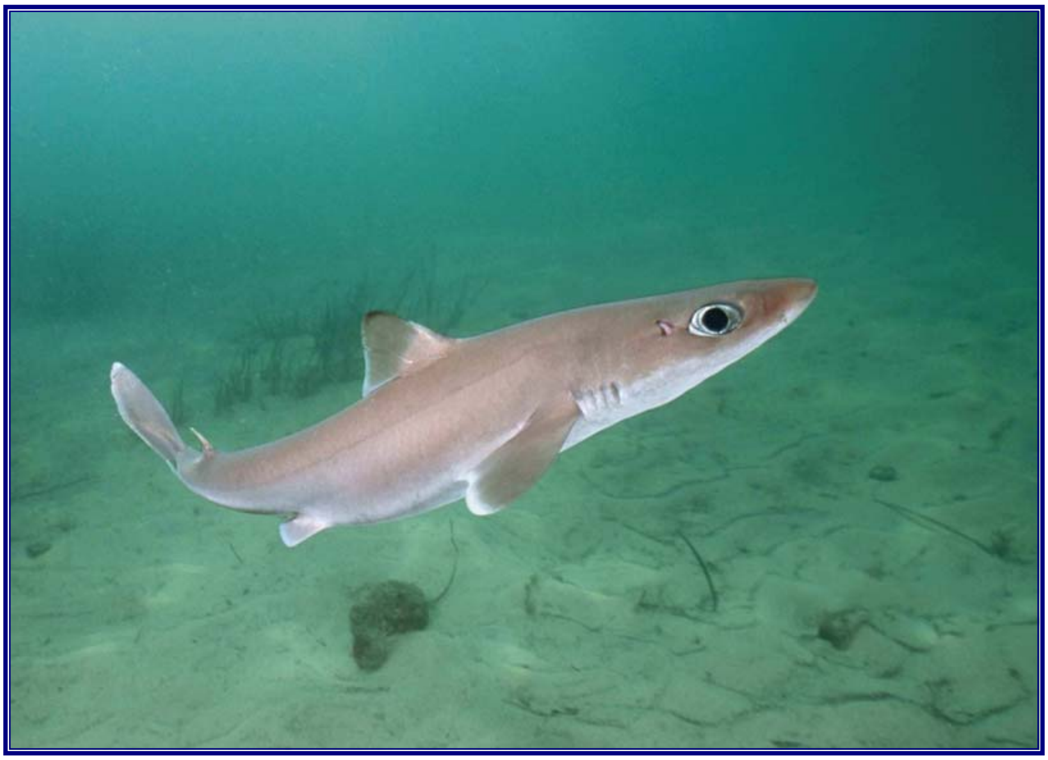
ASSESSMENT OF ECOLOGICAL RISKS FROM EFFECTS OF FISHING TO PIKED SPURDOG (*SQUALUS MEGALOPS*) IN SOUTH-EASTERN AUSTRALIA



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DECLARATION OF AUTHORSHIP

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13 January 2006

Cover image: The piked spurdog, *Squalus megalops* (photo by Kelvin Aitken).

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ABSTRACT

Target species in some Australian shark fisheries are adequately managed, but there has been little attention given to non-target shark species and there is limited information on the biology of their local populations. Among this group of non-target species, the piked spurdog (*Squalus megalops*) is of special interest because it is a dominant and ecologically important species with high natural abundance. Hence, the main purpose of the present research was to improve knowledge of the basic biology of this species and to provide essential data for its management, sustainable use and conservation.

Squalus megalops had a complex population structure, segregating by sex, size and breeding condition. The sex ratio was biased towards females and there was sexual size dimorphism with females attaining a larger maximum size than males. Conversion factors from partial lengths to total length and from partial masses to total mass were determined due to the common commercial fishing practice of eviscerating, beheading and finning sharks. Comparisons of total and partial length–length and mass–length relationships between males and females using different ranges of size showed that there was no effect of size range on measurements reflecting only somatic growth (fork and carcass lengths; carcass, pectoral fin and caudal fin masses). However, for variables reflecting somatic and reproductive growth (total and liver masses), different outcomes can be expected when different ranges of size are compared.

Examination of dietary composition revealed that *S. megalops* is an opportunistic predator that consumes a wide range of prey items. High variability was found when overall importance of prey items was estimated. Dietary composition varied in space and time, exhibiting differences among regions, seasons and size classes. Therefore, the intrinsic natural variability in the dietary composition of *S. megalops* and its spatial and temporal variation in diet suggest that information on the ecological relationships among species is likely to be missed when predator–prey interactions are only inferred from overall diet.

Reproductive parameters were determined for population assessment. For both sexes, length-at-maturity differed depending on the criterion adopted for defining maturity. Mature males are capable of mating throughout the year. Females have a continuous

asynchronous reproductive cycle. The sex ratio of embryos is 1:1 and litter size and near-term embryo size increase with maternal length. Females have an ovarian cycle and gestation period of two years. Although all females are mature at 600 mm, only 50% of them are in maternal condition, contributing to annual recruitment each year. Hence, for chondrichthyan species with reproductive cycles of two, three or more years, if maturity ogives are used in population assessments instead of maternity ogives, the models will over-estimate recruitment rates.

Age and growth information was also determined for population assessment. Precision estimates, the relationship between spine total length and body length, edge analysis, and agreement between counts on the inner dentine layer and the enameled surface support the use of the first dorsal fin spine for the age estimation of *S. megalops*. Based on goodness-of-fit criterion, the best growth model for males and females was a two-phase von Bertalanffy function. However, model selection cannot be based on quality of statistical fit only and results should be interpreted with caution. Regardless of the model used, the growth rate of *S. megalops*, particularly of females, is very low, even within the range of growth rates reported for shark species.

A three-levelled hierarchical risk assessment approach was trialed to evaluate the suitability of the approach for *S. megalops*. Integration of qualitative, semi-quantitative, and quantitative biological and fishing impact data showed that *S. megalops* is potentially highly susceptible to the effects of fishing. A qualitative assessment indicated that the only fishing related activities to have moderate or high impact on *S. megalops* were those associated with ‘capture fishing’ of the otter trawl, Danish seine, gillnet and automatic longline methods. A semi-quantitative assessment ranked *S. megalops* at risk because of its low biological productivity and, possibly, its catch susceptibility from cumulative effects across the separate fishing methods. Finally, a quantitative assessment showed that population growth is slow even under the assumption of density-dependent compensation where the fishing mortality rate equals the natural mortality rate. Therefore, conservation and management for sustainable use of *S. megalops* will require a close control of fishing mortality due to the low capacity of this species to withstand fishing pressure.

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The piked spurdog, *Squalus megalops* (photo by Kelvin Aitken).

CHAPTER 1

CHAPTER 1

GENERAL INTRODUCTION

Global fish production has been increasing since the 1950s, but this increase is mainly due to aquaculture, as production from capture marine fisheries has remained relatively stable. Currently, about 50% of the worldwide major marine fish stocks are fully exploited, another 15–18% are overexploited and 9–10% of stocks have been depleted or are recovering from depletion (FAO 2000*a*). Whereas depleted and recovering teleost and invertebrate stocks may have ample potential for recuperation, this may not be the case for sharks and other chondrichthyans.

Currently, shark species are facing an increasing risk of depletion due to the combination of anthropogenic impacts such as fishing overexploitation and their unique life-history strategies. Sharks are harvested by industrial, artisanal, traditional, and recreational fisheries around the world and these fisheries have contributed to their decline (Walker 1998). Industrial fisheries directed at one or a small number of species of shark have seldom been sustainable, although Walker (1998) concluded that some species can be fished sustainably. However, other researchers (e.g. Holden 1974; Compagno 1990*a*; Musick *et al.* 2000; Stevens *et al.* 2000) claim that most industrial shark fisheries have been characterised by a rapid decline in catch rates or by a complete collapse of the fishery after the initial exploitation.

The decline in shark captures is masked by unreliable and underestimated shark-fishing statistics. A large proportion of world catches of sharks are not recorded in official fishery statistics because they are taken incidentally (retained non-targeted catch or by-product) while fishing for other target species (Bonfil 1994). Although official figures report about 700,000 T of elasmobranchs caught at the end of the 1980s, the actual level is at least in the range of 1.0–1.35 million T including unreported by-product (Bonfil 1994). Moreover, there is a high component of illegal fishing (Compagno 1990*a*; Bonfil 1994).

Even more worrisome, shark species are mostly taken in multispecies fisheries directed at more highly valued teleosts and in most fisheries part or the entire shark catch is discarded

(discarded non-targeted catch or by-catch), mostly dead or severely damaged, at the point of capture (FAO 2000*b*). Shark by-catch is not included in fishery statistics. For instance, Bonfil (1994) reported that in the high seas the estimated annual incidental capture of sharks and rays at the end of the 1980s was 250–270,000 T/year, but another 230–240,000 T/year could have been discarded (by-catch). Besides sharks being taken as by-product and by-catch, there may also be some collateral mortality of sharks that are not actually captured, associated with the fishing gear (Hall 1996). Such mortality does not form part of the fishery catch statistics and is unaccounted fishing mortality.

In addition to the impact of fisheries, there are several reasons why the conservation of sharks is of particular concern. First, most shark species have reproductive and growth characteristics and feeding habits that make their vulnerability to the effects of fishing high compared with teleost fish. Sharks mature late, exhibit low fecundity, long gestation periods and high longevity, and many species have slow growth (Holden 1973). Hence, sharks have low intrinsic rates of population increase and low resilience to fishing mortality (Hoenig and Gruber 1990; Smith *et al.* 1998). Second, most shark fisheries have been managed by population models designed for more productive animals such as teleost fishes, increasing the vulnerability of shark populations to overexploitation (Musick *et al.* 2000). Third, sharks are predators at or near the top of the marine food web and hence they are indirectly affected by the impacts on the species below them in the marine food web. Finally, assessment of shark populations is severely impaired by a lack of biological information (Cortés 1998*a*), especially for non-commercial species.

Therefore, the effects of fishing on most shark populations that are either targeted directly or caught incidentally remain mostly unidentified and unquantified. As a result, there is an increasing concern about the sustainability of shark stocks. International agreements reflect the concern about the sustainable management of sharks; the Food and Agriculture Organisation of the United Nations (FAO) developed the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) to ensure the conservation and management of sharks (targeted and non-targeted species) and their long-term sustainable use (FAO 2000*b*).

As a signatory to the IPOA-Sharks, Australia has developed the Australian National Plan of Action for the Conservation and Management of Sharks to ensure that all Australian shark species are managed sustainably regardless of fishery or jurisdictional boundaries. This need for management is also identified in the *Fisheries Management Act 1991* and the *Commonwealth Environment Protection and Biodiversity Conservation Act 1999*; this latter Act highlights the need for strategic assessment of fisheries operating under Commonwealth jurisdiction for ecological impacts on 1) target and by-product species, 2) by-catch species, 3) threatened, endangered and protected species, 4) marine habitats and 5) marine food webs. Hence, different types of survey, assessments and biological studies are required to meet the terms of the management commitments.

Australian sharks have been exploited by non-industrial and industrial fisheries. Local sharks have been fished by Australian aborigines as a source of food. Since European settlement in Australia, sharks have been captured to consume their meat and to extract oil from their livers for lighting and medicinal purposes (Walker 1998). Local sharks have also been utilized as fertilizer, as a source of Vitamin A and squalene and their leather has been used for making bags, wallets, shoes, and other garments (Walker 1998). Target and non-target shark species are captured in several different fisheries. Sharks are taken by foreign vessels in Australian waters, are captured in two shark control programs (Queensland and New South Wales), are targeted by recreational and game fishers, and are caught as by-catch or by-product or both in more than 70 other commercial fisheries. Furthermore, approximately 3,900 T of whole sharks were potentially finned and discarded during 1998–99 (Rose and McLoughlin 2001). However, most of the Australian recorded shark catch is taken by directed fisheries in the Southern and Eastern Scalefish and Shark Fishery (SESSF). This fishery comprises the South East Trawl Fishery, Great Australian Bight Trawl Fishery, and Gillnet Hook and Trap Fishery (GHATF). Of these fisheries, the GHATF is the most important in terms of shark landings, contributing one-third of Australia’s shark catch (Anonymous 2002). The GHATF deploys demersal gillnets and longlines to harvest several species of temperate-water sharks (Walker 1999). The primary target species are the gummy (*Mustelus antarcticus*) and the school (*Galeorhinus galeus*) sharks. Walker (1999) reported that during the period 1970–97 these two species comprised 88% of the catch; the remaining 12% were by-product species comprising saw shark (*Pristiophorus nudipinnis* and *P. cirratus*) (7%), elephant fish (*Callorhynchus milii*) (2%), and several other species of shark such as bronze whaler (*Carcharhinus brachyurus*), whiskery (*Furgaleus macki*), dusky (*C. obscurus*), broadnose sevengill (*Notorynchus* *cepedianus*), blue (*Prionace glauca*), mako (*Isurus oxyrinchus*), and angel (*Squatina australis*) sharks.

Currently, few studies have addressed the stock assessment of Australian sharks and these studies have only been focused on target species (e.g. Walker 1992; Punt and Walker 1998; Simpfendorfer *et al.* 2000). The models used in these studies are complex and require extensive data collection. However, shark populations can be depleted before collecting sufficient data to undertake reliable stock assessment (Compagno 1990*a*). Although complex models and comprehensive long-term monitoring data are required to reduce uncertainty, in the short-term, ecological risk assessment methods based on simpler data sets and judgement can provide advice on management of species at risk (Walker 2004). Therefore, a different approach is required for the evaluation of non-target species, in which long time-series of data have generally not been recorded. This new approach should involve the development and implementation of ecological risk assessment methods of each non-target shark species.

A risk assessment is a tool that allows quantifying risks to then allocate efforts and regulations to protecting species identified as at risk. An ecological risk assessment approach was originally applied to by-catch elasmobranch species (sharks and rays) in northern Australia by Stobutzki *et al.* (2002) and the methodology was taken a step further by Walker (2004) to make it more compatible with more comprehensive fishery assessment methods. For the assessment of risks to a species, information on the biological productivity and catch susceptibility is needed. Biological productivity is a measure of the population turnover potential or how fast a population can recover after overfishing. Catch susceptibility is a measure of the extent of the impact of a fishing method. In addition, knowledge on the feeding ecology of a species is also needed, as this provides information on the position and function of shark species in marine ecosystems. This knowledge is also important as potential negative effects on the prey of a shark may have negative food web cascading effects through trophic interactions. Furthermore, due to growing awareness of the need of a multispecies approach to fisheries management (Gulland 1978; Botsford *et al.* 1997), feeding ecology information is needed to determine interactions among components of the ecosystem.

Within the group of non-target Australian sharks, which neither the ecological risk nor the status of the stock have been assessed, the piked spurdog (*Squalus megalops*) is of special concern as it is the most caught by-catch shark species by trawling operations on the continental shelf and slopes of New South Wales, Victoria, Tasmania and South Australia (Walker and Gason 2006). Also, a proportion of the captured sharks is landed and retailed as ‘flake’. To date, the current marketed catch within dogfish species in south-eastern Australia is mostly *S. megalops* (Daley *et al.* 2002) and 16 T were marketed in 2004 from the GHATF (Walker and Gason 2005).

Squalus megalops is a member of the family Squalidae and it is one of the most abundant shark species of southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001). It is a demersal species that is distributed off southern and eastern Australia, from Carnarvon (Western Australia) to Townsville (Queensland), including Tasmania (Last and Stevens 1994). It has also been reported off the coasts of Brazil (Vooren 1992) and South Africa (Bass *et al.* 1976) and there are unconfirmed reports off Indo China, New Caledonia and New Hebrides (Last and Stevens 1994). This species inhabits the continental shelf and upper continental slope (depths <510 m) in warm temperate and tropical areas (Last and Stevens 1994). In eastern Australia, the abundance of *S. megalops* has not declined after 20 years of fishery exploitation. Hence, due to the depletion of many harvested shark species and a decline in abundance of most other shark species in southern Australia (Graham *et al.* 2001), *S. megalops* will inevitably become a more sought after species. However, due to little knowledge on its biology and on the effect that fishing has on its local population(s), the conservation status of *S. megalops* is uncertain.

The aim of the present study was to contribute to the ecological risk assessment of *S. megalops*, an important by-catch shark species taken in south-eastern Australia. To investigate the biology and ecological risk of this species, the specific objectives of this research were to:

- determine the population structure of *S. megalops* in south-eastern Australia (Chapter 2),
- determine total and partial length–length, mass–mass and mass–length relationships (Chapter 3),
- analyse stomach contents to determine the feeding ecology of this species and its role in marine ecosystems (Chapter 4),

- describe the reproductive biology of this species with emphasis on the information needed for quantitative population studies (Chapter 5),
- estimate the age and growth rate of *S. megalops* captured in south-eastern Australia (Chapter 6), and
- use qualitative, semi-quantitative and quantitative techniques for the assessment of ecological risks of *S. megalops* (Chapter 7).

