	6	8	8	0.454	0.454	NA	73.0	1 ¹	O	2, 113, 1260,
<i>R. binoculata</i> (NEP)	Deep	2039	1836	900	720	8.0	6.0	26	25	87	69	0.040	0.050	195	0	1 ¹	Om	114-115, 96, 106,
<i>R. brachyura</i> (NEA)	Shelf	1090	1080	836	819	5.5	4.6	8	8	27	24	0.129	0.145	NA	90.0	1 ¹	O	116
<i>R. clavata</i> (NEA1)	Shelf	1044	870	760	658	5.6	5.6	16	16	27	17	0.130	0.210	NA	142	1 ¹	O	116-123
<i>R. clavata</i> (NEA2)	Shelf	930	1650	718	657	6.1	6.1	8	8	37	26	0.093	0.135	NA	NA	1 ³	O	106
<i>R. clavata</i> (NEA3)	Shelf	835	835	784	676	7.5	5.8	10	10	36	24	0.097	0.142	NA	136.0	1 ¹	O	121, 124
<i>R. microocellata</i> (NEA)	Shelf	875	875	578	578	5.0	5.0	9	9	40	40	0.086	0.086	130	57.5	1 ¹	O	51, 120
<i>R. miraletus</i> (MED)	Shelf	717	717	398	350	2.3	2.3	17	15	20	18	0.170	0.190	NA	61.0	1 ¹	O	125-126
<i>R. montagui</i> (NEA1)	Shelf	700	670	634	611	11.0	11.0	18	18	19	18	0.180	0.190	NA	21.3	1 ³	O	116, 118

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Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>R. montagui</i> (NEA2)	Shelf	770	750	574	537	3.4	4.1	7	7	14	11	0.256	0.304	NA	NA	1 ³	O	106 106, 115-
<i>R. montagui</i> (NEP/NEA)	Shelf	740	740	568	568	4.6	4.6	10	10	23	23	0.152	0.152	NA	60.0	1 ¹	O	116, 120
<i>R. rhina</i> (NEP1)	Deep	1246	1220	830	650	9.0	6.0	26	23	58	50	0.060	0.070	145	NA	1 ³	O	114, 127- 73, 127-
<i>R. rhina</i> (NEP2)	Deep	1450	1358	1131	1029	16.0	14.0	24	25	94	62	0.037	0.056	181	NA	1 ¹	O	128
<i>R. rhina</i> (ECP)	Deep	1322	1068	700	615	10.5	7.0	12	13	22	14	0.160	0.250	NA	NA	1 ³	O	129
<i>R. texana</i>	Shelf	630	546	537	444	5.8	5.0	9	8	19	14	0.179	0.249	116	NA	1 ¹	O	130-131
<i>R. undulata</i> (NEA)	Shelf	882	832	762	736	9.0	7.7	13	12	32	35	0.110	0.100	NA	NA	1 ¹	O	132-133
<i>Zearaja chilensis</i> (SEP1)	Deep	1170	930	1060	860	14.0	11.0	21	18	31	26	0.112	0.134	NA	47.0	1 ³	O	134-136
<i>Z. chilensis</i> (SEP2)	Deep	1170	930	1052	878	13.5	10.7	21	17	33	30	0.104	0.116	NA	NA	1 ¹	O	137
<i>Z. chilensis</i> (SEP3)	Deep	1170	930	1056	878	12.8	10.3	22	19	40	32	0.087	0.110	NA	NA	1 ¹	O	137
<i>Z. chilensis</i> (SWA)	Deep	1340	1010	800	750	10.5	9.5	24	17	43	29	0.080	0.121	NA	NA	1 ³	O	138
<i>Z. nasuta</i>	Deep	740 ⁴	680 ⁴	591 ⁴	517 ⁴	5.7	4.3	9	7	22	22	0.160	0.160	NA	NA	1 ⁴	O	2, 92
Family: Urolophidae																		
<i>Trygonoptera mucosa</i>	Shelf	369 ¹	369 ¹	253 ¹	253 ¹	5.0	2.0	17	12	14	7	0.241	0.493	113 ¹	1.1	1 ¹	Vh	139-141
<i>T. personata</i>	Shelf	311 ¹	311 ¹	228 ¹	228 ¹	4.0	4.0	16	10	24	17	0.143	0.203	NA	1.2	1 ¹	Vh	139
<i>Urolophus lobatus</i>	Shelf	277 ¹	277 ¹	201 ¹	201 ¹	4.0	2.0	14	13	9	7	0.369	0.514	NA	1.3	1 ¹	Vh	96, 142
<i>U. paucimaculatus</i>	Shelf	298 ¹	298 ¹	204 ¹	204 ¹	3.0	4.0	10	8	17	8	0.210	0.450	165	12.0	1 ¹	Vh	143-144
Family: Urotrygonidae																		
<i>Urobatis halleri</i>	Shelf	310 ¹	250 ¹	145 ¹	146 ¹	3.8	3.8	14	14	23	39	0.150	0.090	75	3.5	0.5 ¹	VI	48, 145- 146
Family: Dasyatidae																		

Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>Dasyatis americana</i> (WCA)	Shelf	2000 ¹	2000 ¹	775 ¹	500 ¹	5.5	3.5	13	12	32	8	0.110	0.440	NA	4.2	1 ¹	Vh	147-150 2,
<i>D. chrysonota</i> (SEA)	Shelf	711 ¹	531 ¹	505 ¹	395 ¹	4.0	4.0	14	9	50	20	0.070	0.175	NA	4.0	1 ¹	Vh	151,153
<i>D. dipterura</i> (ECP)	Shelf	830 ¹	830 ¹	573 ¹	465 ¹	9.5	6.5	28	19	69	35	0.050	0.100	313 ¹	2.5	1 ¹	Vh	152-154
<i>D. fluviorum</i>	Shelf	762 ¹	651 ¹	630 ¹	412 ¹	13.4	7.0	21	16	35	35	0.100	0.100	NA	NA	1 ²	Vh	155 2, 156-
<i>D. pastinaca</i> (MED)	Shelf	600 ¹	490 ¹	242 ¹	240 ¹	4.5	4.5	12	8	89	85	0.039	0.041	NA	6.2	1 ²	Vh	157
<i>Himantura astra</i> (WCP)	Shelf	782 ¹	660 ¹	462 ¹	469 ¹	8.7	7.3	29	18	87	50	0.040	0.070	180	3.0	1 ⁴	Vh	158-159
<i>Neotrygon annotata</i> (WCP)	Shelf	278 ¹	240 ¹	191 ¹	204 ¹	4.0	4.0	13	9	17	11	0.200	0.310	130 ¹	2.0	1 ⁴	Vh	160 19, 160-
<i>N. kuhlii</i> (WCP1)	Shelf	402 ¹	350 ¹	267 ¹	285 ¹	6.0	6.0	15	10	11	4	0.311	0.831	145 ¹	2.0	1 ¹	Vh	163
<i>N. kuhlii</i> (WCP2)	Shelf	470 ¹	470 ¹	314 ¹	294 ¹	6.3	4.0	17	15	27	17	0.130	0.200	100 ¹	2.0	1 ¹	Vh	163-164
<i>N. picta</i>	Shelf	322 ¹	249 ¹	181 ¹	172 ¹	3.5	3.5	18	11	43	29	0.080	0.120	100 ¹	3.0	1 ⁴	Vh	160
<i>Pteroplatytrygon violacea</i> (MED) Family: Myliobatidae	Pelagic	960 ¹	680 ¹	450 ¹	410 ¹	3.0	3.0	9	7	15	6	0.320	0.800	145 ¹	6.5	1 ²	Vh	165-166 2, 167-
<i>Aetobatus flagellum</i> (NWP)	Shelf	1500 ¹	1000 ¹	900 ¹	900 ¹	6.0	6.0	19	9	31	26	0.111	0.133	352 ¹	3.5	1 ²	Vh	169 51, 170-
<i>Myliobatis californicus</i> Family: Rhinopteridae	Shelf	1800 ¹	915 ¹	881 ¹	536 ¹	5.0	2.5	25	6	35	15	0.100	0.229	263 ¹	7.0	1 ¹	Vh	171
<i>Rhinoptera bonasus</i> (WCA) Family: Mobulidae	Shelf	1025 ¹	960 ¹	653 ¹	642 ¹	4.5	4.5	18	16	46	46	0.075	0.075	350 ¹	1.0	1 ¹	Vh	172-174 161,
<i>Mobula japonica</i>	Pelagic	3100 ¹	3100 ¹	2070 ¹	2100 ¹	NA	NA	14	14	13	13	0.277	0.277	810 ¹	1.0	2 ¹	Vh	175-176
Superorder: Galeomorphii																		
Order: Orectolobiformes																		