Notes on chapter style

Each chapter of this thesis that presents original data (Chapters 2–7) has been written in a style suitable for publication in a scientific journal and can be read as a separate study. Each chapter is preceded by a preamble that briefly describes the content of the chapter, presents information on the publication status of the chapter at the time of thesis submission (where applicable), and describes the contributions of all co-authors to the research therein. Tables and figures appear within the text and all references cited in this thesis are compiled at the end of the thesis and not at the end of each chapter.

The shark gillnet vessel ‘*Ester-J*’ (photo by the author).

CHAPTER 2

CHAPTER 2 PREAMBLE

Chapter 2 describes the population structure of *S. megalops* in south-eastern Australia and shows the segregation pattern and sexual size dimorphism that the species exhibits in this area. At the time this thesis was submitted (January 2006), this chapter was under peer-review with the journal *Ciencias Marinas*, with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide) and Terence I. Walker (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation.

CHAPTER 2

NOTES ON POPULATION STRUCTURE OF THE PIKED SPURDOG (*SQUALUS MEGALOPS*) IN SOUTH-EASTERN AUSTRALIA

2.1 ABSTRACT

The population structure of *Squalus megalops* was studied in south-eastern Australia. A total of 929 sharks was analysed. The sex ratio was biased towards females. There was sexual size dimorphism; females attained a larger maximum size than males. Analyses of sex ratio and length-frequency distributions of selected fishing shots suggested that *S. megalops* had a complex population structure. Despite the opportunistic nature of the sampling design, individual analysis of selected fishing shots suggested that *S. megalops* segregated by sex, size and breeding condition. Small females and males segregated from large females. In addition, large females in the first year of pregnancy seemed to be separated from those in the second year of pregnancy. The segregation pattern exhibited by this species needs to be considered in management plans.

2.2 INTRODUCTION

Most dogfish species (Squalidae) have complex population structures. Segregation in time and space by sex, size and mature condition is a common feature of this group. Pregnant and ovulating females of the roughskin dogfish (*Centroscymnus owstoni*) segregate from immature specimens (Yano and Tanaka 1988). Size and sexual segregation have been reported for the southern laternshark (*Etmopterus granulosus*) (Wetherbee 1996), the black dogfish (*Centroscyllium fabricii*) (Yano 1995), the leafscale gulper shark (*Centrophorus squamosus*), the Portuguese dogfish (*Centroscymnus coelolepis*) (Clarke 2000) and the birdbeak dogfish (*Deania calcea*) (Clark and King 1989; Clarke *et al.* 2002*a*). Among *Squalus* species, the spiny dogfish (*S. acanthias*) exhibits a complex population structure related to its reproductive cycle. Off New Zealand, parturition, ovulation and mating occur in deep water whereas pregnant females spend the first year of gestation in shallow waters before migrating back to deep water during the second year of pregnancy (Hanchet 1988).

A complex size structure is also reported for the piked spurdog (*S. megalops*). In South Africa, this species forms large schools often segregated by sex and size (Compagno

1990*b*). In New South Wales, southeast coast of Australia, large females segregate from males and juveniles, aggregating in deeper waters and different regions (Graham 2005). In Australia, many of the harvested species of sharks have been depleted and the abundance of most other shark species has declined at least in southern Australia (Graham *et al.* 2001). However, *S. megalops* has a high natural abundance (Bulman *et al.* 2001; Graham *et al.* 2001) so this shark will inevitably become a more sought after species. Given that the current marketed catch within dogfish species in south-eastern Australia is mostly *S. megalops* (Daley *et al.* 2002), a better understanding of the population structure of this species is needed.

The aim of the present study was to determine the population structure of *S. megalops* in south-eastern Australia. Due to complex segregation patterns found in *Squalus* species, emphasis is put on separation between sexes, sizes and breeding condition.

2.3 MATERIALS AND METHODS

Male and female *S. megalops* were collected opportunistically from the by-catch of shark gillnet and demersal trawl fishing vessels operating in the Australian Southern and Eastern Scalefish and Shark Fishery during October 2002–April 2004. Samples were mainly collected from Robe, Lakes Entrance and Ulladulla (Fig. 2.1). Shark gillnet fishing gear consisted of monofilament netting of 6½-inch mesh-size, ~4000 m long, and 2.4 m deep deployed for 4–8 hours during night and day. Demersal trawl fishing gear consisted of otter trawl or Danish seine nets. Otter trawl nets had a headline length of 24–50 m with a stretched codend mesh-size of 90 mm and Danish seine nets had a headrope length of 30–59 m with a stretched codend mesh-size of 38 mm. Trawling operations lasted for 3–4 hours during night and day. Fishing depth varied with location and fishing gear between 21 and 238 m. Each individual *S. megalops* was measured (total length, TL) to the nearest millimetre. The reproductive condition of males and females was determined following Braccini *et al.* (2006; see Chapter 5 for description of reproductive stages of males and females).

The sex ratio and the length-frequency distribution of males and females were determined for the entire sample and per fishing shot when depth information was available and sample size per shot was ≥10. For the entire sample, a Chi-square test with Yates' continuity correction and a Kolmogorov-Smirnov test (KS; Zar 1999) were used to test for differences in the sex ratio and the length-frequency distribution of males and females, respectively.

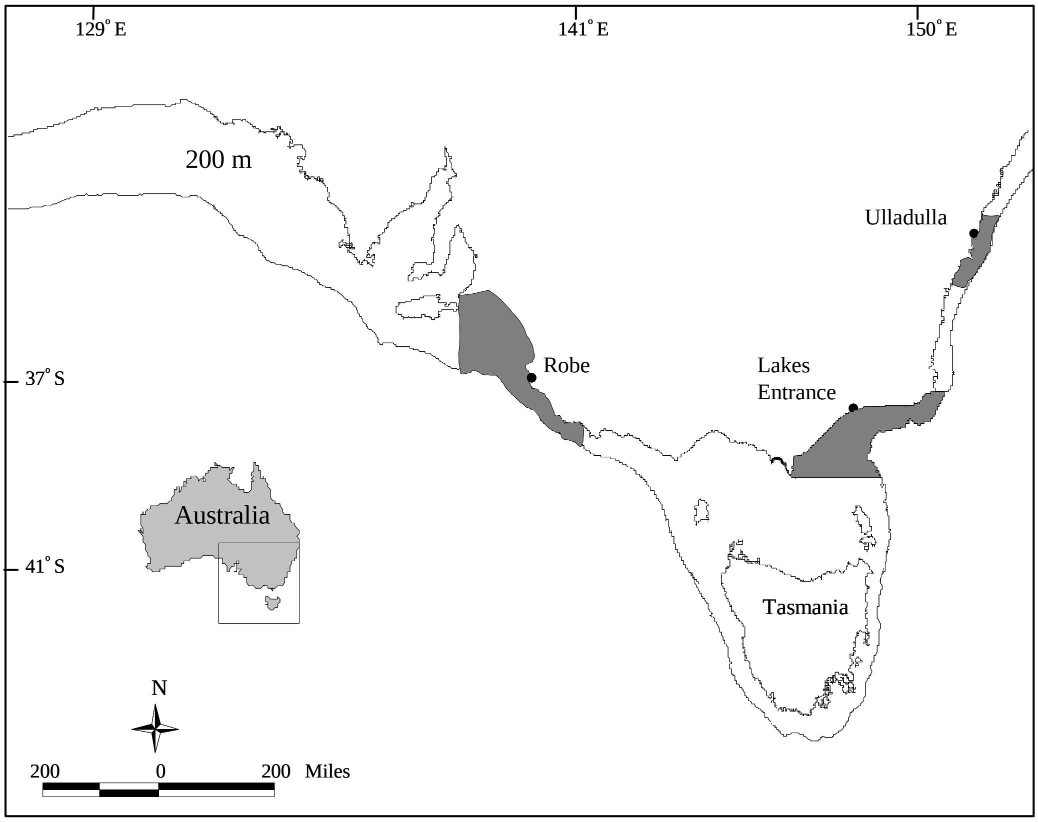


Figure 2.1. Map of sampling area (shaded).

2.4 RESULTS

Data from a total of 929 sharks were analysed. For the entire sample, the sex ratio (males : females) was significantly biased towards females (1 : 3.49, $\chi^2 = 284.39$, d.f = 1, $P < 0.001$). By fishing gear, the sex ratio was also biased towards females (1 : 25.34, $\chi^2 = 133.07$, d.f = 1, $P < 0.001$ for shark gillnets, and 1 : 2.83, $\chi^2 = 175.64$, d.f = 1, $P < 0.001$ for the demersal trawl nets). Size of sharks ranged from 274–470 mm TL for males and 270–635 mm TL for females. There was sexual dimorphism in maximum size; mean TL (± s.e.) of males was 404 (2) mm whereas mean TL of females was 480 (3) mm. The length-frequency distribution was significantly different between males and females (KS, $d_{MAX} = 0.685$, $n_{males} = 207$, $n_{females} = 722$, $P < 0.001$) (Fig. 2.2a). Shark gillnets mainly captured large females (Fig. 2.2b) whereas otter trawl and Danish seine nets caught males and females of a broader range of sizes (Figs. 2.2c, d).

Analyses of sex ratio and length-frequency distributions of selected fishing shots for the trawl method (18 fishing shots in total) suggested that *S. megalops* had a complex schooling pattern. In some cases, males and small females (<460 mm TL) were trawled together (Fig. 2.3a; Table 2.1, shots 146, 155), but in other shots mainly small immature females (Fig. 2.3b; Table 2.1, shot 205) or large females were captured (Fig. 2.3c; Table 2.1, shots 497, 509, 540). Among large females, those in the first year of pregnancy tended to be separated from females in the second year of pregnancy (Table 2.1, shots 497, 509, 540). In one shot, a school of large males was caught (Fig. 2.3d; Table 2.1, shot 491).

Analyses of length-frequency distributions of selected fishing shots for the gillnet method (8 fishing shots in total) also revealed a complex schooling pattern as only large females were captured (Figs. 2.3e, f; Table 2.1, shots 467, 521); however, it may be possible that in these shots small females and males were not sampled by the gillnet due to the size-selectivity of this fishing gear.

Table 2.1. Sample details for selected fishing shots showing the number of immature (I) and mature (M) males and the number of immature (I), first year of pregnancy (Year 1), second year of pregnancy (Year 2), and ovulating and post-partum (O & P-p) females.

Shot	Location	Month	Gear	Mean depth (m)	Number						Sex ratio	Mean size (± s.e.)	
					Male		Female					Male	Female
					I	M	I	Year 1	Year 2	O & P-p			
146	LE	February	Ds	73	22	5	28	2	1	0	1 : 1.1	386 (5)	421 (8)
509	LE	February	Ds	68.5	0	0	10	29	4	1	—	—	500 (5)
155	LE	March	Ds	38	3	6	7	2	0	2	1 : 1.2	434 (4)	476 (12)
205	LE	April	Ds	40.5	3	5	29	2	1	3	1 : 4.4	406 (6)	438 (7)
491	Queenscliff	February	Tn	75	1	33	0	0	0	0	—	416 (2)	—
467	Robe	January	Gn	87	0	2	23	17	5	3	1 : 24	416 (0)	528 (7)
521	Robe	March	Gn	90	0	0	1	20	5	1	—	—	573 (5)
497	Ulladulla	February	Tn	210.5	0	2	3	0	9	0	1 : 6	429 (17)	491 (16)
540	Ulladulla	March	Tn	164	0	1	1	23	3	0	1 : 27	433 (0)	506 (5)

LE (Lakes Entrance); Ds (Danish seine net); Tn (trawl net); Gn (gillnet).

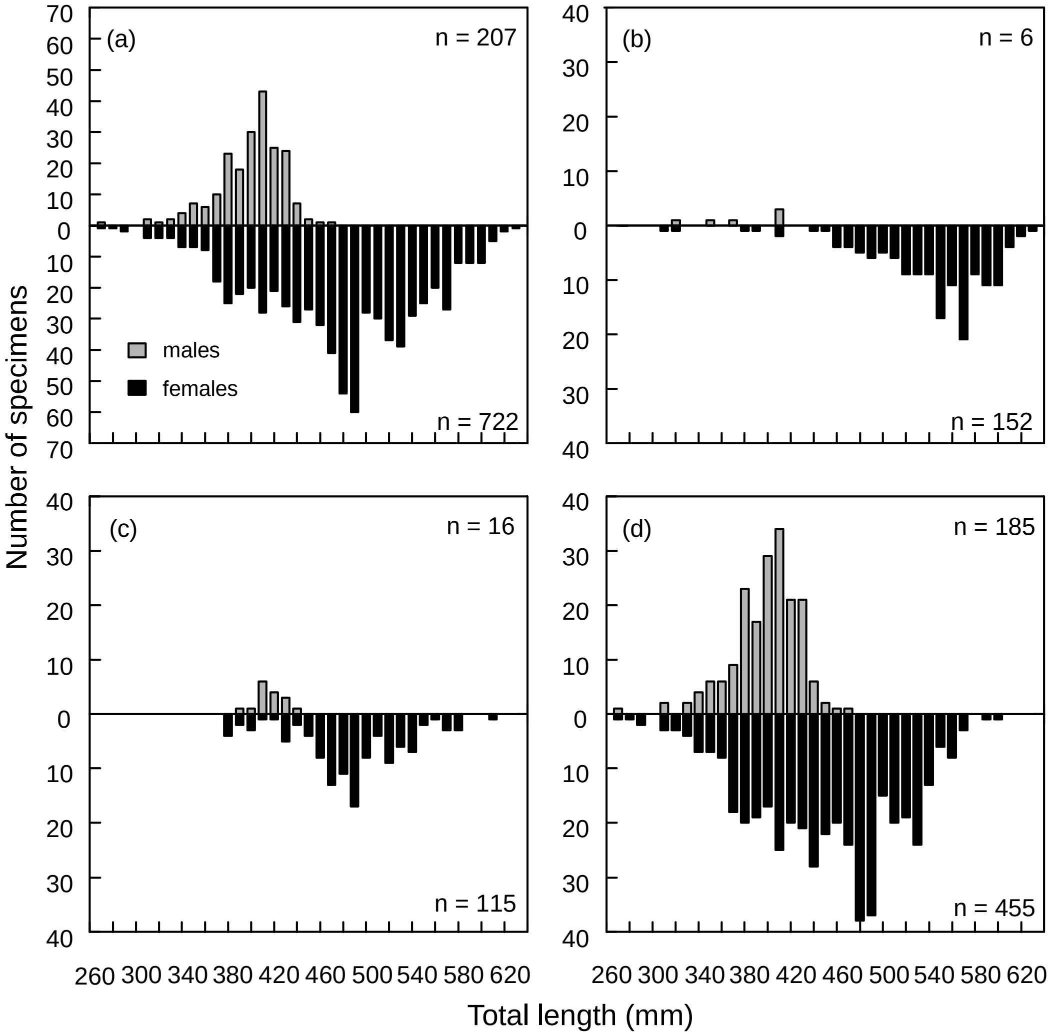


Figure 2.2. Length-frequency distribution of *Squalus megalops* for (a) the entire sample, and by fishing gear: (b) shark gillnet, (c) otter trawl net, and (d) Danish seine net.

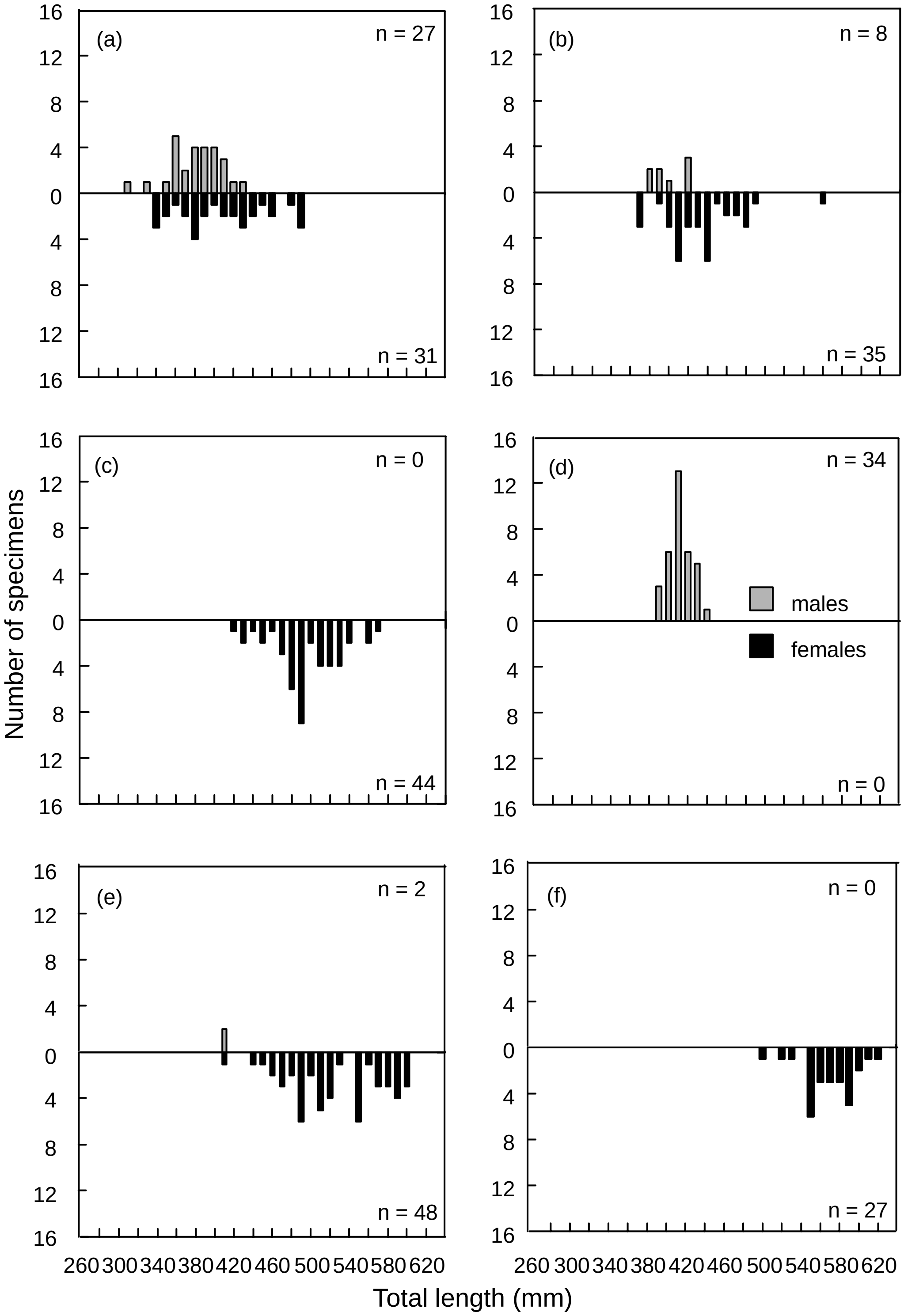


Figure 2.3. Length-frequency distribution of some of the selected fishing shots (location, gear and season): (a) 146 (Lakes Entrance, Danish seine net, summer), (b) 205 (Lakes Entrance, Danish seine net, autumn), (c) 509 (Lakes Entrance, Danish seine net, summer), (d) 491 (Queenscliff, Danish seine net, summer), (e) 467 (Robe, gillnet, summer), and (f) 521 (Robe, gillnet, autumn).

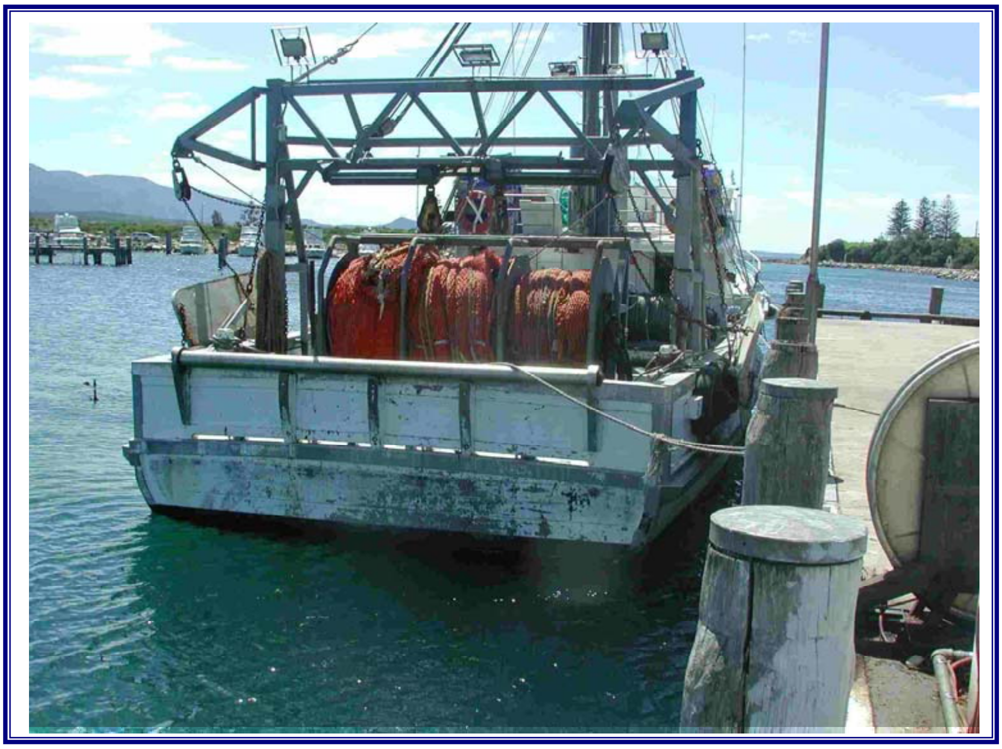
2.5 DISCUSSION

The present study provides evidence of a complex population structure for *S. megalops* in south-eastern Australia. Although the opportunistic nature of the sampling design did not allow for the effects of time, region, depth or sampling gear to be rigorously tested, individual analysis of selected fishing shots suggested that *S. megalops* segregates by sex, size and breeding condition. Sexual and size segregation is a common characteristic of many shark species where juveniles, adult males and adult females separate into different groups (Springer 1967). Male and small female *S. megalops* were sampled together and did not occur with large females. Furthermore, in one of the shots, a school of only large mature males was collected and on other occasions, schools of only large females were captured. Graham (2005) reported a similar pattern off New South Wales where large females and males occur in different regions and depths. In addition, large females in the first year of pregnancy seemed to be separated from those in the second year of pregnancy. Similarly, large female *S. acanthias* segregate by breeding condition. Pregnant females spend the first year of pregnancy in shallow waters, perhaps due to warmer water requirements for early embryo development, and migrate to deeper offshore waters during the second year of pregnancy (Hanchet 1988).

Female *S. megalops* attained larger sizes than males. Sexual size dimorphism is frequently observed in sharks and it is more common among viviparous species where for females, due to their more energetically demanding reproductive mode, there is a strong selection pressure for a larger body size (Sims 2003). Many species that have sexual size dimorphism also exhibit sexual segregation (Sims 2003). In sexually dimorphic mammals, males attain a larger size and seek habitats with higher food availability, whereas females prefer habitats safe from predation (Main *et al.* 1996). Sex-specific habitat use has been reported for several shark species (e.g. McLaughlin and O'Gower 1971; Sims *et al.* 2001). Female scalloped hammerhead sharks (*Sphyrna lewini*) select habitats with more abundant, energy-rich prey (Klimley 1987). Large female *S. megalops* had a different diet and consumed more energy-rich prey than males and small females during summer and autumn (Braccini *et al.* 2005; Chapter 4). Hence, if large females have different energetic requirements, selection of different diet quality may lead to sexual size segregation (Main *et al.* 1996). In this way, large females may inhabit areas with higher food availability while males and small females trade off food preference for areas with fewer predators (Bowyer 2004). However, other hypotheses, such as migration, differences in swimming capabilities, male-avoidance, or absence of aggression between similar sized individuals have also been proposed to explain segregation among sharks (Springer 1967; Sims 2003). Given that *S. megalops* is the most commonly taken by-catch shark species by demersal trawlers in south-eastern Australia (Walker and Gason 2006), further information is needed on the location of parturition areas, and the spatial distribution of juveniles, males and females in different breeding condition. A more rigorous sampling design would allow the extent of the segregation pattern of *S. megalops* to be determined and testing the hypotheses proposed to explain this phenomenon.

Small *S. megalops* were not collected by the sampling gears. The small length-classes are often missing in dogfish studies (Clarke 2000). Gillnets select for larger-sized specimens, but demersal trawl nets are likely to catch the smaller *S. megalops* as it was shown that, when present, the small size-classes are retained by the 90-mm mesh-size codend (Graham 2005). Hence, small individuals probably occur outside the trawling grounds, being unavailable to the trawl gear. A pelagic phase has been proposed for juvenile *S. megalops* (Compagno *et al.* 1991). This life strategy would decrease predation risk as predation by larger sharks and teleosts most likely occurs near the seabed (Graham 2005).

The sex ratio suggests that either females are more common in the population or they are more vulnerable to fishing than males. In the latter case, this must be considered in the management of this species, as the selective removal of females may have a disproportionate effect on the reproductive output of the population. Furthermore, the segregation pattern of *S. megalops* also needs to be considered in management plans. Different management of males and females has already been proposed for mammals with sexual segregation (Bowyer 2004).



One of several trawlers that assisted in sampling (photo by the author).

CHAPTER 3

CHAPTER 3 PREAMBLE

Chapter 3 presents conversion factors from partial lengths and masses to total length and mass due to the common fishing practices of eviscerating, beheading and finning sharks. Also, different ranges of size are used for testing sexual differences in length–length and mass–length relationships to distinguish variables related only to somatic growth from variables related to somatic and reproductive growth. At the time this thesis was submitted (January 2006), this chapter was accepted for publication in the journal *Fisheries Research* (*in press*), with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide) and Terence I. Walker (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation. Permission from the publisher (Elsevier Ltd) to reproduce this manuscript has been granted (see Appendix A).

Contributions and signatures of authors

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CHAPTER 3

TOTAL AND PARTIAL LENGTH–LENGTH, MASS–MASS AND MASS–LENGTH RELATIONSHIPS FOR THE PIKED SPURDOG (*SQUALUS MEGALOPS*) IN SOUTH-EASTERN AUSTRALIA

3.1 ABSTRACT

Common commercial fishing practices of eviscerating, beheading and finning sharks create the need for using conversion factors from partial lengths to total length and from partial masses to total mass. In the present paper, these conversion factors were calculated for *Squalus megalops*. In addition, total and partial length–length and mass–length relationships of male and female *S. megalops* were compared using different ranges of size. There was no effect of size range on measurements reflecting only somatic growth (fork and carcass lengths; carcass, pectoral fin and caudal fin masses) but for variables reflecting somatic and reproductive growth (total and liver masses), different outcomes can be expected when different ranges of size are compared.

3.2 INTRODUCTION

Fisheries taking sharks are common throughout the world. Given that commercial shark species are normally beheaded, eviscerated and landed in one of two forms: with fins attached (‘carcass’) or without fins attached (‘trimmed carcass’), only partial lengths and masses can be recorded after landing (FAO 2000*b*). Furthermore, due to increases in worldwide demand for shark fins, in many fisheries only the fins are retained whereas the rest of the animal is discarded. Due to these fishing practices, relationships between partial lengths and total length and between partial masses and total mass of shark are needed to determine the length and mass composition of captured sharks. Therefore, conversion to live weight and length equivalent units using appropriate conversion factors is an essential requirement for fisheries monitoring programmes and stock assessments.

Size relationships and size conversion factors have several biological applications and are commonly used in fishery management. Size relationships, particularly total mass–total length relationship, are commonly reported in biological studies of sharks (e.g. Stevens and McLoughlin 1991; Kohler *et al.* 1995). Many studies test for differences between sexes in these relationships; in some cases, significant differences are found (e.g. Chiaramonte and Pettovello 2000; Walker 2005), whereas other studies show no differences (e.g. Bridge *et al.* 1998; Francis and Stevens 2000). Many species of sharks exhibit sexual dimorphism in maximum size, females being larger and heavier than males (e.g. Cortés 2000). For these species, size relationship comparisons are thus made between groups of different ranges of size so similarities or differences in these relationships may be an artefact of comparing smaller individuals (males) with larger individuals (females).

In the present study, length–length and mass–length relationships of male and female piked spurdogs (*Squalus megalops*), an abundant shark of southern Australia (Graham *et al.* 2001), were compared using different ranges of size. In addition, due to the common fishing practice of eviscerating, beheading and finning sharks, conversion factors from partial lengths and partial masses to total length and total mass were determined.

3.3 MATERIALS AND METHODS

Male and female *S. megalops* were collected from the by-catch of shark and demersal trawl fishery vessels operating in the Australian Southern and Eastern Scalefish and Shark Fishery during October 2002–April 2004. Total (TL), fork (FL) and carcass (CL) lengths were measured to the nearest millimetre. Fork length was measured from the tip of the snout to the caudal fork and CL was measured from the fifth gill-slit to the precaudal pit. Total (TM), carcass (CM), liver (LM), pectoral fins (PFM) and caudal fin (CFM) masses were recorded to the nearest gram. All length and mass measures were recorded in the laboratory. Differences between sexes were tested by Student *t*-test on the slopes and intercepts of the linear regression of FL and CL against TL and the linear regression of ln (TM), ln (CM), ln (LM) ln (PFM), and ln (CFM) against ln (TL) or ln (CL) (Kleinbaum *et al.* 1988). A factor is used to correct for biases caused by natural logarithmic transformation (Beauchamp and Olson 1973).

Squalus megalops showed sexual dimorphism in maximum size, ranging from 274–470 mm TL (86–465 g TM) and 270–635 mm TL (84–1411 g TM) for males and females, respectively. Hence, samples of different ranges of size were selected for statistical comparisons. The following groups were compared: males (n = 207), all females (n = 721) and small females (≤470 mm TL, n = 297). Geometric mean regressions (Ricker 1973) were used to determine conversion factors from partial lengths and partial masses to total length and total mass and from total length and total mass to partial lengths and partial masses.

3.4 RESULTS

There were no significant differences in the FL–TL, CL–TL, CM–TL, PFM–TL, CFM–TL, and CM–CL relationships between males and all females and between males and small females (*t*-test, $P > 0.05$ for comparisons of slopes and intercepts). Therefore, sexes and sizes were pooled for calculation of conversion factors, shown in Table 3.1. The conversion factors estimated are applicable to the size range analysed (270–635 mm TL), which covers most of the population size range, with the exception of neonates (TL <270 mm).

There were significant differences in the TM–TL relationship between males and all females (*t*-test, d.f. = 902, $t = 5.06$, $P < 0.05$ for comparison of slopes and $t = 5.01$, $P < 0.05$ for comparison of intercepts; Fig. 3.1). However, when animals of the same size range were compared (males and small females), no differences were detected (*t*-test, d.f. = 500, $t = 1.78$, $P > 0.05$ for comparison of slopes and $t = 1.74$, $P > 0.05$ for comparison of intercepts; Fig. 3.1). There were no differences in the LM–TL relationship between males and all females (*t*-test, d.f. = 873, $t = 0.89$, $P > 0.05$ for comparison of slopes and $t = 0.86$, $P > 0.05$ for comparison of intercepts; Fig. 3.1), but significant differences were detected between males and small females (*t*-test, d.f. = 481, $t = 4.51$, $P < 0.05$ for comparison of slopes and $t = 4.47$, $P < 0.05$ for comparison of intercepts; Fig. 3.1). To standardize for the effects of size, CM and LM were expressed as a proportion of TM. Carcass mass expressed as a proportion of TM (CMP) decreased with TL for all females (Fig. 3.2), whereas the CMP–TL relationship showed no trend for males and a slight decrease for small females (not shown). Liver mass expressed as a proportion of TM (LMP) increased with TL for small females (Fig. 3.2). For males and all females, the LMP–TL relationship showed no trend (not shown).

Table 3.1. Conversion factors derived from geometric mean regressions. Estimated parameters for converting (a) partial lengths and partial masses to total length and total mass and (b) total length and total mass to partial lengths and partial masses. Values for parameters (and standard error) derived from the equation Y = *a* + *b* X.

Variables		n	*b* ± s.e.	*a* ± s.e.
X	Y			
(a)				
Fork length	Total length	547	1.138 ± 0.005	5.736 ± 1.857
Carcass length	Total length	490	1.587 ± 0.017	26.764 ± 4.419
Carcass mass	Total mass	851	1.939 ± 0.011	–58.518 ± 3.537
Pectoral fin mass	Total mass	351	64.437 ± 0.962	–87.998 ± 9.119
Caudal fin mass	Total mass	352	82.529 ± 0.948	–136.357 ± 7.562
(b)				
Total length	Fork length	547	0.878 ± 0.004	–4.972 ± 1.651
Total length	Carcass length	490	0.630 ± 0.007	–16.901 ± 2.959
Total mass	Carcass mass	851	0.516 ± 0.003	30.230 ± 1.676
Total mass	Pectoral fin mass	351	$0.016 \pm 2.31 \times 10^{-4}$	1.367 ± 0.123
Total mass	Caudal fin mass	352	$0.013 \pm 1.43 \times 10^{-4}$	1.467 ± 0.076

a and *b* are parameters and n is sample size.