Appendix A

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
Family: Hemiscylliidae																		
<i>Chiloscyllium plagiosum</i> (NWP)	Shelf	850	950	649	656	4.5	4.4	7	7	15	16	0.224	0.212	132	NA	1 ¹	O	177-179
Family: Rhincodontidae																		
<i>Rhincodon typus</i>	Pelagic	18000	18000	9800	4850	22.0	20.0	80	80	108	108	0.032	0.032	595	300	2 ²	VI	179-183
Order: Lamniformes																		
Family: Odontaspidae																		
																		96, 184-
<i>Carcharias taurus</i> (NWA1)	Shelf	3180	2500	2250	1925	6.0	4.5	11	8	24	20	0.142	0.174	1000	2.0	2 ²	Va	186
<i>C. taurus</i> (NWA2)	Shelf	2770	2480	2250	1925	9.5	6.5	17	15	32	22	0.110	0.160	1000	2.0	2 ²	Va	56, 187
<i>C. taurus</i>	Shelf	2670	2360	2265	1930	6.9	6.9	12	12	25	25	0.136	0.136	1000	2.0	2 ²	Va	2, 179, 188
Family: Alopiidae																		
<i>Alopias pelagicus</i>	Pelagic	3652	3237	2870	2715	8.6	7.5	29	20	41	29	0.085	0.118	1740	2.0	1 ²	Vo	179, 189, 179,
<i>A. superciliosus</i>	Pelagic	4610	3780	3365	2790	13.0	9.5	20	19	38	39	0.092	0.088	1375	2.0	1 ²	Vo	190-194
<i>A. vulpinus</i> (NEP)	Pelagic	6300	6300	3150	3330	3.5	4.5	15	15	22	16	0.158	0.215	1360	3.0	1 ²	Vo	195-196
<i>A. vulpinus</i>	Pelagic	4150	5730	3575	3140	5.8	5.0	22	10	28	19	0.124	0.184	1360	4.5	1 ²	Vo	51, 56
Family: Cetorhinidae																		
<i>Cetorhinus maximus</i>	Pelagic	10000	10000	8900	6000	18.0	13.5	50	51	56	56	0.062	0.062	1750	6.0	3 ²	Vo*	30, 51, 179, 197-199
Family: Lamnidae																		
<i>Carcharodon carcharias</i> (SEA)	Shelf	6000	5000	4450	3670	12.5	9.0	40	40	53	53	0.065	0.065	1475	6.0	2 ²	Vo	29, 200-201

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>C. carcharias</i> (NEP)	Shelf	5639	5500	4570	4260	9.5	9.5	27	28	60	60	0.058	0.058	1215	9.0	2 ²	Vo	2, 15, 51, 96, 202
<i>C. carcharias</i> (NWP)	Shelf	6000	5000	4500	3100	7.0	4.0	22	18	22	18	0.159	0.196	1507	6.0	2 ²	Vo	2, 203
<i>Isurus oxyrinchus</i> (ECP)	Pelagic	3850	3850	2730	2730	15.0	15.0	21	21	69	69	0.050	0.050	720	12.5	3 ¹	Vo	51, 204-206
<i>I. oxyrinchus</i> (NEP)	Pelagic	3510	3510	2300	2300	7.5	7.5	17	17	48	48	0.072	0.072	653	11.8	3 ³	Vo	15
<i>I. oxyrinchus</i> (NWA)	Pelagic	3280	2980	2800	2800	7.0	7.0	12	5	17	13	0.203	0.266	750	13.5	3 ¹	Vo	15, 96, 206-207
<i>I. oxyrinchus</i> (NWA/WCA)	Pelagic	3610	2800	2960	1995	18.0	8.0	29	32	38	21	0.087	0.125	865	13.5	3 ³	Vo	208
<i>I. oxyrinchus</i> (WCP/ECP)	Pelagic	3575	2860	2560	1560	17.2	5.2	20	14	39	22	0.090	0.160	720	11.8	3 ³	Vo	179, 209-210
<i>I. oxyrinchus</i>	Pelagic	3510	3510	1815	1815	7.5	7.5	31	31	48	48	0.072	0.072	653	9.5	3 ¹	Vo	48, 179, 195, 205, 211
<i>Lamna ditropis</i> (ALL1)	Pelagic	3050	3050	1970	1433	8.0	4.0	19	22	20	15	0.170	0.230	725	4.0	1 ⁴	Vo	48
<i>L. ditropis</i> (ALL2)	Pelagic	2600	2600	2028	1625	9.0	5.0	17	25	25	20	0.136	0.171	735	5.0	1 ⁴	Vo	51, 56
<i>L. nasus</i> (NWA)	Pelagic	3650	3650	2500	1750	13.0	8.0	24	25	57	43	0.061	0.080	710	4.0	1 ¹	Vo	2, 51, 206, 212-214
Order: Carcharhiniiformes																		
Family: Scyliorhinidae																		
<i>Galeus melastomus</i> (NEA)	Deep	670	643	560	490	2.2	2.2	5	5	6	6	0.570	0.570	90	13.0	1 ¹	Om	15, 215-218
<i>G. sauteri</i> (NWP)	Shelf	498	432	405	345	9.1	7.6	14	12	21	12	0.374	0.392	67	2.0	1 ¹	O	15, 219-220
<i>Scyliorhinus canicula</i> (NEA)	Shelf	720	750	550	560	7.9	4.0	12	11	23	23	0.150	0.150	100	2.0	1 ¹	O	15, 221-222