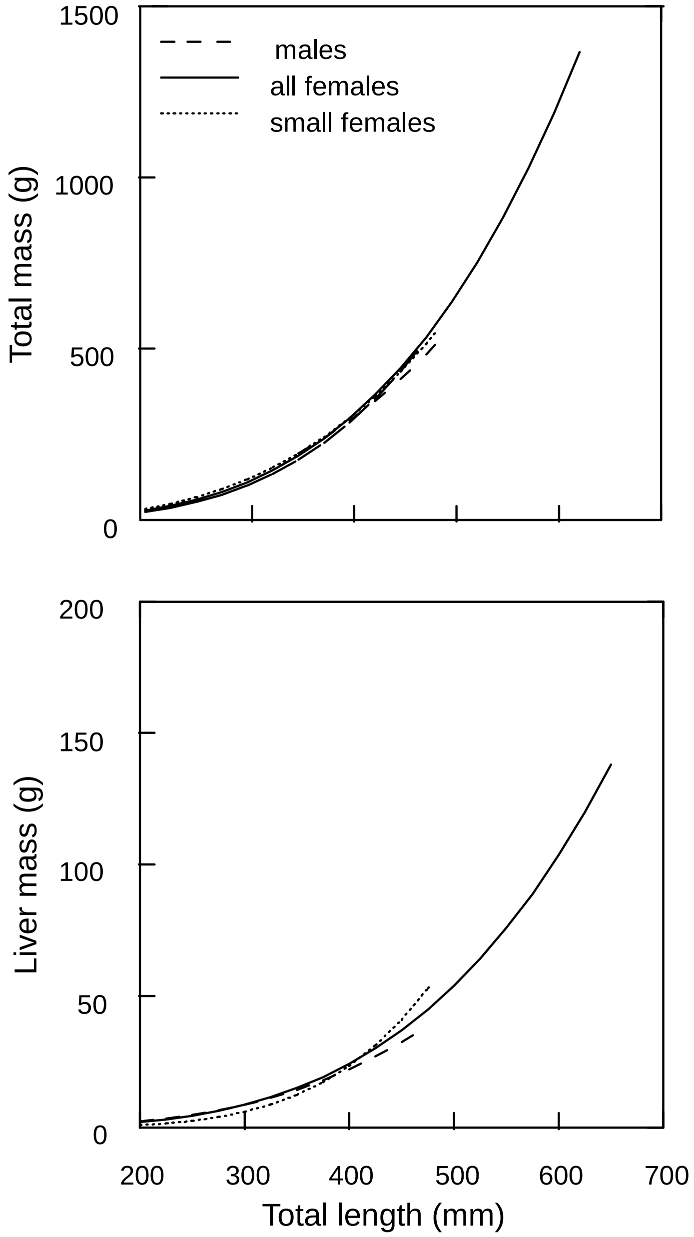

Figure 3.1. Predicted relationship between total mass and total length and between liver mass and total length for males, all females and small females. Values for parameters are given in Table 3.2.

Table 3.2. Estimated parameters (and standard error) for the relationship between total mass (TM) and total length (TL) and between liver mass (LM) and total length (TL) for males, all females and small females, derived from the equation TM = $a\ c\ \mathrm{TL}^b$ and LM = $a\ c\ \mathrm{TL}^b$.

Shark group	*a* (s.e. range)	*b* (± s.e.)	*c*	n	r^2
TM–TL					
Males	2.15 (1.44–3.20) × 10^{-6}	3.124 (0.07)	1.003	205	0.91
All females	2.54 (2.18–2.96) × 10^{-7}	3.482 (0.03)	1.005	699	0.97
Small females	8.09 (5.76–11.40) × 10^{-7}	3.290 (0.06)	1.006	297	0.92
LM–TL					
Males	7.15 (1.34–38.20) × 10^{-8}	3.257 (0.28)	1.034	196	0.41
All females	1.05 (0.59–1.87) × 10^{-8}	3.587 (0.09)	1.065	679	0.69
Small females	1.03 (0.41–2.63) × 10^{-11}	4.743 (0.16)	1.031	287	0.76

a and *b* are parameters, *c* is the (Beauchamp and Olson 1973) correction factor for logarithmic transformation, n is sample size and r^2 is square of correlation coefficient.

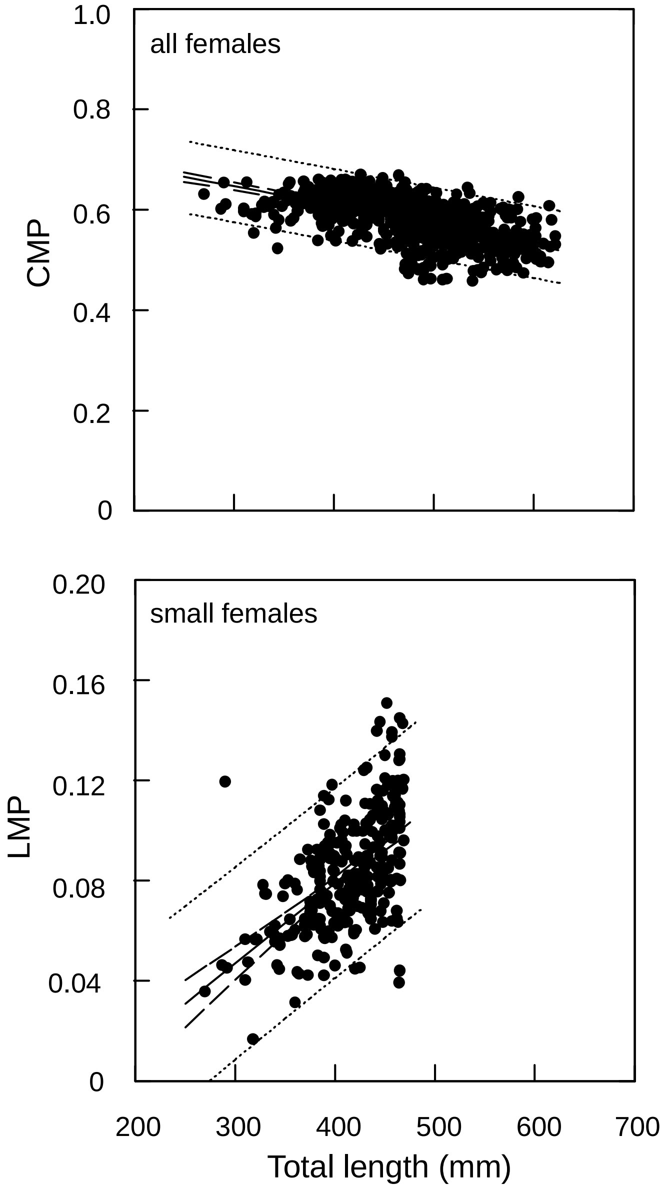

Figure 3.2. Relationship between carcass mass as a proportion of total mass (CMP) and total length (TL) for all females and between liver mass as a proportion of total mass (LMP) and TL for small females with 95% confidence intervals around the mean (– – –) and 95% predicted intervals around the data (········). All females: CMP = 0.758 (0.01) – 3.723 (0.21) × 10^{-4} TL, n = 660, $r^2 = 0.32$, and small females: LMP = –0.049 (0.01) + 3.211 (0.28) × 10^{-4} TL, n = 279, $r^2 = 0.32$.

3.5 DISCUSSION

There were no sex or size effects in the FL–TL, CL–TL, CM–TL, PFM–TL, CFM–TL, and CM–CL relationships. These length and mass measures reflect structural size and somatic growth with little trade-off between somatic and reproductive growth. Otherwise, the relatively larger increase in reproductive tissue experienced by adult female sharks (e.g. Yano 1995) would be coupled with a decrease in their somatic tissue, particularly carcass mass, expecting differences in the CM–TL and CM–CL relationships of all females compared with males or small females. Hence, for measurements that only reflect somatic growth (e.g. partial lengths, fin masses), comparing different ranges of size had no effect on the relationships between these variables and TL.

Total mass and LM reflect somatic growth and reproductive investment. As the costs of reproduction are different between males and females (Stearns 1992), different outcomes can be expected when testing for differences between sexes if different ranges of size are compared. This is of particular concern for species that exhibit sex and size segregation, such as *S. megalops* (Graham 2005; Chapter 2), for which the full size range of the population may not be adequately represented. Male and small female *S. megalops* had a similar TM–TL relationship, but this relationship was different from the TM–TL relationship of all females. Thus, if sampling is biased towards particular size-classes due to size-selectivity of the sampling gear or size or sex segregation of sharks, comparisons between sexes may not reflect real differences or similarities in the TM–TL relationship. Hence, given the opportunistic sampling nature of most biological studies of sharks and the small sample size of many studies, care must be taken when determining mass–length relationships. If the size range is not fully represented, mass–length relationships may be biased, affecting predictions of population assessments that use these relationships as inputs to the models. Likewise, the LM–TL relationship of *S. megalops* differed between the sexes depending on the ranges of size compared. For some squalid sharks (Yano 1995; Clarke *et al.* 2001) and other elasmobranchs (e.g. Craik 1978), size of liver varies with reproductive stage, being relatively smaller for pregnant females. Liver lipid reserves are used for vitellogenesis (Craik 1978); hence, an increase in liver lipids and liver mass is expected for females entering first maturation. This was reflected in the larger slope of the LM–TL relationship and the increase in LMP with TL for small females. This pattern was obscured when small and large females were pooled as no trend was observed for this relationship when using all females and also no differences were found in the LM–TL relationship of males and all females. Therefore, the relationships between variables that reflect somatic growth and reproductive dynamics and TL are affected by the ranges of size used.

Most life-history parameters used in shark stock and demographic assessments are determined as a function of TL or TM (e.g. maturity and maternity ogives, fecundity). Also some shark fisheries use minimum and maximum size limits to regulate the catch. However, commercial shark species are normally beheaded, eviscerated and finned so only the mass and length of the carcass or the mass of the fins can be recorded after landing. It is, therefore, essential to determine how these partial lengths and masses can be converted to TL or TM (FAO 2000*b*). When measurements reflect only somatic growth, conversion factors to TL or TM can be determined by pooling sexes and sizes, but for measurements that reflect both somatic and reproductive growth, conversion factors should be determined for sexes and sizes separately. Although many studies provide TM–TL relationships, few present conversion factors to allow calculating TL or TM from partial length or partial mass measures. Geometric mean regressions were used to determine conversion factors for several length–length and mass–mass relationships for *S. megalops*. These conversion factors are essential for assessment of this species. Given the depletion of many of the harvested species of sharks and a decline in abundance of most other shark species in southern Australia (Graham *et al.* 2001), *S. megalops* will inevitably become a more sought after species.

Some of the prey items found in the stomach of *Squalus megalops* (photos by the author).

CHAPTER 4

CHAPTER 4 PREAMBLE

Chapter 4 studies the range of variability around the estimate of the overall importance of prey items of *Squalus megalops*. The chapter also tests the relative and interactive effects of potential sources of variation in the feeding ecology of this predator. This chapter was published in the journal *ICES Journal of Marine Science* in 2005 (vol 62: 1076–1094), with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide) and Terence I. Walker (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation. Permission from the publisher (Elsevier Ltd) to reproduce this manuscript has been granted (see Appendix A).

Contributions and signatures of authors

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CHAPTER 4

SOURCES OF VARIATION IN THE FEEDING ECOLOGY OF THE PIKED SPURDOG (*SQUALUS MEGALOPS*): IMPLICATIONS FOR INFERRING PREDATOR–PREY INTERACTIONS FROM OVERALL DIETARY COMPOSITION

4.1 ABSTRACT

Sources of variation in dietary composition were examined in the piked spurdog (*Squalus megalops*). This species is an opportunistic predator that consumed a wide range of prey items. When importance of prey was measured by weight or occurrence, *S. megalops* preyed largely on molluscs and teleosts. However, when number of prey was considered, the main items were crustaceans. A bootstrap analysis showed that considerable variability can be expected in the importance of prey items in the species' overall diet. Regional, seasonal and ontogenetic differences in dietary composition were found, but there were no differences between mature and immature sharks or between males and females. The spatial and temporal variation in diet exhibited by *S. megalops* and the intrinsic natural variability of the dietary composition of this opportunistic predator suggest that studies that infer predator–prey interactions from overall diet are likely to miss information on the ecological relationships among species and thus account for only part of these interactions.

4.2 INTRODUCTION

The feeding ecology of marine animals has been studied to determine the ecological roles and position of animals within foodwebs and to understand predator–prey interactions (Caddy and Sharp 1986; Pauly *et al.* 1998; Cortés 1999). Interactions among species affect population dynamics and also cause indirect ecological effects (Alonzo *et al.* 2003). Hence, if interactions among species were determined, ecosystems could be managed with higher certainty (Yodzis 1994). Traditional single-species fishery management ignores fishery impacts on ecosystems (Agardy 2000). As an alternative, ecosystem-based fishery management has been proposed to account for such impacts (Gulland 1978; Caddy and Sharp 1986; Fulton *et al.* 2003). Many ecosystem models use dietary information as a proxy for the interactions among species (e.g. Christensen 1995; Walters *et al.* 1997;

Yodzis 1998). However, most models use overall diet data, ignoring many sources of variation that can affect the dietary composition of predators.

Natural systems are dynamic and vary in time and space (Paine 1988). It is, therefore, expected that diet of predators, and hence predator–prey interactions, may also vary in time and space. Trophic interactions are determined by the size of predators and their prey (Floeter and Temming 2003), but little is known about predator–prey size relationships of large marine predators such as sharks. Also for sharks, the effects of time and space and their interactions with other potential sources of variation in their diet, such as sex or maturity condition, have been little studied. Although some studies have reported regional, seasonal, or ontogenetic differences in diet (see Wetherbee and Cortés 2004, for a review), many studies on the diet of sharks have been limited to simple lists of prey items (Heithaus 2004). Moreover, variation in diet has often been reported qualitatively with little statistical support (Ferry and Cailliet 1996; Cortés 1997; Wetherbee and Cortés 2004). Hence, a more rigorous and quantitative approach is required to study the feeding ecology of sharks.

The piked spurdog (*Squalus megalops*) is a suitable species to test for the effects of potential sources of variation in the dietary composition of predators, as it is a very abundant shark in southern Australia (Jones 1985; Bulman *et al.* 2001; Graham *et al.* 2001). *Squalus megalops* inhabits waters of the continental shelf and upper continental slope to 510 m (Last and Stevens 1994). Off South Africa, females grow larger (782 mm total length, TL) than males (572 mm TL) and attain 50% maturity at 15 years, and 50% of males are mature at 9 years old (Watson and Smale 1999). Given its high natural abundance, which has remained stable since it was first surveyed (Graham *et al.* 2001), *S. megalops* is a dominant and ecologically important species (Bulman *et al.* 2001) that is likely to make an important contribution to the structure and function of an ecosystem. Nevertheless, information on its feeding habits is scarce. Its overall diet has been described for animals caught off South Africa and eastern Australia, where it preys mainly on teleosts and cephalopods, but also consumes crustaceans and elasmobranchs (Bass *et al.* 1976; Ebert *et al.* 1992; Bulman *et al.* 2001). Although those studies offer a preliminary description of the diet of this shark, more quantitative analyses are needed.

The purpose of this study was to investigate the effects of several sources of variation in the feeding ecology of *S. megalops*. The specific objectives were to: (i) quantify its overall dietary composition and account for how much variability would be expected when calculating overall prey importance; (ii) examine relationships between prey and predator size; and (iii) test for the effects of region, maturity condition, sex, season and ontogenetic variation on its dietary composition.

4.3 MATERIALS AND METHODS

Sampling

Squalus megalops were obtained from the by-catch of shark and trawl vessels operating in the Australian Southern and Eastern Scalefish and Shark Fishery (Fig. 4.1). Samples were collected monthly between October 2002 and April 2004, with the exception of the period July–September (Table 4.1), when *S. megalops* seems to move off the fishing grounds and weather conditions restricted sampling. The specimens were sexed, measured (TL ±1 mm) and weighed on an electronic balance (±0.1 g). Maturity of males was determined on the basis of clasper calcification, condition of testes and vas efferens, and presence of semen in seminal vesicles. Maturity of females was determined on the basis of the condition of oviducal glands and ovarian follicles, and the presence of *in utero* eggs or embryos.

Diet and data analyses

Diet was studied by prey identification and analysis of stomach contents. The stomach of each fish was removed, and the contents were identified to the lowest taxon practical. When possible, to correlate size of prey and predator, body width (BW) of worms, TL of fish, mantle length (ML) of cephalopods, and shield length (SL) of hermit crabs were measured to the nearest millimetre. Where these lengths could not be measured, TL of fish, ML of cephalopods, and SL of hermit crabs were estimated from hard tissue pieces found in stomach contents by linear and allometric relationships determined by regression, using a personal reference collection and the fish and crustacean reference collections of the South Australian Museum, Australia, and Museum Victoria, Australia. Prey items that digest more speedily than other prey items or soft-bodied prey may be under-represented if the more persistent hard parts are included in the analyses (Bigg and Fawcett 1985; Bigg and Perez 1985). Hence, hard parts (e.g. beaks, vertebrae, chelipeds) were only used for estimating prey item size and describing the overall dietary spectrum, but they were excluded from further analyses.