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Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
<i>S. canicula</i> (MED) Family: Triakidae	Shelf	600	600	420	405	4.0	3.0	17	17	15	10	0.230	0.340	85	2.0	1 ¹	O	15, 223-226
<i>Furgaleus macki</i> (EI)	Shelf	1450	1450	1125	1075	6.5	4.5	11.5	10.5	9	8	0.369	0.423	245	19.0	2 ¹	VI	51, 227-228
<i>Galeorhinus galeus</i> (SWA/SEP/EI)	Shelf	1645	1645	1311	1311	12.6	12.6	36	36	33	33	0.105	0.105	300	25.0	3 ¹	VI	2, 229-234
<i>G. galeus</i> (SWA)	Shelf	1550	1480	1230	1120	15.8	11.8	36	36	46	38	0.075	0.092	300	23.0	3 ¹	VI	15, 51, 229-230, 234
<i>G. galeus</i> (SWP/EI)	Shelf	1740	1710	1350	1260	12.0	9.0	53	41	28	28	0.124	0.124	315	29.0	3 ¹	VI	15, 234-236
<i>G. galeus</i> (SWP)	Shelf	1680	1750	1375	1300	14.0	14.5	25	25	40	23	0.086	0.154	315	29.0	3 ³	VI	15, 231-233
<i>Mustelus antarcticus</i> (EI1)	Shelf	1750	1750	1120	1120	6.4	6.4	16	16	40	40	0.086	0.086	NA	16.0	1 ¹	Vlh	237
<i>M. antarcticus</i> (EI2)	Shelf	1852	1482	1105	953	8.0	8.0	16	13	28	14	0.123	0.253	330	29.0	2 ¹	Vlh	15, 233, 238
<i>M. antarcticus</i> (EI3)	Shelf	1770	1450	850	800	5.0	4.0	16	16	28	12	0.122	0.266	330	24.0	2 ¹	Vlh	51, 56, 235, 239
<i>M. asterias</i> (MED)	Shelf	1500	1500	960	750	2.4	2.4	15	15	15	15	0.230	0.230	290	17.5	2 ¹	Vlh	15, 240-241
<i>M. californicus</i> (NEP)	Shelf	1630	1160	788	610	2.5	1.5	9	6	16	10	0.218	0.350	250	9.5	1 ¹	Vp	2, 15, 48, 242-244

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>M. canis</i> (NWA1)	Shelf	1320	1320	1020	860	5.5	2.5	16	10	12	8	0.292	0.439	NA	9.5	1 ¹	Vp	245-246 15, 241,
<i>M. canis</i> (NWA2)	Shelf	1500	1100	975	750	2.4	1.6	10	7	10	7	0.335	0.490	365	12.0	1 ¹	Vp	247 15, 96,
<i>M. griseus</i>	Shelf	1010	870	800	665	5.7	5.7	9	9	7	7	0.480	0.480	290	10.5	1 ¹	Vp	241, 247 15, 242-
<i>M. henlei</i> (ECP)	Shelf	1000	795	590	570	2.5	3.0	13	7	15	12	0.225	0.285	280	8.0	1 ¹	Vp	243, 248 15, 241,
<i>M. lenticulatus</i>	Shelf	1370	1140	950	850	7.5	5.5	20	20	29	29	0.119	0.119	300	10.7	1 ¹	Vlh	249-252
<i>M. manazo</i> (NWP1)	Shelf	865	707	649	594	4.0	4.0	9	5	28	15	0.124	0.233	275	5.0	1 ¹	Vlh	253-255 15, 29,
<i>M. manazo</i> (NWP2)	Shelf	865	707	630	630	5.0	4.0	9	9	50	35	0.070	0.100	300	5.0	1 ¹	Vlh	254-257 15, 255,
<i>M. manazo</i> (NWP3)	Shelf	1070	950	820	735	3.5	4.0	10	8	31	22	0.113	0.120	250	6.0	1 ¹	Vlh	258
<i>M. mustelus</i> (SEA)	Shelf	1640	1280	1325	1025	13.5	7.5	24	17	58	29	0.060	0.120	390	11.5	1 ¹	Vp	259-260 51, 261-
<i>Triakis megalopterus</i> (WI)	Shelf	2075	1520	1450	1326	15.3	10.9	25	25	35	29	0.100	0.120	435	9.7	2.5 ¹	VI	262 15, 48, 243,
<i>T. semifasciata</i> Family: Carcharhinidae	Shelf	1980	1600	1175	1025	10.0	7.0	24	24	47	39	0.073	0.089	210	23.5	1 ¹	VI	263-264
<i>Carcharhinus acronotus</i> (WCA1)	Shelf	1324	1324	1135	1062	4.5	4.3	13	11	19	17	0.180	0.210	415	3.5	2 ¹	Vp	2, 265- 266 15, 56,
<i>C. acronotus</i> (WCA2)	Shelf	1540	1640	1200	1100	3.5	3.0	5	6	25	30	0.138	0.117	475	5.0	2 ¹	Vp	266, 269 15, 56, 96, 247,
<i>C. acronotus</i> (WCA3)	Shelf	1300	1220	1040	960	3.0	2.5	3	3	10	6	0.352	0.590	490	5.0	2 ¹	Vp	266, 269

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Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
<i>C. acronotus</i> (WCA4)	Shelf	1300	1220	1100	1030	3.0	2.5	5	5	17	7	0.237	0.771	415	4.5	1 ¹	Vp	15, 269, 270
<i>C. acronotus</i> (SWA)	Shelf	1460	1240	1000	1000	6.0	6.0	15	15	25	29	0.140	0.12	457	4.0	1 ²	Vp	267-268
<i>C. amblyrhynchos</i> (ECP)	Shelf	1870	1740	1370	1325	6.0	8.0	12	12	12	12	0.294	0.294	600	4.5	2 ²	Vp	2, 15, 271
<i>C. amboinensis</i> (WCP)	Shelf	2800	2800	2150	2100	13.0	12.0	30	26	41	38	0.085	0.091	625	9.0	1 ²	Vp	19, 51, 272-273
<i>C. brachyurus</i>	Shelf	2950	2950	2450	2350	19.5	16.0	25	30	90	90	0.039	0.039	650	16.0	2 ²	Vp	15, 19, 48, 274-276
<i>C. brevipinna</i> (WCA)	Shelf	2176	2105	1480	1540	7.6	6.8	18	14	32	50	0.110	0.070	650	8.5	2 ¹	Vp	2, 277-278
<i>C. brevipinna</i> (NWP)	Shelf	2990	3040	2225	2205	7.8	7.9	21	17	23	17	0.151	0.203	650	8.5	2 ¹	Vp	279
<i>C. cautus</i> (EI)	Shelf	1330	1330	1007	1007	6.0	4.0	16	12	18	12	0.198	0.287	350	4.2	2 ¹	Vp	280
<i>C. falciformis</i> (WCA1)	Pelagic	3050	2720	2250	2150	8.0	6.5	14	13	23	23	0.153	0.153	725	12.5	2 ²	Vp	15, 281
<i>C. falciformis</i> (WCA2)	Pelagic	3060	3140	2385	2250	12.0	10.0	22	20	38	35	0.091	0.098	760	11.0	2 ³	Vp	15, 282
<i>C. falciformis</i> (NWP)	Pelagic	2390	2560	2150	2125	9.6	9.3	11	14	41	41	0.084	0.084	695	11.0	2 ³	Vp	283
<i>C. falciformis</i>	Pelagic	2840	2245	1950	1820	6.5	5.5	18	18	23	23	0.148	0.148	580	6.5	2 ²	Vp	51, 281-282, 284
<i>C. galapagensis</i>	Shelf	3000	2670	2300	2045	7.5	7.0	15	15	20	20	0.172	0.172	685	8.7	2.5 ²	Vp	48, 247, 285-286
<i>C. isodon</i>	Shelf	1596	1440	1350	1300	3.9	4.3	8	8	14	8	0.244	0.412	530	4.0	2 ¹	Vp	15, 287-288

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
<i>C. leucas</i> (WCA/WI/SEA)	Shelf	3002	3002	2250	2150	18.0	14.5	28	23	28	21	0.124	0.169	700	9.9	2 ²	Vp	2, 289-293
<i>C. leucas</i> (WI)	Shelf	3000	3000	1930	1900	21.0	20.0	32	29	49	49	0.071	0.071	790	9.0	2 ²	Vp	15, 290, 293
<i>C. leucas</i> (WCP)	Shelf	3180	2840	2200	2300	9.5	9.5	26	22	42	42	0.082	0.082	678	7.0	2 ²	Vp	19, 272, 293
<i>C. limbatus</i> (WCA1)	Shelf	1830	1605	1600	1345	6.5	4.5	10	9	18	13	0.197	0.276	560	4.9	2 ²	Vp	15, 294, 296, 298
<i>C. limbatus</i> (WCA2)	Shelf	2000	1900	1525	1300	7.5	4.5	9	6	13	13	0.274	0.274	580	4.6	2 ²	Vp	15, 298
<i>C. limbatus</i> (WCA3)	Shelf	1840	1524	1420	1310	6.7	5.0	16	14	22	17	0.160	0.210	NA	NA	2 ²	Vp	297
<i>C. limbatus</i> (WI)	Shelf	2470	2460	2060	1990	7.0	6.0	11	10	17	17	0.210	0.200	670	6.0	3 ²	Vp	15, 294-295
<i>C. limbatus</i>	Shelf	2600	2600	2100	2035	5.7	4.5	12	10	14	13	0.240	0.270	490	6.0	3 ²	Vp	48, 51, 294-297
<i>C. longimanus</i> (SWA)	Pelagic	2500	2350	1850	1850	6.5	6.5	17	13	35	35	0.099	0.099	NA	NA	2 ²	Vp	15, 51, 299
<i>C. longimanus</i> (WCP)	Pelagic	2720	2400	1820	1820	4.5	4.5	11	11	34	34	0.103	0.103	700	6.2	2 ²	Vp	51, 300
<i>C. obscurus</i> (EI)	Shelf	3300	3200	2755	2775	19.5	21.5	32	25	81	77	0.043	0.045	885	NA	3 ²	Vp	301
<i>C. obscurus</i> (NWA)	Shelf	3710	3600	2840	2790	21.0	19.0	39	39	89	91	0.039	0.038	925	11.0	3 ²	Vp	15, 302-303
<i>C. obscurus</i> (WI)	Shelf	3890	3240	2800	2800	20.5	20.5	34	34	74	74	0.047	0.047	850	9.9	3 ²	Vp	15, 275, 304
<i>C. plumbeus</i> (NWA)	Shelf	2340	2260	1822	1855	15.5	15.5	25	18	40	40	0.086	0.087	630	8.4	2 ³	Vp	15, 56, 305
<i>C. plumbeus</i> (NWP/NWA)	Shelf	2265	2265	1760	1760	7.5	8.2	21	20	20	20	0.170	0.170	650	7.9	2 ¹	Vp	305-308
<i>C. plumbeus</i> (ECP)	Shelf	1970	1780	1543	1458	10.0	8.0	23	19	35	29	0.100	0.120	630	5.5	2 ³	Vp	161, 309
<i>C. plumbeus</i> (EI)	Shelf	2026	2014	1518	1424	16.2	13.8	25	19	89	79	0.039	0.044	582	NA	2 ¹	Vp	161, 310-311

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Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>C. porosus</i> (SWA)	Shelf	1280	1000	700	710	6.0	6.0	12	12	34	34	0.101	0.101	300	4.5	2 ²	Vp	312-314
<i>C. signatus</i> (SWA)	Pelagic	2600	2600	2025	1850	10.0	8.0	17	17	30	28	0.114	0.124	668	11.1	2 ⁴	Vp	315-317 15, 318-
<i>C. sorrah</i> (WCP)	Shelf	1520	1310	950	900	2.5	3.0	7	5	10	3	0.340	1.170	525	3.1	1 ¹	Vp	319 19, 318-
<i>C. tilstoni</i> (WCP/EI)	Shelf	1800	1800	1150	1100	3.5	3.5	12	8	25	18	0.140	0.190	600	3.0	1 ¹	Vp	319 15, 320-
<i>Galeocerdo cuvier</i> (NWA)	Shelf	4500	3610	3175	3100	10.0	10.0	22	20	28	26	0.124	0.131	610	55.0	2 ²	VI	321 15, 321-
<i>G. cuvier</i> (WI)	Shelf	4100	3700	3400	2900	11.0	8.0	13	11	17	17	0.202	0.202	735	35.0	2 ²	VI	322 2, 320-
<i>G. cuvier</i>	Shelf	4100	4100	3335	3335	10.0	10.0	23	23	19	19	0.184	0.184	710	31.5	2 ²	VI	325
<i>Isogomphodon oxyrhynchus</i> (SWA)	Shelf	1520	1520	1150	1030	6.5	5.5	12	7	29	29	0.121	0.121	430	5.5	2 ²	Vp	326-327 2, 247,
<i>Negaprion acutidens</i>	Shelf	2936	2936	2390	2390	12.7	12.7	20	20	58	58	0.060	0.060	600	7.4	2 ¹	Vp	328 2, 48,
<i>N. brevirostris</i> (WCA/NWA)	Shelf	3200	3200	2400	2250	12.7	11.6	18	20	58	63	0.060	0.055	625	11.0	2 ¹	Vp	329-330 161, 247,
<i>N. brevirostris</i> (WCA)	Shelf	3480	3480	2400	2250	9.7	8.6	45	45	45	45	0.077	0.077	610	11.0	2 ¹	Vp	329, 331 332- 334,
<i>Prionace glauca</i> (SWA/NEA/NWA)	Pelagic	2830	3100	2280	2250	5.0	5.0	14	14	22	22	0.157	0.157	564	30.0	1 ²	Vp	336-337