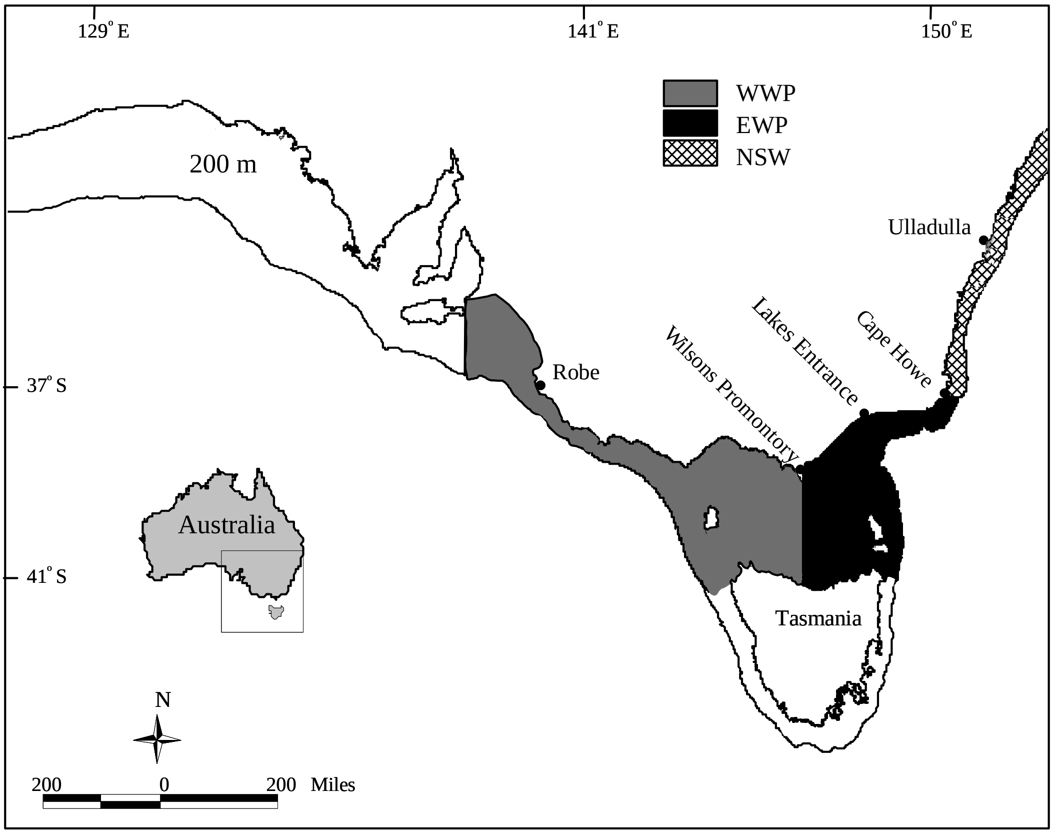

Figure 4.1. Map of sampling area showing the three biogeographic regions and ports – west of Wilsons Promontory (WWP), east of Wilsons Promontory (EWP), New South Wales (NSW).

Taxonomic classification of prey items does not account for differences in habitat utilization of a predator. Therefore, data analyses were carried out by main zoological group (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, Teleostei) and ecological group separately. The ecological groups considered were benthic infauna (prey species living in the sediment), benthic epifauna (prey species living on the sediment surface), benthic (prey species living on the bottom), demersal benthic (prey species living near the bottom but not linked to it), demersal pelagic (prey species with extensive diel vertical migration), and pelagic (prey species living in the upper layers of the water column).

Overall diet

Stomach fullness (SF) and number of prey found in each stomach were recorded to determine the feeding pattern of *S. megalops*. Stomach fullness was recorded using a quarterly scale (0, empty; 1, 0–25% filled; 2, 26–50% filled; 3, 51–75% filled; 4, 76–100% filled). Chi-square tests with Yates' continuity correction (Zar 1999) were used to test for differences in the distribution of SF.

To obtain a precise description of the overall diet of a predator, it is important to determine the minimum number of stomachs required (Ferry and Cailliet 1996; Cortés 1997). The number of *S. megalops* collected was tested to determine whether sufficient sharks were sampled. Items such as sponges, hydroids, and algae were considered incidental, and were excluded from the analysis. The cumulative number of randomly pooled stomachs was plotted against the cumulative diversity of stomach contents. Diversity was calculated using the pooled quadrat method based on the Brillouin Index of diversity (HZ; Pielou 1966). To ensure that curves reached an asymptotic value, 10 random orders of stomachs (curves) were calculated (Koen Alonso *et al.* 2002). Diversity curves were considered asymptotic if at least two previous values to the total sample diversity were in the range of asymptotic diversity ±0.05 (Koen Alonso *et al.* 2002). Diversity curves were calculated for each combination of factors considered in the analyses of variation in dietary composition.

Table 4.1. Sampling sites (see Fig. 4.1), collection time, and sample sizes collected for the spatial, temporal, ontogenetic, maturity condition, and sexual components of the study (sample sizes for the analyses may be smaller because of the occurrence of empty stomachs).

Factor	Site	Collection time	Sample size
Spatial (large females ≥471 mm TL)			
West Wilsons Promontory (WWP)	Robe	Autumn 2004	36
East Wilsons Promontory (EWP)	Lakes Entrance	Autumn 2004	60
New South Wales (NSW)	Ulladulla	Autumn 2004	41
Temporal (seasonal)			
Summer	Lakes Entrance	December 2002, February 2003, 2004	116
Autumn		March 2003, 2004, April, May 2003	98
Winter		June 2003	24
Spring		October 2002, November 2003	71
Size (ontogenetic)*			
Small male (≤400 mm TL)	Lakes Entrance	Spring 2002, 2003, Summer 2003, 2004, Autumn 2003, 2004	30
Small female (≤400 mm TL)			51
Medium-sized females (401–470 mm TL)			92
Large male (401–470 mm TL)			37
Large female (≥471 mm TL)			100
Maturity condition			
Immature	Lakes Entrance	Spring 2002, 2003, Summer 2003, 2004, Autumn 2003, 2004	174
Mature			131

Table 4.1. Continued…

Factor	Site	Collection time	Sample size
Sexual			
Male	Lakes	Spring 2002, 2003,	67
Female	Entrance	Summer 2003, 2004,	242
		Autumn 2003, 2004	

[*] *Squalus megalops* has a tendency to segregate by sex/size and this was reflected in the size frequency distribution of some of the fishing shots analysed. Hence, the size classes compared are based on this segregation pattern.

No single method of analysis of stomach contents completely describes the diet of a predator (Hyslop 1980); hence, the importance of prey items was evaluated using percentage weight (%W), percentage number (%N), percentage frequency of occurrence (%FO), and percentage Index of Relative Importance (%IRI; Pinkas *et al.* 1971; Cortés 1997). Bootstrap methods (1000 replicates) were used to estimate confidence intervals (2.5th and 97.5th percentiles) around the dietary parameters (mean %W, %N, %FO, and %IRI; Haddon 2001). From the original data matrix, random samples of the observations (i.e. each individual stomach) with replacement were generated to obtain the probability distribution of the dietary parameter estimates for each prey item.

Predator–prey size relationship

The relationship between prey size and shark size was determined using the Spearman rank correlation coefficient (r_s). The length variables for the different taxonomic groups were considered. Relative and cumulative frequency histograms of prey size:predator size ratios were plotted to examine the patterns of prey size consumed by *S. megalops* (Bethea *et al.* 2004). For this latter analysis, only teleost and cephalopod prey were used.

Variation in dietary composition

Regional comparisons of diet were made for large females (471–650 mm TL) collected in autumn (Table 4.1). A one-way non-parametric multivariate analysis of variance (NP-MANOVA) using Bray–Curtis distances (Anderson 2001) on weight and number data for sharks collected at the same time (autumn 2004) was used to test for regional effects on the diet of *S. megalops*. Weight and number data were transformed to fourth root and standardized to z-scores to minimize differences attributable to stomach size. Region was treated as a fixed factor. Equal sample sizes were used (n = 30 for the analysis of zoological groups, n = 28 for the analysis of ecological groups). If significant differences were found, *a posteriori* pairwise comparisons were made (Anderson 2001).

Maturity condition was evaluated, and sexual, seasonal, and ontogenetic comparisons were made on sharks collected from Lakes Entrance between October 2002 and March 2004 (Table 4.1). Non-parametric multidimensional scaling (nMDS) on Bray–Curtis similarity measures using fourth root transformed data (Clarke 1993) were used to visualize patterns of variation in dietary composition. Mean percentage weight and number of zoological and ecological groups were used.

The relative and interactive effects of maturity condition, sex, season, and size were evaluated in a similar way to the regional analysis using weight and number. *Squalus megalops* is sexually dimorphic, females attaining larger sizes than males; hence, separate analyses were undertaken for each sex to investigate the effects of maturity condition on dietary composition. The effects of maturity condition (mature, immature) and season (summer, autumn, spring; Table 4.1) were investigated using individuals within the 382–406 and 433–509 mm TL range for males and females, respectively. These ranges covered the sizes of the smallest mature and largest immature specimen of each sex. For the analysis of males, season was not included as a factor because of the low number of replicates for any season, except summer. Hence, the analysis was done using data collected only during the latter season. For females, maturity condition was treated as fixed and orthogonal to the random factor season (i.e. every level of the factor “maturity”, mature or immature, is present in every level of the factor “season”, summer, autumn, or spring; Table 4.1). Similar sample sizes (n = 7 for males, n = 8 for females) were used for each combination of factors.

To test for sexual, ontogenetic (size), and seasonal differences, sharks of similar size (<471 mm TL) were used in a three-way NP-MANOVA (factors: sex, size, and season). Sex (males, females) and size (small and large males, small and medium-sized females) were treated as fixed and orthogonal to the random factor season (summer, autumn, spring; Table 4.1). Equal sample sizes (n = 6) were used for each combination of factors. As small and large males and small and medium-sized females had similar diets (see “Results”), data were pooled to test for ontogenetic and seasonal differences between small (<471 mm TL) and large (≥471 mm TL) animals. A two-way NP-MANOVA (factors: size and season) with equal sample sizes (n = 26) was used for each combination of factors. Finally, winter samples could only be collected for small specimens, so to include winter in the seasonal study, a one-way NP-MANOVA was undertaken for small *S. megalops* using a balanced design (n = 24).

4.4 RESULTS

The stomach contents and fullness of 937 *S. megalops* were examined. In all, there were 77 small males (274–400 mm TL), 105 small females (270–400 mm TL), 129 large males (400–470 mm TL), 193 medium-sized females (401–470 mm TL), and 433 large females (471–650 mm TL).

Overall diet

Of the 937 stomachs examined, 603 (65.3%) contained food, from which >60% contained a single prey item. For stomachs with >1 item, the number of prey items ranged from two to ten. For stomachs with prey, the distribution of stomach fullness was relatively even (~25%) and there were no significant differences among the frequency of individuals in each SF category ($\chi^2 = 2.150$, n = 603, $P = 0.542$).

Of the 603 stomachs with food, 111 were excluded because they contained only hard parts, sponges, hydroids, algae, or unidentified material. The prey diversity curve for the overall diet reached a stable level at about 350 stomachs (Fig. 4.2a), so the sample size of 492 was large enough to describe the overall diet of *S. megalops*.

The stomachs contained 107 taxonomic levels of prey item: six polychaetes, two sipunculids, 29 crustaceans, 17 molluscs, 47 fish, remains of sea lion, and other items such as echiurids, algae, sponges, hydroids and brittle stars (Appendix 4.a). Arrow squid (family Ommastrephidae) was the dominant prey item, contributing the highest values of %W (20.03%), %N (7.54%), %FO (8.76%), and %IRI (32.05%). Octopus (*Octopus* spp) was the second most important prey item by weight (12.55%), frequency of occurrence (7.66%) and relative importance (19.37%). The third major prey was fish of the family Triglidae (gurnards) in terms of weight (9.77%), number (5.33%), frequency of occurrence (5.97%) and relative importance (12.00%). Shrimps (Caridea) and hermit crabs (Diogenidae) were important by number (6.88% and 5.90%, respectively), but not in terms of weight or occurrence.

A similar pattern was observed when data were analysed by main zoological group (Appendix 4.a). Molluscs were the most important item by weight (56.43%), frequency of occurrence (35.89%), and relative importance (50.31%). However, the most numerous items were crustaceans (31.61%). Teleosts were the second most important item in terms of weight (38.32%), frequency of occurrence (34.03%), and relative importance (37.27%). When data were analysed by ecological group, the most important group by weight was demersal pelagic prey (40.25%), followed by benthic (36.95%), and demersal benthic (11.04%) prey (Appendix 4.a). In contrast, benthic epifauna dominated by number (41.15%) and frequency of occurrence (29.41%), followed by benthic prey (21.10% by number and 25.35% by frequency of occurrence). Finally, for %IRI, the main ecological group was benthic prey (33.96%), followed by benthic epifauna (30.70%), demersal pelagic (26.52%) and demersal benthic (6.27%) prey. Pelagic and benthic infauna were less important.

Irrespective of analysing prey items by zoological or ecological group, considerable variability was found around the estimation of overall mean prey importance (Appendix 4.a). For important prey such as molluscs or teleosts, there was ~20% of variability within the upper and lower 95% confidence intervals. However, for less important prey such as crustaceans, variability was ~50%. When the mean values obtained from bootstrapping were compared with those obtained from point estimates of overall diet, variability ranged from 1–14% (not shown). A similar pattern was observed for ecological groups.

Predator–prey size relationship

Squalus megalops consumed prey of a wide range of sizes (Fig. 4.3). More than 60% of teleosts and cephalopods consumed were less than 30% and 24% of *S. megalops* total length (TL), respectively, but *S. megalops* also consumed fish and cephalopods up to 60% of its TL.

No correlation was found between predator TL and shield length of hermit crabs (r_s = 0.119, n = 65, $P > 0.05$), TL of teleosts (r_s = 0.157, n = 39, $P > 0.05$), or body width of worms (r_s = 0.273, n = 14, $P > 0.05$). However, there was a positive correlation between predator TL and mantle length of cephalopods (r_s = 0.455, n = 43, $P < 0.05$) (Fig. 4.3).

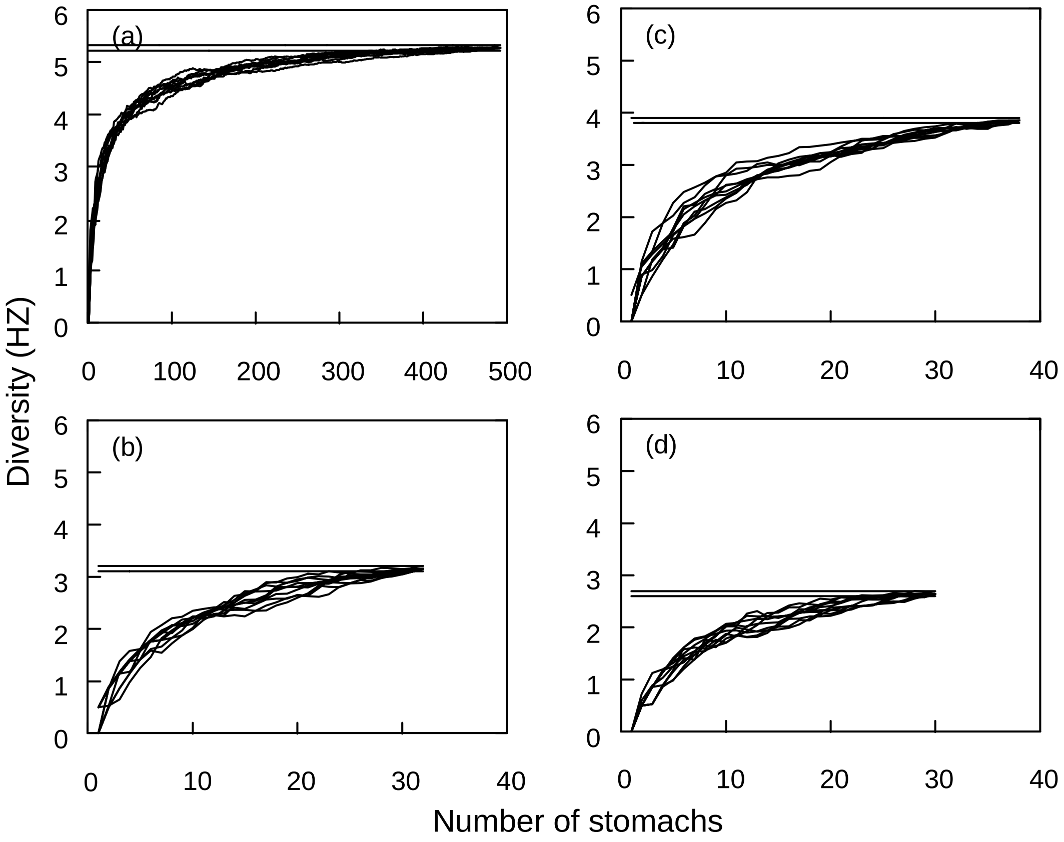

Figure 4.2. Cumulative diversity (HZ) of prey items for (a) the overall diet of *S. megalops* and for the three regions analysed: (b) west of Wilsons Promontory, (c) east of Wilsons Promontory, and (d) New South Wales. The straight lines indicate the range of asymptotic diversity ±0.05.