Species	Habitat	S_{max}		S_m		T_m		$^0T_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male					
<i>P. glauca</i> (NWA1)	Pelagic	3751	3751	2400	2400	5.0	5.0	15	16	27	19	0.130	0.180	NA	39.0	1 ²	Vp	334-335 247, 286,
<i>P. glauca</i> (NWA2)	Pelagic	3270	3400	2210	2250	4.5	6.0	13	16	23	22	0.150	0.160	450	39.0	1 ²	Vp	337-339 15, 56,
<i>P. glauca</i> (NWP)	Pelagic	3000	3000	1850	1790	5.5	4.5	16	16	24	27	0.144	0.129	360	NA	1 ²	Vp	337 19,161,
<i>Rhizoprionodon acutus</i> (WI)	Shelf	1020	890	750	700	2.0	1.6	5	3	6	5	0.605	0.646	325	4.9	1 ¹	Vp	340
<i>R. acutus</i> (WCP)	Shelf	940	931	780	742	1.8	1.1	8	5	6	4	0.630	0.940	424	4.5	1 ¹	Vp	19, 341 19, 342-
<i>R. taylori</i> (WCP)	Shelf	784	784	575	575	1.0	1.0	7	6	3	3	1.013	1.337	240	4.5	1 ¹	Vp	344
<i>R. terraenovae</i> (WCA1Ca)	Shelf	1000	1000	758	726	1.6	1.3	10	7	6	4	0.630	0.850	320	5.0	1 ¹	Vp	2, 345 15, 346-
<i>R. terraenovae</i> (WCA1Co)	Shelf	1070	1050	875	825	4.0	3.0	6	6	10	10	0.359	0.359	325	5.0	1 ⁴	Vp	347
<i>R. terraenovae</i> (NWA/WCA)	Shelf	1034	985	811	816	3.0	3.0	10	9	7	7	0.490	0.500	NA	3.9	1 ¹	Vp	348 15, 247,
<i>Scoliodon laticaudus</i> (WI) Family: Sphyrnidae	Shelf	690	580	340	300	1.6	1.2	7	7	10	9	0.358	0.405	140	7.5	1 ¹	Vp	349 2, 15,
<i>Sphyrna lewini</i> (WCA)	Shelf	3100	3000	2500	1800	15.0	9.5	17	12	47	47	0.073	0.073	475	35.0	1 ¹	Vp	281, 352 15, 351-
<i>S. lewini</i> (NWP)	Shelf	3240	3050	2100	1980	4.1	3.8	14	11	14	16	0.249	0.222	470	26.0	1 ¹	Vp	352
<i>S. lewini</i> (WCP)	Shelf	2898	2898	1471	1471	5.7	5.7	21	21	46	21	0.076	0.163	514	NA	1 ²	Vp	356
<i>S. lewini</i> (SWP)	Shelf	2898	2898	2043	2043	8.9	8.9	21	21	46	37	0.076	0.093	NA	NA	1 ²	Vp	356
<i>S. lewini</i> (SWA)	Shelf	2170	2340	2040	1920	15.0	10.0	32	30	69	69	0.050	0.050	490	NA	1 ¹	Vp	352, 357 2, 350-
<i>S. lewini</i>	Shelf	3310	3310	2200	1665	5.8	4.3	19	19	22	22	0.156	0.131	NA	20.1	1 ²	Vp	355

Appendix A

Species	Habitat	S_{max}		S_m		T_m		$^oT_{max}$		$^T T_{max}$		k		S_{birth}	l	I_i	R_m	Source
		Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male							
<i>S. mokarran</i> (WCP/SWP)	Shelf	4391	3691	2279	2279	8.3	8.3	39	32	44	44	0.079	0.079	700	NA	2 ²	Vp	2, 356-358
<i>S. tiburo</i> (WCA1)	Shelf	1040	820	825	690	2.7	2.0	7	6	9	7	0.370	0.530	274	9.3	1 ¹	Vp	15, 359-361
<i>S. tiburo</i> (WCA2)	Shelf	1160	890	875	800	2.2	2.0	7	6	10	6	0.340	0.580	347	8.9	1 ¹	Vp	15, 359
Superorder: Holocephali																		
Order: Chimaeriformes																		
Family: Callorhynchidae																		
<i>Callorhynchus capensis</i> (SEA)	Shelf	600 ²	601 ²	496 ²	496 ²	4.2	3.3	10	5	20	20	0.170	0.170	NA	22.0	1 ¹	O	2, 362-363
<i>C. callorynchus</i> (SEP)	Shelf	700 ³	620 ³	502 ³	437 ³	6.5	4.5	28	9	18	7	0.193	0.473	NA	NA	1 ¹	O	364
<i>C. milii</i> (SWP)	Shelf	970 ²	760 ²	710 ²	560 ²	5.6	3.4	9	5	15	7	0.224	0.466	NA	20.0	1 ¹	O	19, 365-367
Family: Chimaeridae																		
<i>Chimaera monstrosa</i> (NEA1)	Deep	571 ⁵	503 ⁵	459 ⁵	402 ⁵	11.7	9.5	17	15	35	25	0.100	0.140	100 ⁵	6.5	1 ²	O	30, 368-369
<i>C. monstrosa</i> (NEA2)	Deep	740 ⁵	740 ⁵	480 ⁵	500 ⁵	11.2	13.4	26	30	52	52	0.067	0.067	100 ⁵	NA	1 ²	O	30, 369-370

*assumed due to only one record of a pregnant female

FAO Fisheries Areas

NWA	Northwest Atlantic
NEA	Northeast Atlantic
WCA	Western Central Atlantic

ECA	Eastern Central Atlantic
MED	Mediterranean and Black Sea
SWA	Southwest Atlantic
SEA	Southeast Atlantic
WI	Western Indian Ocean
EI	Eastern Indian Ocean
NWP	Northwest Pacific
NEP	Northeast Pacific
WCP	Western Central Pacific
ECP	Eastern Central Pacific
SWP	Southwest Pacific
SEP	Southeast Pacific
AP	Antarctic Pacific

Table A.2: Deepwater species habitat data. All depths are in metres: *Depth_U* - Usual or typical depth limit that a population has been reported to occur, *Depth_M* - Maximum depth limit that a population has been reported to occur, *Depth_{RU}* - Usual depth range across which a species is reported to occur, *Depth_{RM}* - Maximum depth range across which a species has been reported to occur. Longitudinal range and latitudinal range are the respective ranges across which a population is reported to occur and are in degrees.

Species	<i>Depth_U</i>	<i>Depth_M</i>	<i>Depth_{RU}</i>	<i>Depth_{RM}</i>	<i>Long.Range</i>	<i>Lat.Range</i>	<i>Region</i>
<i>Squalus acanthias</i> (NWA)	200	1446	200	1446	293	129	North Atlantic
<i>S. acanthias</i> (NEA1)	200	1446	200	1446	293	129	North Atlantic
<i>S. acanthias</i> (NEA2)	200	1446	200	1446	293	129	North Atlantic
<i>S. acanthias</i> (SWP)	200	1446	200	1446	293	129	South Pacific
<i>S. blainville</i> (MED)	440	440	424	424	60	79	North Atlantic
<i>S. megalops</i> (SEA)	732	732	732	732	187	83	South Atlantic
<i>S. megalops</i> (SWP/EI)	732	732	732	732	187	83	South Pacific
<i>S. megalops</i> (ECA)	732	732	732	732	187	83	North Atlantic
<i>S. mitsukurii</i> (NWP1)	500	954	400	950	293	104	North Pacific

Appendix A

Species	Depth _U	Depth _M	Depth _{R_U}	Depth _{R_M}	Long.Range	Lat.Range	Region
<i>S. mitsukurii</i> (NWP2)	500	954	400	950	293	104	North Pacific
<i>S. mitsukurii</i> (NWP3Ta)	500	954	400	950	293	104	North Pacific
<i>S. mitsukurii</i> (NWP3Wi)	500	954	400	950	293	104	North Pacific
<i>S. mitsukurii</i> (ECP)	500	954	400	950	293	104	North Pacific
<i>S. suckleyi</i>	200	1446	200	1446	118	29	North Pacific
<i>Centrophorus acus</i> (NWP)	950	950	750	800	23	18	North Pacific
<i>C. granulatus</i> (MED)	600	1440	400	1390	254	94	North Atlantic
<i>C. squamosus</i> (NEA)	1000	2400	200	2170	125	123	North Atlantic
<i>Deania calcea</i> (NEA)	900	1470	500	1400	360	113	North Atlantic
<i>D. calcea</i> (SWP)	900	1470	500	1400	360	113	South Pacific
<i>Etmopterus baxteri</i> (SWP)	1500	1500	1250	1250	42	10	South Pacific
<i>E. pusillus</i> (NEA)	1000	1998	726	726	353	90	North Atlantic
<i>E. spinax</i> (NEA)	500	2000	300	1930	55	108	North Atlantic
<i>E. spinax</i> (MED)	500	2000	300	1930	55	108	North Atlantic
<i>Centroselachus crepidater</i> (SWP)	2080	2080	1580	1810	248	109	South Pacific
<i>Squatina occulta</i> (SWA)	500	500	480	480	10	10	South Atlantic
<i>Bathyraja albomaculata</i> (SWA)	861	861	806	806	20	21	South Atlantic
<i>B. aleutica</i> (NEP)	700	700	609	609	85	15	North Pacific
<i>B. brachyurops</i> (SWA)	604	604	576	576	14	12	South Atlantic
<i>B. griseocauda</i> (SWA)	941	941	859	859	12	28	South Atlantic
<i>B. kincaidi</i>	1372	1372	1317	1317	35	29	North Pacific
<i>B. minispinosa</i> (NWP)	1420	1420	1270	1270	15	6	North Pacific
<i>B. parmifera</i> (NWP)	1425	1425	1405	1405	40	10	North Pacific

Species	Depth_U	Depth_M	Depth_{R_U}	Depth_{R_M}	Long.Range	Lat.Range	Region
<i>B. scaphiops</i> (SWA)	159	509	55	405	14	19	South Atlantic
<i>B. trachura</i>	2550	2550	2150	2150	85	25	North Pacific
<i>Rhinoraja interrupta</i> (NEP)	1100	1100	1077	1077	85	31	North Pacific
<i>Amblyraja radiata</i> (NWA)	439	1400	412	1382	241	39	North Atlantic
<i>A. radiata</i> (NEA)	439	1400	412	1382	241	39	North Atlantic
<i>A. georgiana</i> (AP)	800	800	780	780	135	20	South Pacific
<i>Dipturus batis</i> (NEA)	1000	1000	900	900	72	57	North Atlantic
<i>D. cerva</i> (EI)	470	470	450	450	10	12	South Pacific
<i>D. innominatus</i> (SWP)	1310	1310	1295	1295	28	27	South Pacific
<i>D. laevis</i> (NWA)	430	430	430	430	42	18	North Atlantic
<i>D. pullopunctatus</i> (SEA)	300	457	200	452	11	12	South Atlantic
<i>D. trachyderma</i> (SEP)	450	450	357	357	57	55	South Pacific
<i>Leucoraja naevus</i> (NEA1)	500	500	480	480	54	45	North Atlantic
<i>L. naevus</i> (NEA2)	500	500	480	480	54	45	North Atlantic
<i>L. wallacei</i> (SEA)	300	500	150	430	27	1	South Atlantic
<i>Malacoraja senta</i> (NWA)	914	914	868	868	34	14	North Atlantic
<i>M. senta</i> (NEA)	914	914	868	868	34	14	North Atlantic
<i>Raja asterias</i> (MED)	343	343	333	333	45	10	North Atlantic
<i>R. binoculata</i> (NEP)	800	800	797	797	63	30	North Pacific
<i>R. rhina</i> (NEP1)	1000	1000	975	975	70	39	North Pacific
<i>R. rhina</i> (NEP2)	1000	1000	975	975	70	39	North Pacific
<i>R. rhina</i> (ECP)	1000	1000	975	975	70	39	North Pacific
<i>Zearaja chilensis</i> (SEP1)	500	500	472	472	14	9	South Pacific
<i>Z. chilensis</i> (SEP2)	500	500	472	472	14	9	South Pacific
<i>Z. chilensis</i> (SEP3)	500	500	472	472	14	9	South Pacific
<i>Z. chilensis</i> (SWA)	500	500	472	472	14	9	South Atlantic

Species	Depth _U	Depth _M	Depth _{R_U}	Depth _{R_M}	Long.Range	Lat.Range	Region
<i>Z. nasutus</i>	1500	1500	1490	1490	25	15	South Pacific
<i>Galeus melastomus</i> (NEA)	500	1440	300	1385	55	50	North Atlantic
<i>Galeorhinus galeus</i> (SWA/SEP/EI)	470	800	468	800	286	128	South Atlantic
<i>G. galeus</i> (SWA)	470	800	468	800	286	128	South Atlantic
<i>G. galeus</i> (SWP/EI)	470	800	468	800	286	128	South Pacific
<i>G. galeus</i> (SWP)	470	800	468	800	286	128	South Pacific
<i>Chimaera monstrosa</i> (NEA1)	500	1000	200	950	67	48	North Atlantic
<i>C. monstrosa</i> (NEA2)	500	1000	200	950	67	48	North Atlantic

Table A.3: Growth constant (k), age at maturity (T_m) and longevity (observed and theoretical) for deep, pelagic and shelf habitats. These values are the direct output of the linear mixed effects model (LMEM) where the LMEM coefficient values (\pm se) for the pelagic and shelf habitats are relative to the intercept value for the deep habitats.

Habitat	k		T_m		$^oT_{max}$		$^T T_{max}$	
	Fem	Male	Fem	Male	Fem	Male	Fem	Male
Deep	-2.058	-1.670	1.818	1.399	2.634	2.314	3.310	2.903
Intercept	(0.175)	(0.201)	(0.254)	(0.241)	(0.209)	(0.214)	(0.185)	(0.209)
Pelagic	0.479	0.526	-0.498	-0.491	-0.325	-0.304	-0.457	-0.507
	(0.186)	(0.198)	(0.168)	(0.158)	(0.145)	(0.158)	(0.190)	(0.197)
Shelf	0.383	0.380	-0.257	-0.238	-0.169	-0.208	-0.375	-0.375
	(0.120)	(0.127)	(0.111)	(0.104)	(0.097)	(0.105)	(0.122)	(0.127)

Table A.4: Litter size (l), size at birth (S_{birth}) and interbirth interval (I_i) for deep, pelagic and shelf habitats. As transformation made no difference to the significance levels for S_{birth} and l , for ease of interpretation untransformed results are presented for these two parameters. The coefficient values (\pm se) for the pelagic and shelf habitats are relative to the intercept value for the deep habitats and are the direct output values from the LMEM analyses. The magnitude of difference in deep habitat traits from those in the other two habitats is presented as predicted ratios with the significance level; the LMEM coefficient values of traits for the pelagic and shelf habitats were added to the intercept value of the traits for the deep habitat. The resultant values were used to calculate the ratio.

Value	l			S_{birth}			I_i		
	Value	Value	Ratio	Value	Value	Ratio	Value	Value	Ratio
	LMEM	(number)		LMEM	(mm)		LMEM	(yrs)	
Deep	12.2	12.2		167.1	167.1		0.188	1.21	
Intercept	(10.0)			(88.7)			(0.164)		
Pelagic	-5.1	7.1	1.72	27.5	194.6	0.86	-0.067	1.13	1.07
	(3.8)		$p=0.173$	(49.5)		$p=0.191$	(0.08)		$p=0.330$
Shelf	-5.0	7.2	1.70	20.4	187.5	0.89	-0.041	1.16	1.04
	(2.7)		$p=0.060$	(36.7)		$p=0.416$	(0.05)		$p=0.410$

Table A.5: Regional patterns in deep habitat litter size (l) and male growth constant (k_M) in relation to size at maturity (S_{mat}). The coefficient values (\pm se) for the North Pacific, South Atlantic and South Pacific are relative to the intercept value for the North Atlantic and are the direct output values from the LMEM analyses. The magnitude of difference in the North Atlantic traits from those in the other Regions is presented as predicted ratios with the significance level; the LMEM coefficient values of traits for each of the Regions were added to the intercept value of the traits for the North Atlantic. The resultant values were back-transformed and used to calculate the ratio.