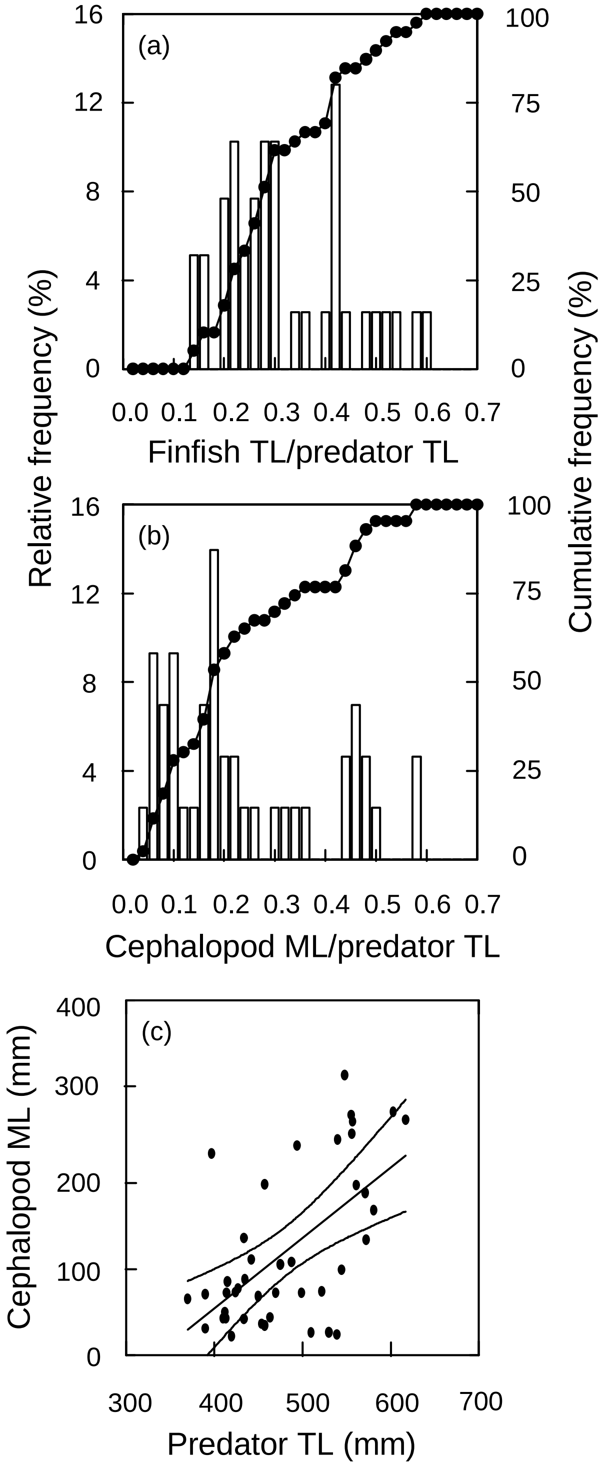

Figure 4.3. Changes in prey size with predator size. Distribution of prey size:predator size ratios for (a) teleosts and (b) cephalopods. (c) Relationship between cephalopod mantle length (ML) and predator total length (TL) and 95% confidence limits. ML = 0.6894 TL – 218.68; $r^2 = 0.37$. Open bars = relative frequencies at 0.02 intervals. Filled circles = cumulative frequencies at 0.02 intervals.

Variation in dietary composition

Prey diversity for sharks collected from WWP (~3.10; Fig. 4.2b) and NSW (~2.64; Fig. 4.2d) was lower than for sharks from EWP (~3.85; Fig. 4.2c), suggesting a more diverse diet at EWP. The prey diversity curves reached a stable level for each of the three regions analysed, indicating that the sample was large enough to describe the diet of sharks from each region.

There was a regional pattern in the diet of *S. megalops* (Table 4.2). Significant differences in dietary composition were found between sharks collected from WWP and EWP, irrespective of the use of weight or number of zoological or ecological groups (Fig. 4.4; pairwise comparisons). Significant differences were also found between sharks collected from WWP and NSW when weight of zoological group and weight or number of ecological group were used (Fig. 4.4; pairwise comparisons). No differences were found between the diets of sharks collected from EWP and NSW (Fig. 4.4; pairwise comparisons). For EWP and NSW, *S. megalops* consumed mainly teleosts, molluscs and crustaceans, and also small amounts of worms and chondrichthyans for EWP. However, for WWP, *S. megalops* preyed largely on molluscs and, to a lesser extent, teleosts. For ecological groups, *S. megalops* collected from WWP preyed mostly on demersal pelagic prey, whereas those collected from EWP and NSW preyed mostly on benthic organisms.

Most prey diversity curves (not shown) showed asymptotes or trends towards an asymptote for each combination of maturity condition and season. Irrespective of the use of weight or number of a zoological or an ecological group, there were no significant differences in dietary composition between immature and mature *S. megalops* (Table 4.3). Therefore, immature and mature sharks were pooled for subsequent analyses.

Most prey diversity curves (not shown) showed asymptotes or trends towards an asymptote for each combination of sex, size and season. A significant seasonal pattern in the dietary composition of *S. megalops* was found for the three-way analysis, but there were no sexual or ontogenetic differences (Table 4.4). Therefore, both sexes and sizes (small and large males, and small and medium-sized females) were pooled for subsequent analyses.

Table 4.2. NP-MANOVA testing for the effects of region (east of Wilsons Promontory, west of Wilsons Promontory, New South Wales) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, and Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of *S. megalops*.

		Weight		Number	
Factor	d.f.	F	*P*	F	*P*
Zoological group					
Region	2	4.965	<0.001	3.580	0.011
Residual	87				
Ecological group					
Region	2	6.561	<0.001	6.990	<0.001
Residual	81				

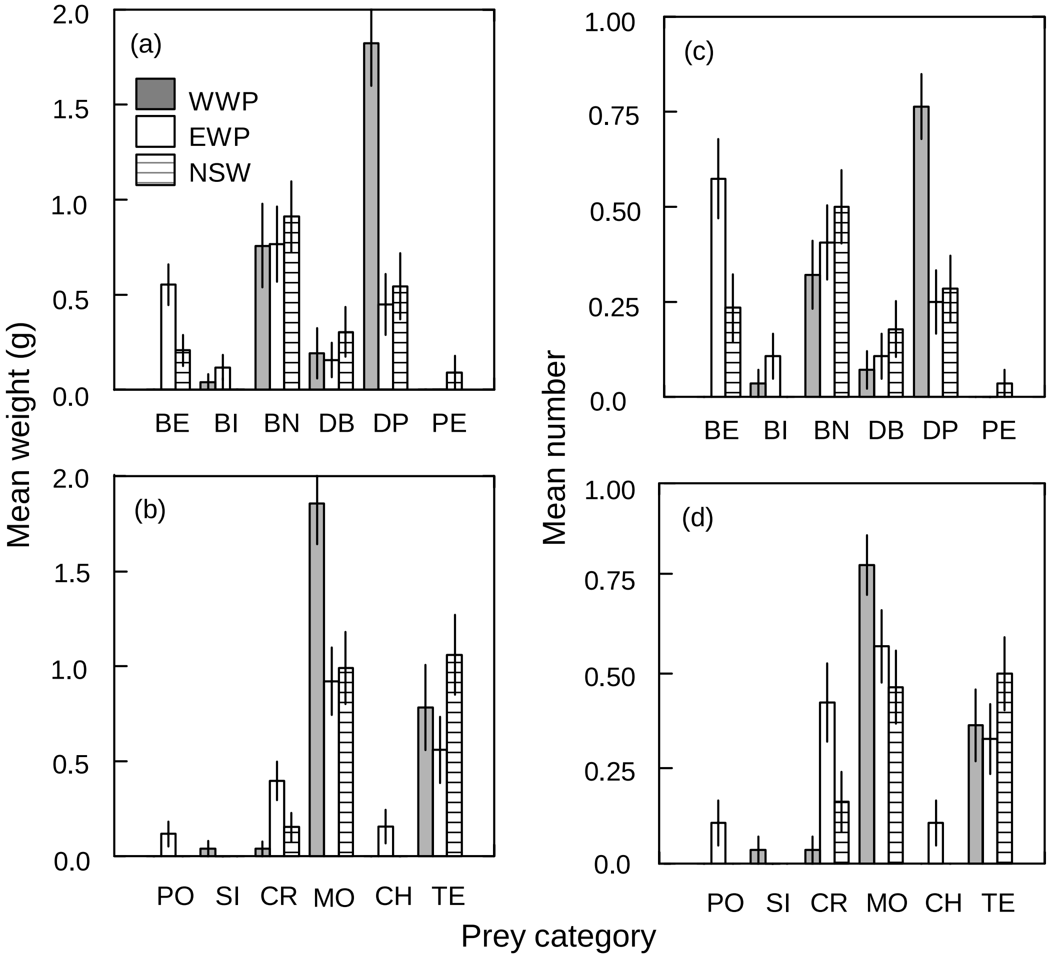

Figure 4.4. Main prey groups found in the diet of *S. megalops* collected from west of Wilsons Promontory (WWP), east of Wilsons Promontory (EWP), and New South Wales (NSW). Mean weight of fourth root transformed data (±s.e.) of prey sorted by (a) ecological and (b) zoological group, and mean number of fourth root transformed data (±s.e.) of prey sorted by (c) ecological and (d) zoological group. BE, benthic epifauna; BI, benthic infauna; BN, benthic; DB, demersal benthic; DP, demersal pelagic; PE, pelagic. PO, polychaetes; SI, sipunculids; CR, crustaceans; MO, molluscs; CH, chondrichthyans; TE, teleosts.

Table 4.3. NP-MANOVA testing for the effects of maturity condition (mature, immature) and season (summer, autumn, spring), females only, on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, and Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of male and female *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	*P*	F	*P*	F	*P*	F	*P*
Male									
Maturity	1	1.045	0.394	1.094	0.391	0.488	0.730	0.543	0.738
Residual	12								
Female									
Maturity	1	3.122	0.080	3.551	0.080	1.779	0.307	1.742	0.289
Season	2	1.843	0.077	1.800	0.107	1.374	0.190	1.370	0.206
Maturity × season	2	0.559	0.804	0.471	0.827	0.460	0.912	0.385	0.930
Residual	42								

Table 4.4. NP-MANOVA testing for the effects of sex (male, female), size (small and large for males, small, medium-sized, and large for females), and season (summer, autumn, spring) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, and Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	*P*	F	*P*	F	*P*	F	*P*
3-way analysis for sharks <471 mm TL									
Sex	1	0.505	0.619	0.508	0.602	2.622	0.190	2.764	0.189
Size	1	0.741	0.520	0.667	0.537	3.938	0.120	4.205	0.120
Season	2	5.130	<0.001	5.579	<0.001	3.963	<0.001	4.378	<0.001
Sex × size	1	0.315	0.782	0.211	0.841	1.161	0.390	1.085	0.425
Sex × season	2	0.750	0.582	0.826	0.516	0.583	0.817	0.569	0.804
Size × season	2	1.980	0.077	2.172	0.062	0.565	0.841	0.545	0.840
Sex × size × season	2	2.227	0.051	2.245	0.057	1.660	0.094	1.693	0.098
Residual	60								
2-way analysis for all sizes including large females (≥471 mm TL)									
Size	1	4.407	0.059	4.189	0.094	5.157	0.018	6.557	0.017
Season	2	6.935	<0.001	6.983	<0.001	8.978	<0.001	8.220	<0.001
Size × season	2	6.051	<0.001	7.826	<0.001	1.984	0.048	2.495	0.017
Residual	150								

Prey diversity curves for each size–season combination reached a stable level and had similar values of diversity, except for small sharks collected in winter that showed lower values (Fig. 4.5). After including all sizes in the analysis, significant ontogenetic and seasonal effects were detected. Also, a significant interaction between size and season was found for weight and number of prey items for both zoological and ecological groups (Figs. 4.6, 4.7; Table 4.4). The ordination showed two separate groups when zoological data and ecological number data were used (Fig. 4.6). Large sharks tended to be separated from small ones, and samples collected in summer and autumn were separated from those collected in spring. However, no clear visual pattern was observed when the analysis was done for ecological groups using weight data. Large and small *S. megalops* had different diets in summer and autumn but similar diets in spring (Fig. 4.7; pairwise comparisons). In summer and autumn, large sharks consumed mainly molluscs, whereas small sharks consumed mainly crustaceans. For ecological groups in summer, large *S. megalops* preyed mainly on demersal pelagic prey whereas small sharks preyed on benthic organisms. In spring, both size classes had a similar feeding pattern, consuming mainly teleosts, followed by molluscs and crustaceans. By ecological group, large and small sharks collected in spring preyed mainly on benthic organisms. When winter was included in the seasonal analyses, the seasonal pattern was similar (Table 4.5). Dietary composition in summer, autumn and winter was similar, but significant differences were observed among these three seasons and spring (pairwise comparisons).

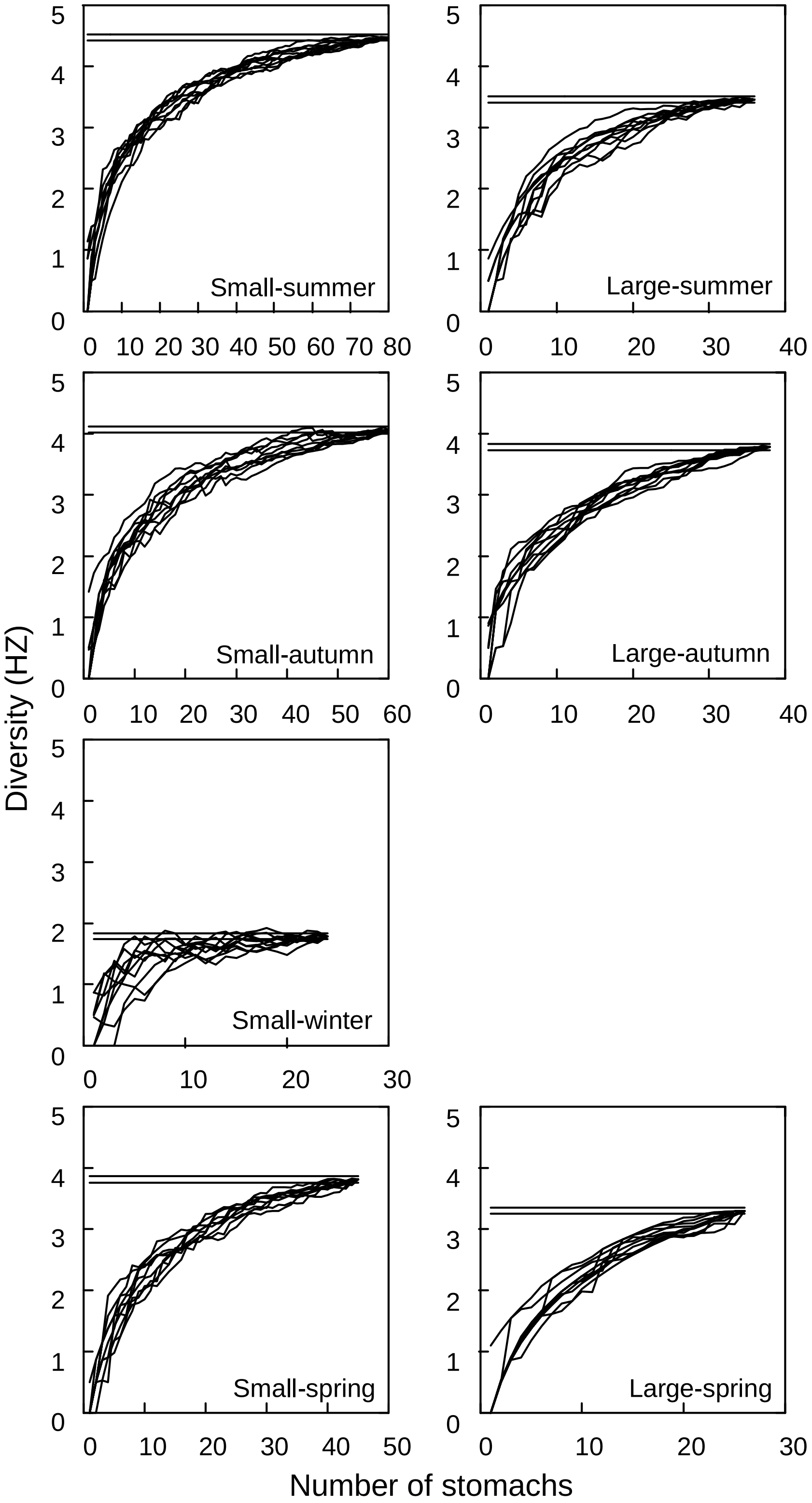

Figure 4.5. Cumulative diversity (HZ) of prey items for small and large sharks from each season. The straight lines indicate the range of asymptotic diversity ±0.05.