Region	l			k_M		
	Value LMEM	Value (#)	Ratio	Value LMEM	Value (k_M)	Ratio
North Atlantic	1.891	6.625		-1.515	0.219	
Intercept	(0.436)			(0.360)		
North Pacific	-0.396 (0.204)	4.457	1.49 $p=0.062$	-0.185 (0.193)	0.182	1.20 $p=0.343$
South Atlantic	-0.663 (0.249)	3.517	1.88 $p=0.017$	-0.367 (0.222)	0.152	1.44 $p=0.106$
South Pacific	-0.329 (0.198)	4.768	1.39 $p=0.107$	0.021 (0.200)	0.224	0.98 $p=0.918$

Table A.6: Regional patterns in deep habitat predicted ratios of female and male maximum body size (S_{\max}), size at maturity (S_m), age at maturity (T_m), observed longevity (${}^0T_{\max}$). The predicted ratios with the significance level are compared to the North Atlantic. The magnitude of difference in North Atlantic traits from those in the other Regions is presented as predicted ratios with the significance level; the LMEM coefficient values of traits for each of the Regions were added to the intercept value of the traits for the North Atlantic. These values were back-transformed and used to calculate the ratio.

Region	S_{\max}		S_m		T_m		${}^0T_{\max}$	
	Female	Male	Female	Male	Female	Male	Female	Male
North Pacific	0.86	0.87	0.81	0.87	0.84	0.89	0.87	0.86
	$p=0.216$	$p=0.191$	$p=0.056$	$p=0.168$	$p=0.217$	$p=0.433$	$p=0.346$	$p=0.320$
South Atlantic	0.82	0.88	0.90	0.92	0.74	0.78	0.71	0.76
	$p=0.117$	$p=0.309$	$p=0.392$	$p=0.475$	$p=0.057$	$p=0.0126$	$p=0.057$	$p=0.131$
South Pacific	0.89	0.92	0.86	0.90	0.77	0.85	0.81	0.99
	$p=0.318$	$p=0.458$	$p=0.162$	$p=0.283$	$p=0.072$	$p=0.266$	$p=0.195$	$p=0.962$

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Appendix B

Table B.1: Deepwater chondrichthyans known to occur in the Great Barrier Reef Marine Park. Source: A. Great Barrier Reef Marine Park (Chin *et al.* 2010); B. Eastern King Prawn fishery in the Great Barrier Reef, Department of Agriculture and Fishery Observer Program 2005-2010 (Pears *et al.* 2012); C. Eastern King Prawn fishery in the Swain Reefs area of the Great Barrier Reef (the present study). Australian endemic (source: Last and Stevens, 2009): noted if restricted to waters offshore from Queensland-New South Wales (QLD-NSW) or Queensland (QLD).

Family	Species	Common name	GBRMP ^A	EKP ^B	EKP ^C	Australian endemic	IUCN Status	
Chimaeridae	<i>Chimaera macrospina</i>	Longspine chimaera	X			Yes	Least Concern	
	<i>Chimaera obscura</i>	Shortspine chimaera	X			QLD-NSW	Least Concern	
	<i>Hydrolagus lemures</i>	Blackfin ghostshark	X	X	X	Yes	Least Concern	
	<i>Hydrolagus marmoratus</i>	Marbled ghostshark	X			QLD-NSW	Data Deficient	
Hexanchidae	<i>Heptanchias perlo</i>	Sharpnose sevengill shark	X			No	Near Threatened	
	<i>Hexanchus griseus</i>	Bluntnose sixgill shark	X			No	Near Threatened	
	<i>Hexanchus nakamurai</i>	Bigeye sixgill shark	X			No	Data Deficient	
Echinorhinidae	<i>Echinorhinus cookei</i> ^a	Prickly shark	X			No	Near Threatened	
Squalidae	<i>Squalus albifrons</i>	Eastern highfin spurdog	X			QLD-NSW	Data Deficient	
	<i>Squalus grahami</i>	Eastern longnose spurdog	X			QLD-NSW	Near Threatened	
	<i>Squalus megalops</i>	Piked spurdog				X	No	Near Threatened
	<i>Squalus montalbani</i>	Philippine spurdog	X			No	Vulnerable	
	<i>Squalus notocaudatus</i>	Bartail spurdog	X			QLD	Data Deficient	
Centrophoridae	<i>Centrophorus moluccensis</i>	Endeavour dogfish	X			No	Near Threatened	
	<i>Centrophorus niaukang</i>	Taiwan gulper shark	X			No	Not assessed	
Etmopteridae	<i>Etmopterus brachyurus</i> ^a	Short-tail lanternshark	X			No	Data Deficient	
	<i>Etmopterus dianthus</i>	Pink lanternshark	X			No	Least Concern	
	<i>Etmopterus dislineatus</i>	Lined lanternshark	X			QLD	Least Concern	

Appendix B

Family	Species	Common name	GBRMP ^A	EKP ^B	EKP ^C	Australian endemic	IUCN Status
	<i>Etmopterus lucifer</i>	Blackbelly lanternshark	X			No	Least Concern
Dalatiidae	<i>Dalatias licha</i>	Black shark	X			No	Near Threatened
Squatinae	<i>Squatina albipunctata</i>	Eastern angelshark	X		X	QLD-NSW	Vulnerable
Pristiophoridae	<i>Pristiophorus delicatus</i>	Tropical sawshark	X		X	QLD	Least Concern
Narcinidae	<i>Narcine nelsoni</i>	Eastern numbfish	X			QLD	Least Concern ⁸
Torpedinidae	<i>Torpedo macnelli</i>	Short-tail torpedo ray	X			Yes	Data Deficient
	<i>Torpedo tokionis</i>	Longtail torpedo ray	X			No	Data Deficient
Arhynchobatidae	<i>Insentiraja laxipella</i>	Eastern looseskin skate	X			QLD	Data Deficient
	<i>Notoraja ochroderma</i>	Pale skate	X			QLD	Data Deficient
	<i>Pavoraja mosaica</i>	Mosaic skate	X			QLD	Least Concern
	<i>Pavoraja pseudonitida</i>	False peacock skate	X			QLD	Least Concern
Rajidae	<i>Dipturus apricus</i>	Pale tropical skate	X	X	X	QLD	Least Concern
	<i>Dipturus melanospilus</i>	Blacktip skate	X			QLD-NSW	Data Deficient
	<i>Dipturus polyommata</i>	Argus skate	X	X	X	QLD	Least Concern
	<i>Dipturus queenslandicus</i>	Queensland deepwater skate	X			QLD	Data Deficient
	<i>Dipturus wengi</i>	Weng's skate	X			Yes	Least Concern
Anacanthobatidae	<i>Sinobatis filicauda</i>	Eastern leg skate	X			QLD	Data Deficient
Plesiobatidae	<i>Plesiobatis daviesi</i>	Giant stingaree	X			No	Least Concern
Urolophidae	<i>Urolophus bucculentus^b</i>	Sandyback stingaree	X	X	X	Yes	Vulnerable
	<i>Urolophus piperatus</i>	Coral Sea stingaree	X		X	QLD	Least Concern
Hexatrygonidae	<i>Hexatrygon bickelli</i>	Sixgill stingray	X			No	Least Concern