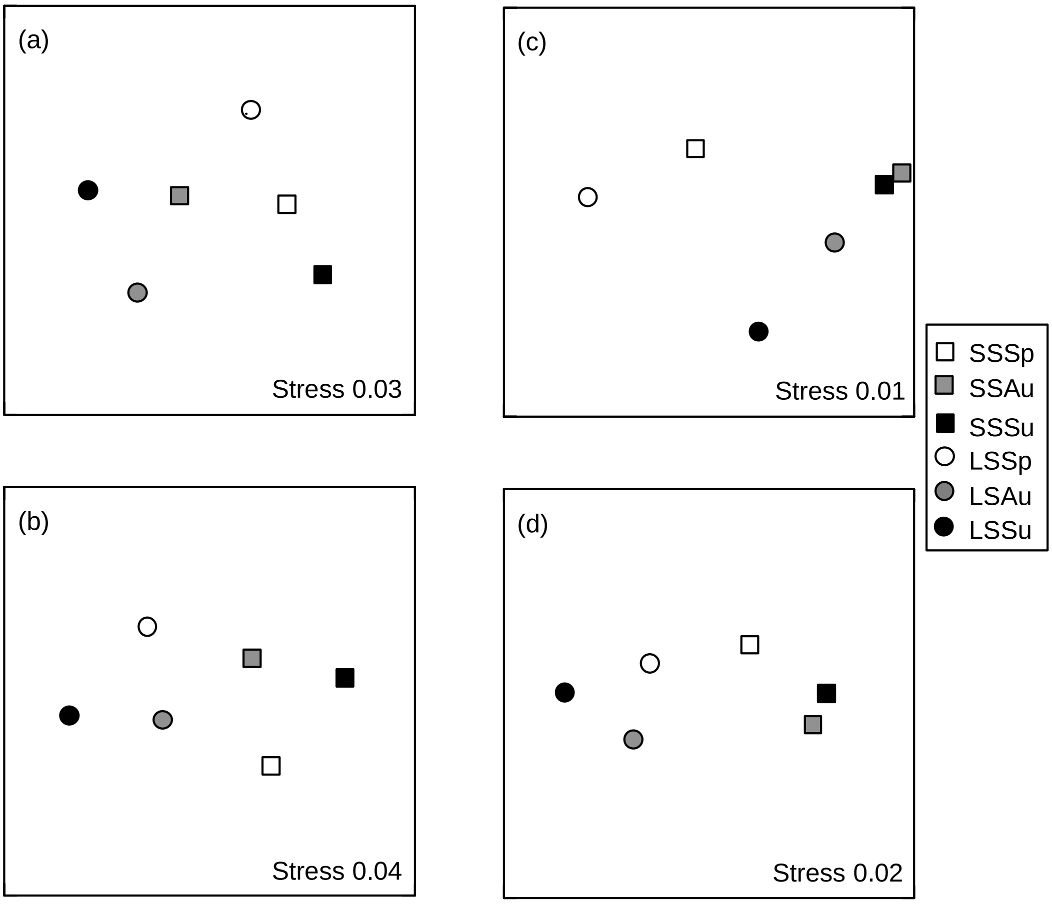

Figure 4.6. Non-parametric multidimensional scaling (nMDS) ordination of the stomach contents of small sharks from spring (SSSp), autumn (SSAu), and summer (SSSu), and large sharks from spring (LSSp), autumn (LSAu), and summer (LSSu). Mean %W of (a) ecological and (b) zoological group, and mean %N of (c) ecological and (d) zoological group.

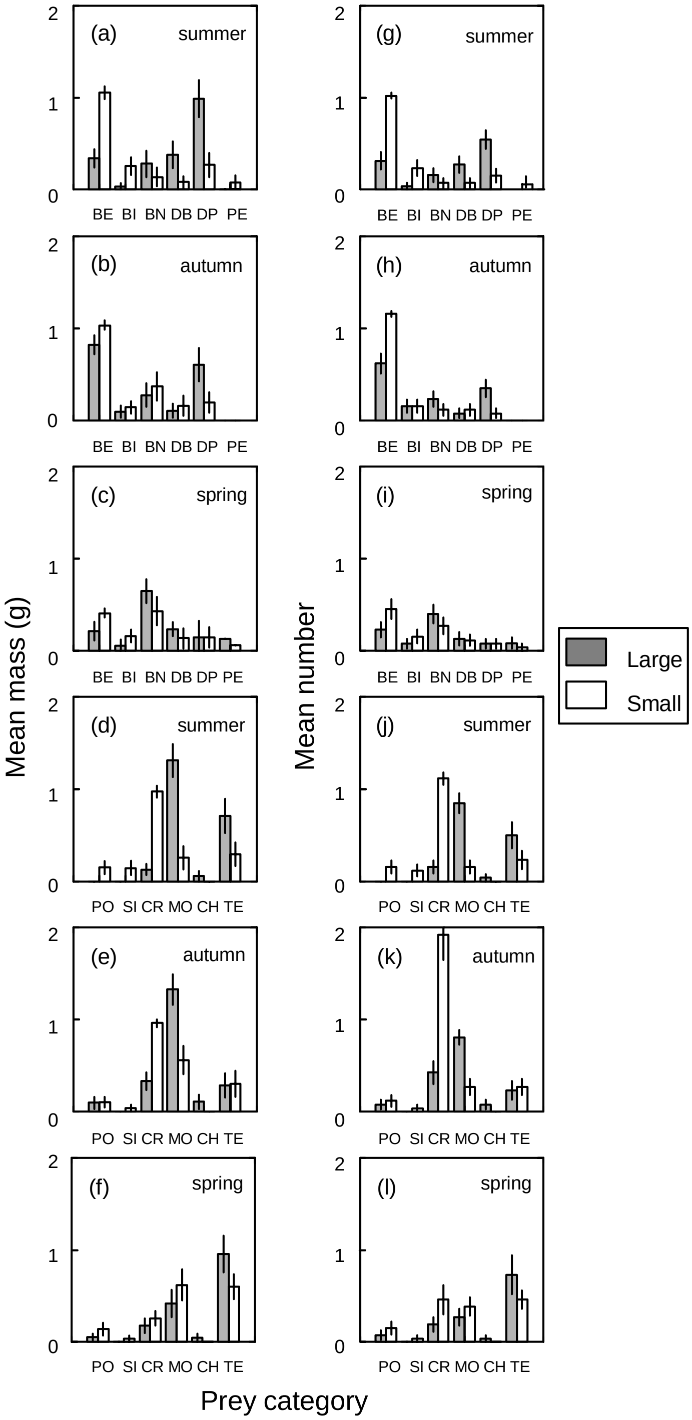

Figure 4.7. Size and seasonal effects in the diet of large and small *S. megalops* caught in summer, autumn, and spring. Mean weight of fourth root transformed data (±s.e.) of prey sorted by ecological (a, b and c) and zoological group (d, e and f), and mean number of fourth root transformed data (±s.e.) of prey sorted by ecological (g, h and i) and zoological group (j, k and l). BE, benthic epifauna; BI, benthic infauna; BN, benthic; DB, demersal benthic; DP, demersal pelagic; PE, pelagic. PO, polychaetes; SI, sipunculids; CR, crustaceans; MO, molluscs; CH, chondrichthyans; TE, teleosts.

Table 4.5. NP-MANOVA testing for the effects of season (summer, autumn, winter, spring) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, and Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of small (<471 mm TL) *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	*P*	F	*P*	F	*P*	F	*P*
Season	3	6.274	<0.001	7.366	<0.001	4.314	<0.001	5.483	<0.001
Residual	92								

4.5 DISCUSSION

Dietary studies of sharks commonly report a high proportion of empty stomachs and few prey items per stomach, most of them in advanced stages of digestion (Wetherbee *et al.* 1990; Ebert *et al.* 1992; Simpfendorfer *et al.* 2001*a*). Therefore, many shark species are considered intermittent feeders. For these species, short periods of active feeding are followed by longer periods of reduced predatory activity (Wetherbee *et al.* 1990; Wetherbee and Cortés 2004). The present study supports this hypothesis. Almost 35% of stomachs examined were empty, and for stomachs with prey, >60% contained a single prey item, suggesting that feeding is intermittent. However, further research on the feeding duration, total digestion time, and gastric evacuation rates using captive *S. megalops* would allow estimates of feeding frequency and feeding periodicity.

There was a wide range of food items in the stomachs of *S. megalops*, which meant that many stomachs were needed to describe overall diet. When diversity curves have been used to determine the sample size required for a precise description of the diet of sharks, most studies have found stable levels of diversity at <200 stomachs sampled (Carrassón *et al.* 1992; Gelsleichter *et al.* 1999; Koen Alonso *et al.* 2002; Morato *et al.* 2003; Bethea *et al.* 2004). However, prey diversity was high for *S. megalops*, and at least 350 stomachs had to be sampled to describe its overall diet. *Squalus megalops* can be considered a generalist and opportunistic feeder given that portions of large teleosts, cephalopods, and sharks were found in many stomachs, and that they consumed abundant prey such as arrow squid (Triantafillos *et al.* 2004) and gurnards (Triglidae; M. Gomon, pers. comm.). Other studies also suggest sharks are generalist and opportunistic feeders that consume the most abundant prey (Wetherbee *et al.* 1990; Hanchet 1991; Ellis *et al.* 1996; Koen Alonso *et al.* 2002).

Overall, results differed when average prey importance was analysed using weight, number, or frequency of occurrence of prey groups. If importance of prey is to be deduced on the basis of weight or frequency of occurrence, *S. megalops* preyed largely on molluscs and teleosts. However, if number of prey is to be used, the main items were crustaceans. Analyses done by ecological group showed that *S. megalops* was a versatile predator that used a wide range of habitats. The most important items by weight were demersal pelagic and benthic prey, whereas benthic epifauna and benthic prey were the most consumed items by number and occurrence. Therefore, number, weight, and frequency of occurrence measures provided different information on feeding habits (MacDonald and Green 1983; Bigg and Perez 1985; Cortés 1998*b*). Ferry and Cailliet (1996) suggest using multiple measures when prey items differ in size. For generalist and opportunistic feeders that consume a wide range of prey, like *S. megalops*, the use of multiple measures allows a better representation of overall diet.

Irrespective of which diet descriptor was used, the bootstrap analysis showed a wide range of variability around the estimate of overall importance of prey. In general, studies on the diet of sharks obtain samples opportunistically, and in many cases small sample sizes are collected. However, as sharks are considered opportunistic predators (Wetherbee *et al.* 1990), large sample sizes would be needed for a comprehensive description of diet. Also, many studies have reported a high proportion of empty stomachs (Wetherbee *et al.* 1990), and some studies only described diet in terms of number or occurrence of prey, whereas other studies only used weight. However, for *S. megalops*, number, occurrence, and weight of prey showed different patterns of importance of prey. Therefore, a combination of small sample size, high proportion of empty stomachs, the use of different descriptors of importance of prey, and the opportunistic predatory nature of many shark species, is likely to result in high variability in the dietary composition and hence in evaluation of predator–prey interactions. Accurate characterization of predator–prey interactions inferred from diet data is crucial for ecosystem-based models and in their increasing use as tools for fisheries management. However, if overall diet data do not incorporate a measure of the natural variability in dietary composition exhibited by many shark species, predatory interactions and hence model predictions may be misleading. For example, if overall diet data are used to describe the predatory relationships of *S. megalops* in southern Australia, the main interactions will be with molluscs, in terms of %W, or with crustaceans, in terms of %N. However, the main interactions will be with teleosts, if sampling is done only in spring, or with molluscs, if only large sharks are collected in summer and autumn, or with crustaceans, if only small sharks are collected in summer and autumn. The same pattern of variability is reported for other shark species. Simpfendorfer *et al.* (2001*b*) compared the diet of tiger sharks (*Galeocerdo cuvier*) from four sites off Western Australia. Overall, the main predatory interactions by %FO were with turtles, teleosts, and sea snakes. However, for one site, North West shelf, the interactions with teleosts and sea snakes were not as important as with dugongs, and for another site, Ningaloo, tiger sharks interact almost exclusively with turtles. The observed variability in the diet of sharks is particularly relevant when using overall diet data as a descriptor of their predator–prey interactions, because the use of overall data may obscure site-, size-, or sex-specific interactions. Also, given that ecosystem-based models tend to use %W data from overall diet as inputs, the occurrence of a few heavy prey items, for example, may overestimate the importance of the interaction between the predator and those particular prey, and underestimate the importance of the interactions with other prey.

Size-dependent predation can regulate population and community level dynamics (Brooks and Dodson 1965), but size-selective feeding has been little studied in sharks. In the present study, *S. megalops* preyed on a wide range of prey sizes (4–60% of its TL) and, except for cephalopod items, the total length of *S. megalops* was not correlated with size of prey. Other studies found that shark diets consisted of relatively small prey (in most cases, <36% of the sharks TL), and that prey size was correlated to predator size (Cortés *et al.* 1996; Scharf *et al.* 2000; Bethea *et al.* 2004). However, the present study showed that *S. megalops* had little size preference for prey, supporting the belief that this shark is a generalist and opportunistic predator.

Predation can be highly variable in space and time (Bax 1998). There was regional, seasonal, and ontogenetic variation in the diet of *S. megalops*, and this pattern was consistent despite analyses being conducted on weight or number of zoological or ecological prey groups. Variation was not explained by the effects of sex or maturity condition, but this could be due to the low number of replicates for each combination of factors (e.g. $n = 6$ for the sex × size × season analysis), and hence low statistical power (Ferry and Cailliet 1996). Some authors have found differences in the diet of sharks between sexes (Hanchet 1991; Stillwell and Kohler 1993; Simpfendorfer *et al.* 2001*b*; Koen Alonso *et al.* 2002) and maturity condition (Koen Alonso *et al.* 2002). However, some of these studies may have confounded the effects of sex or maturity condition with other factors such as space and time because, although samples were obtained opportunistically across a wide spatial and temporal scale, space and time were not considered in the analyses.

Feeding plasticity of sharks results in regional, seasonal, and ontogenetic variation in diet that complicates an accurate description of their feeding ecology (Wetherbee and Cortés 2004). However, most studies on the feeding ecology of sharks have described only overall dietary composition. Some studies have reported regional, seasonal, or ontogenetic variation (Jones and Geen 1977*a*; Lyle 1983; Laptikhovsky *et al.* 2001; Simpfendorfer *et al.* 2001*a*; Ebert 2002), but most of them have done so qualitatively (Wetherbee and Cortés 2004). When a quantitative approach was taken (Cortés *et al.* 1996; Simpfendorfer *et al.* 2001*b*; Vögler *et al.* 2003; White *et al.* 2004), region, season, or ontogeny were evaluated independently of each other even though samples were collected across wide spatial and temporal scales. When sampling is opportunistic across wide spatial and temporal scales, if the interactive effects of space and/or time are not considered, it is likely that differences in diet attributed to a certain factor (e.g. size) are unknowingly confounded by the effects of other factors (e.g. region) not included in the analysis. Furthermore, if a factor is analysed independently but many factors are involved, the analysis should, at least, be undertaken on standardized data to remove the effects of the other factors not considered.

Standardized data for the effects of season, sex, and size showed regional variation in the diet of large females collected in autumn. Sharks from WWP fed largely on demersal pelagic prey (mainly ommastrephid squid), but those from EWP and NSW had a more varied diet, also consuming benthic prey (teleosts and crustaceans). A demersal pelagic diet implies that a demersal shark such as *S. megalops* undergoes vertical feeding migrations to exploit pelagic prey such as squid or preys on squid while aggregated near the seabed (Roper and Young 1975). These findings suggest that *S. megalops* would have different patterns of habitat utilization in different areas, interacting in different ecological communities and acting as an energy linkage between them. Although squid occur across the three regions (Norman and Reid 2000), information on their abundance at a lower scale (regional level) is scarce. Several other shark species show regional variation in dietary composition, switching between prey types with changes in prey availability (Medved *et al.* 1985; Cortés and Gruber 1990; Stillwell and Kohler 1993; Simpfendorfer *et al.* 2001*b*). Therefore, it is unclear whether the regional differences found in the diet of *S. megalops* reflect different patterns in feeding and habitat utilization or rather the natural pattern of prey availability. In any case, the present findings reinforce the importance of considering spatial variation as a common phenomenon affecting the feeding ecology of sharks.