Appendix B

Family	Species	Common name	GBRMP ^A	EKP ^B	EKP ^C	Australian endemic	IUCN Status
Myliobatidae	<i>Myliobatis hamlyni</i>	Purple eagle ray	X			Yes	Endangered
Brachaeluridae	<i>Brachaelurus colcloughi</i> ^c	Colcough's shark	X	X	X	QLD-NSW	Vulnerable
Orectolobidae	<i>Orectolobus maculatus</i> ^c	Spotted wobbegong	X	X	X	No	Near Threatened
Scyliorhinidae	<i>Apristurus australis</i>	Pinocchio catshark	X			Yes	Data Deficient
	<i>Apristurus longicephalus</i>	Smoothbelly catshark	X			No	Data Deficient
	<i>Apristurus platyrhynchus</i>	Bigfin catshark	X			No	Data Deficient
	<i>Asymbolus pallidus</i>	Pale spotted catshark	X	X	X	QLD	Least Concern
	<i>Cephaloscyllium signourum</i>	Flagtail swellshark	X			No	Data Deficient
	<i>Cephaloscyllium variegatum</i>	Saddled swellshark	X	X	X	QLD-NSW	Near Threatened
	<i>Cephaloscyllium zebrum</i>	Narrowbar swellshark	X			QLD	Data Deficient
	<i>Figaro striatus</i>	Northern sawtail shark	X			QLD	Data Deficient
	<i>Galeus gracilis</i>	Slender sawtail shark	X			Yes	Data Deficient
	<i>Parmaturus bigus</i>	Short-tail catshark	X			QLD	Data Deficient
Pseudotriakidae	<i>Pseudotriakis microdon</i>	False catshark	X			No	Data Deficient
Triakidae	<i>Hemitriakis abdita</i>	Darksnout houndshark	X			QLD	Data Deficient
	<i>Iago garricki</i>	Longnose houndshark	X ⁵⁴			No	Least Concern
	<i>Mustelus walkeri</i>	Eastern spotted gummy shark	X	X	X	QLD	Data Deficient
Carcharhinidae	<i>Carcharhinus altimus</i>	Bignose shark	X			No	Data Deficient

^a additional deepwater species in GBRMP (Last and Stevens 2009)

^b *Urolophus flavomosaicus* previously recorded from GBRMP are likely to be *U. bucculentus*

^c consider these shelf species, based on Last and Stevens (2009).

Table B.2: Depth and distribution range of deepwater chondrichthyans observed from Swain Reefs EKP Fishery. Restricted to waters offshore from Queensland – QLD. Source: Last and Stevens, 2009.

Species	Depth range (m)	Distribution range	Australian endemic
<i>S. megalops</i>	0-732	Atlantic to Indo-West Pacific: in Australia south of Whitsundays continuous to the north west shelf of Western Australia	No
<i>D. polyommata</i>	135-320	Rockhampton to Townsville, probably further north	Yes- QLD
<i>A. pallidus</i>	225-400	Swain Reefs to Cairns	Yes- QLD
<i>M. walkeri</i>	50-400	Moreton Island to Hinchinbrook, possibly further north and south	Yes- QLD
<i>U. piperatus</i>	170-370	Moreton Island to Cairns	Yes- QLD
<i>P. delicatus</i>	245-405	Rockhampton to Cairns	Yes- QLD
<i>H. lemures</i>	200-700	Cairns continuous to Scott Reef , Western Australia	Yes
<i>U. bucculentus</i>	65-265	Beachport South Australia to Stradbroke Island, Queensland- extended to Swain Reefs, Queensland	Yes
<i>S. albipunctata</i>	35-415	Lakes Entrance, Victoria to Cairns, Queensland	Yes
<i>D. apricus</i>	240-695	Broken Bay, New South Wales to Marion Plateau, Queensland	Yes
<i>C. variegatum</i>	115-605	Tathra, New South Wales to Rockingham Bay, Queensland	Yes

Appendix C

Table C.1: Life history traits of *Squalus megalops* in different regions. L_{\max} , maximum size; L_{50} , size at maturity; A_{50} , age at maturity; ${}^{\circ}L_{\max}$, observed longevity; k , von Bertalanffy growth function; S_{birth} , size at birth; l , litter size; I_i , interbirth interval

Country	Ocean	L_{\max} (mm)		L_{50} (mm)		A_{50} (years)		${}^{\circ}L_{\max}$ (mm)		k (year ⁻¹)		S_{birth} (mm)	l	I_i (years)	Source
		Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem				
Australia	Indo-West Pacific	470	635	386	484	10.0	15.5	15	28	0.158	0.042	218	3.0	2	Braccini <i>et al.</i> 2006, 2007
Australia	Indo-West Pacific	510	630	383	483								2.0		Graham, 2005
South Africa	Atlantic	572	782	400	490	9.0	15.0	29	32	0.089	0.033	255	3.0	2	Watson and Smale, 1998, 1999
Canary Islands	Atlantic	640	825	490	647	12.0	20.0	26	32	0.053	0.040	226	3.5	2	Pajuelo <i>et al.</i> 2011
Brazil	Atlantic	645	890	445	590								4.1		Hazin <i>et al.</i> 2006
Tunisia	Atlantic	690	760	444	564										Marouani <i>et al.</i> 2014

Table C.2: Female reproductive data for *S. megalops* and *S. montalbani* U, unknown sex

Maternal L_{ST} (mm)	Embryos							% maternal L_{ST}	Comments
	Number	Uterus		Sex			Size		
		L	R	M	F	U	L_{ST} (mm)		
<i>S. megalops</i>									
423	2	1	1	1	1		157–158	37.1	Near term pups, 1 yolked follicle (32 mm each diameter) in each ovary
<i>S. montalbani</i>									
849	9	4	5				110–115		Embryos, 10 yolked follicles, numerous undeveloped follicles and an atretic follicles

Additional breeding animals observed at sea (Ken Graham, Australian Museum, pers. comm. 2015)

CSIRO 2009 gulper survey (Williams *et al.* 2012)

Maternal L_{ST} (mm)	Embryos						Size L_{ST} (mm)	% maternal L_{ST}	Comments
	Number	Uterus		Sex					
		L	R	M	F	U			
800	6	3	3	1	5		234–245	29.3–30.6	Near term embryos, 5 yolked follicles
870	12	6	6						12 New candles, embryos not visible
CSIRO 2011 gulper survey (Williams <i>et al.</i> 2013), from Recorder Seamount, southern Queensland									
1080	12	6	6	7	5		120–130		No yolked follicles
1100	16	7	9	8	8		140–150		No yolked follicles

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Williams, A., Green, M., Graham, K., Upston, J., Barker, B., and Althaus, F. (2013) Determining the distribution of gulper sharks on Australia’s eastern seamount chain and the selectivity of power handline fishing in regard to seamount populations of Blue-eye Trevalla and Harrison’s Dogfish. Final Report to AFMA, CSIRO Marine and Atmospheric Research, Hobart, Tasmania