Large and small *S. megalops* exploited different resources during part of the year. In summer and autumn, large sharks preyed mostly on demersal pelagic prey (mainly ommastrephid squid), whereas small sharks consumed mainly benthic crustaceans. These ontogenetic differences may be attributed to morphological limitations of small sharks (e.g. gape-limited), better foraging ability of large fish, or differences in the habitat occupied by the two size classes. In spring, however, both size classes had a more varied diet, consuming mainly benthic organisms. Demersal pelagic prey such as squid occur throughout the year, but they show large, unpredictable fluctuations in abundance (Anderson and Rodhouse 2001). Therefore, the decline in squid consumption shown by large *S. megalops* during spring may be due to a decline in the availability of squid. Collection of data on the seasonal variation in the abundance of squid in the studied area is needed for a better understanding of the seasonal pattern exhibited by large *S. megalops*. Seasonal and ontogenetic variation in diet is common, and it has been reported for a related species, the spiny dogfish (*S. acanthias*) (Jones and Geen 1977*a*; Hanchet 1991; Koen Alonso *et al.* 2002), and for many other shark species (e.g. Cortés and Gruber 1990; Simpfendorfer *et al.* 2001*b*; White *et al.* 2004). Cortés *et al.* (1996) found an interaction between season and size of shark on the diet of the bonnethead shark (*Sphyrna tiburo*). However, no other study on the diet of sharks has analysed the interaction of these factors when samples from different seasons and size classes were compared. In the present study, an interaction between size and season was found; large and small *S. megalops* had different diets in summer and autumn, but consumed similar prey items in spring. Therefore, the differences found in the dietary composition of large and small *S. megalops* suggest that large and small individuals would exhibit, at least during part of the year, different predator–prey interactions and ecological roles within the marine ecosystem. Hence, if only the overall diet data are used in an ecosystem model as a proxy for the predator–prey interactions of *S. megalops*, some of the interactions exhibited by this species throughout its lifespan would be ignored.

In conclusion, high variability was found when the overall importance of prey items was estimated. Furthermore, the dietary composition of *S. megalops* varied in space and time, exhibiting differences among regions, seasons, and size classes. Therefore, the intrinsic natural variability in the dietary composition of *S. megalops*, and the spatial and temporal variation in diet exhibited by this opportunistic predator, suggest that studies that infer predator–prey interactions from overall diet are likely to miss information on the ecological relationships among species and therefore account for only part of these interactions. Understanding predator–prey interactions is required for long-term strategic ecosystem management (Bax 1998). Hence, given that natural variability is intrinsic to ecological systems, the natural variability of predation should be considered when predatory interactions are used to model ecosystem dynamics.

Appendix 4.a.

Overall dietary compositions. Prey item sorted by (upper panel) taxonomic groups and (lower panel) ecological groups. Mean percentage weight (%W), mean percentage number (%N), mean percentage frequency of occurrence (%FO), and mean percentage Index of Relative Importance (%IRI), and 95% confidence intervals. Unid.: unidentifiable; n = 492.

Taxonomic groups	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Polychaeta	0.62	0.24	1.04	3.26	1.72	4.39	4.32	3.05	5.65	0.27	0.15	0.40
Unid. Polychaeta	0.15	0.04	0.30	1.25	0.60	2.06	1.49	0.72	2.47	0.28	0.09	0.56
Lumbrineridae	0.05	0.01	0.09	0.75	0.25	1.36	0.88	0.29	1.60	0.10	0.02	0.22
Lumbrineris spp	0.00	0.00	0.01	0.13	0.00	0.39	0.15	0.00	0.46	0.00	0.00	0.01
Nereididae	0.06	0.00	0.16	0.38	0.00	0.86	0.43	0.00	0.91	0.03	0.00	0.08
Eunicidae	0.04	0.00	0.11	0.24	0.00	0.64	0.30	0.00	0.75	0.01	0.00	0.05
Aphroditidae	0.40	0.07	0.89	0.63	0.12	1.21	0.74	0.15	1.47	0.10	0.02	0.25
Sipuncula	0.67	0.22	1.10	1.79	0.90	2.63	1.98	1.11	2.91	0.08	0.03	0.15
Unid. Sipuncula	0.58	0.12	1.22	1.38	0.63	2.17	1.60	0.77	2.55	0.42	0.16	0.82
Sipunculus robustus	0.11	0.00	0.32	0.24	0.00	0.63	0.28	0.00	0.73	0.01	0.00	0.05
Echiura	0.02	0.00	0.07	0.13	0.00	0.39	0.15	0.00	0.57	0.00	0.00	0.02
Crustacea	2.33	1.70	3.22	31.61	28.15	34.86	22.11	19.15	24.79	11.99	9.70	14.22

Appendix 4.a. Continued…

Prey	%W			%N			%FO			%IRI		
	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Unid. Crustacea	0.06	0.00	0.14	0.99	0.13	2.32	0.73	0.15	1.46	0.10	0.01	0.30
Decapoda	0.04	0.01	0.08	0.99	0.36	1.77	1.19	0.45	2.08	0.16	0.05	0.37
Caridea	0.36	0.09	0.74	6.88	2.49	12.22	1.62	0.74	2.56	1.57	0.44	3.18
Palaemonidae	0.00	0.00	0.01	0.26	0.00	0.66	0.30	0.00	0.75	0.01	0.00	0.04
Alpheidae	0.01	0.00	0.04	0.12	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Brachyura	0.02	0.00	0.04	0.38	0.00	0.87	0.44	0.00	1.02	0.02	0.00	0.08
Leucosiidae	0.01	0.00	0.02	0.12	0.00	0.38	0.15	0.00	0.46	0.00	0.00	0.01
Ebalia intermedia	0.01	0.00	0.02	0.12	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.01
Portunidae	0.01	0.00	0.04	0.25	0.00	0.76	0.15	0.00	0.45	0.01	0.00	0.03
Pilumnus spp	0.02	0.00	0.07	0.25	0.00	0.78	0.15	0.00	0.46	0.01	0.00	0.03
Dendrobranchiata	0.10	0.00	0.27	0.26	0.00	0.65	0.31	0.00	0.75	0.01	0.00	0.05
Solenoceridae	0.01	0.00	0.01	0.38	0.00	0.86	0.45	0.00	1.01	0.02	0.00	0.08
Haliporoides sibogae	0.00	0.00	0.00	0.13	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.02
Penaeidae	0.14	0.02	0.32	1.85	0.62	3.84	1.31	0.57	2.23	0.35	0.09	0.83
Penaeus spp	0.02	0.00	0.06	0.26	0.00	0.63	0.30	0.00	0.75	0.01	0.00	0.04

Appendix 4.a. Continued…

Prey	%W			%N			%FO			%IRI		
	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Palinuridae	0.03	0.00	0.11	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Anomura	0.00	0.00	0.01	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01
Diogenidae	0.34	0.16	0.56	5.90	3.62	8.25	3.79	2.41	5.18	3.15	1.70	4.90
Dardanus arrosor	0.10	0.02	0.21	0.86	0.27	1.50	1.03	0.42	1.86	0.13	0.03	0.30
Strigopagurus strigimanus	0.59	0.19	1.13	2.48	1.40	3.72	2.64	1.59	3.85	1.08	0.53	1.84
Paguristes spp	0.21	0.12	0.34	5.30	3.02	7.85	3.53	2.35	4.95	2.60	1.32	4.42
Paguristes sulcatus	0.02	0.00	0.05	0.25	0.00	0.63	0.29	0.00	0.74	0.01	0.00	0.04
Pagurus spp	0.03	0.00	0.06	0.37	0.00	0.86	0.43	0.00	1.03	0.02	0.00	0.08
Distosquilla miles	0.03	0.00	0.08	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Austrosquilla osculans	0.01	0.00	0.02	0.12	0.00	0.38	0.15	0.00	0.57	0.00	0.00	0.02
Isopoda	0.06	0.00	0.14	0.62	0.13	1.26	0.73	0.15	1.46	0.07	0.01	0.17
Cirolanidae	0.04	0.01	0.10	0.87	0.24	1.65	0.88	0.29	1.64	0.11	0.02	0.26
Cirolana spp	0.04	0.01	0.08	1.00	0.38	1.77	1.17	0.45	2.05	0.16	0.04	0.35
Cirolana capricornica	0.01	0.00	0.02	0.25	0.00	0.63	0.29	0.00	0.73	0.01	0.00	0.04

Appendix 4.a. Continued…

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Mollusca	56.43	50.66	62.47	31.45	28.84	34.44	35.89	33.17	38.35	50.31	44.57	54.64
Cephalaspidea	0.15	0.00	0.41	0.37	0.00	0.89	0.45	0.00	1.01	0.03	0.00	0.10
Philine angasi	0.09	0.02	0.19	0.74	0.23	1.37	0.89	0.29	1.76	0.10	0.02	0.24
Volutidae	0.26	0.10	0.49	1.51	0.75	2.43	1.78	0.87	2.85	0.42	0.17	0.80
Fasciolariidae	0.63	0.22	1.13	2.27	1.06	3.81	1.92	0.90	2.97	0.75	0.29	1.42
Turbinidae	0.02	0.00	0.04	0.36	0.00	0.79	0.43	0.00	0.92	0.02	0.00	0.06
Unid. Cephalopoda	2.74	1.32	4.74	2.87	1.84	4.03	3.40	2.14	4.77	2.54	1.37	4.19
Octopus spp	12.55	7.73	18.03	6.47	4.70	8.23	7.66	5.78	9.54	19.37	12.67	26.35
Octopus pallidus	5.53	1.94	10.02	1.52	0.74	2.42	1.80	0.88	2.80	1.69	0.61	3.32
Octopus warringa	0.78	0.19	1.55	0.75	0.24	1.37	0.90	0.29	1.66	0.19	0.04	0.43
Octopus berrima	1.44	0.44	2.73	1.25	0.50	2.12	1.48	0.60	2.44	0.53	0.18	1.11
Ommastrephidae	20.03	13.84	26.55	7.54	5.76	9.40	8.76	6.73	11.09	32.05	23.78	41.99
Nototodarus gouldi	9.56	4.92	15.38	2.83	1.81	4.01	3.41	2.13	4.75	5.65	2.67	9.39
Todarodes filippovae	0.90	0.06	2.10	0.51	0.12	1.00	0.59	0.14	1.20	0.11	0.01	0.30

Appendix 4.a. Continued…

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Todaropsis eblanae	0.70	0.00	2.17	0.37	0.00	0.84	0.44	0.00	1.03	0.06	0.00	0.23
Ommastrephes bartramii	1.27	0.16	3.32	0.88	0.36	1.53	1.05	0.31	1.80	0.30	0.06	0.75
Histioteuthis spp	0.05	0.00	0.15	0.13	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Bivalvia	0.01	0.00	0.05	0.13	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01
Chondrichthyes	1.64	0.50	3.22	1.54	0.52	2.46	1.67	0.83	2.86	0.08	0.03	0.18
Unid. Chondrichthyes	0.03	0.00	0.10	0.13	0.00	0.49	0.15	0.00	0.46	0.00	0.00	0.02
Squalus spp	0.05	0.00	0.17	0.13	0.00	0.45	0.14	0.00	0.45	0.00	0.00	0.02
Mustelus antarcticus	0.57	0.00	1.91	0.12	0.00	0.39	0.15	0.00	0.45	0.01	0.00	0.08
Urolophidae	0.48	0.00	1.47	0.25	0.00	0.66	0.29	0.00	0.76	0.03	0.00	0.11
Urolophus spp	0.03	0.00	0.08	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Narcine tasmaniensis	0.31	0.00	0.80	0.49	0.00	1.17	0.45	0.00	0.91	0.05	0.00	0.14
Rajidae	0.28	0.00	0.75	0.24	0.00	0.65	0.29	0.00	0.75	0.02	0.00	0.07
Osteichthyes	38.32	32.71	43.92	30.34	26.95	33.51	34.03	30.74	36.98	37.27	32.73	42.93
Unid. Osteichthyes	2.58	1.43	4.14	4.61	3.24	6.05	5.45	3.83	7.18	5.23	3.21	7.74
Anguilliformes	0.04	0.00	0.14	0.13	0.00	0.39	0.15	0.00	0.46	0.00	0.00	0.02

Appendix 4.a. Continued…

Prey	%W			%N			%FO			%IRI		
	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Scolecenchelys spp	0.13	0.00	0.33	0.37	0.00	0.86	0.44	0.00	1.03	0.03	0.00	0.09
Scolecenchelys breviceps	0.05	0.00	0.12	0.36	0.00	0.87	0.44	0.00	1.04	0.02	0.00	0.08
Serrivomer spp	0.17	0.01	0.41	0.50	0.12	1.04	0.59	0.14	1.20	0.05	0.00	0.14
Congridae	0.24	0.00	0.77	0.12	0.00	0.38	0.15	0.00	0.45	0.01	0.00	0.04
Clupeidae	2.03	0.74	3.68	1.51	0.61	2.58	1.47	0.59	2.53	0.70	0.26	1.41
Paraulopus nigripinnis	0.54	0.00	1.49	0.25	0.00	0.64	0.29	0.00	0.74	0.03	0.00	0.11
Myctophidae	0.46	0.00	1.15	0.36	0.00	0.85	0.44	0.00	1.02	0.05	0.00	0.14
Macrouridae	1.49	0.21	3.09	0.77	0.25	1.43	0.92	0.30	1.64	0.28	0.07	0.63
Caelorinchus spp	0.24	0.00	0.64	0.24	0.00	0.63	0.28	0.00	0.75	0.02	0.00	0.07
Lepidorhynchus denticulatus	0.54	0.13	1.09	0.85	0.24	1.69	0.87	0.15	1.65	0.16	0.03	0.38
Macruronus novaezelandiae	0.18	0.00	0.62	0.13	0.00	0.49	0.15	0.00	0.45	0.01	0.00	0.03
Cyttidae	1.25	0.00	3.34	0.24	0.00	0.64	0.29	0.00	0.75	0.06	0.00	0.24
Cyttus australis	0.27	0.00	0.89	0.12	0.00	0.38	0.14	0.00	0.45	0.01	0.00	0.04
Macroramphosidae	0.22	0.01	0.65	0.50	0.11	1.08	0.59	0.14	1.29	0.06	0.00	0.16
Macroramphosus scolopax	0.17	0.01	0.42	0.51	0.12	1.02	0.60	0.14	1.21	0.06	0.01	0.15

Appendix 4.a. Continued…

Prey	%W			%N			%FO			%IRI		
	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Centriscops spp	0.30	0.00	0.98	0.12	0.00	0.39	0.15	0.00	0.46	0.01	0.00	0.04
Triglidae	9.77	6.02	13.83	5.33	3.83	7.07	5.97	4.25	7.71	12.00	7.51	17.14
Lepidotrigla spp	0.11	0.00	0.37	0.13	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Lepidotrigla mulhalli	0.34	0.00	0.87	0.36	0.00	0.84	0.43	0.00	1.02	0.04	0.00	0.12
Lepidotrigla modesta	1.37	0.17	3.21	0.75	0.13	1.53	0.74	0.15	1.45	0.21	0.03	0.54
Chelidonichthys kumu	0.27	0.00	0.84	0.13	0.00	0.39	0.15	0.00	0.45	0.01	0.00	0.04
Platycephalidae	0.13	0.00	0.39	0.25	0.00	0.64	0.30	0.00	0.76	0.01	0.00	0.05
Neoplatycephalus conatus	0.37	0.00	0.89	0.38	0.00	0.85	0.45	0.00	1.01	0.05	0.00	0.13
Scorpaenidae	0.22	0.00	0.75	0.13	0.00	0.39	0.15	0.00	0.46	0.01	0.00	0.04
Helicolenus percoides	0.39	0.00	1.24	0.24	0.00	0.78	0.14	0.00	0.45	0.01	0.00	0.06
Perciformes	0.18	0.00	0.61	0.12	0.00	0.40	0.15	0.00	0.47	0.01	0.00	0.03
Acropomatidae	0.88	0.00	2.59	0.25	0.00	0.63	0.29	0.00	0.74	0.04	0.00	0.16
Apogonops anomalus	2.38	1.32	3.71	4.48	2.81	6.40	4.12	2.80	5.61	3.77	2.15	5.88
Gempylidae	1.88	0.53	3.56	1.35	0.58	2.29	1.45	0.60	2.33	0.63	0.22	1.22
Thyrsites atun	0.50	0.00	1.27	0.24	0.00	0.62	0.29	0.00	0.74	0.03	0.00	0.10

Appendix 4.a. Continued…

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Sillago flindersi	0.29	0.00	0.98	0.12	0.00	0.38	0.15	0.00	0.57	0.01	0.00	0.04
Parequula melbournensis	1.43	0.32	2.92	1.12	0.25	2.17	0.90	0.29	1.66	0.31	0.07	0.66
Carangidae	0.28	0.00	0.87	0.23	0.00	0.63	0.29	0.00	0.74	0.02	0.00	0.07
Trachurus sp.	0.40	0.00	1.28	0.13	0.00	0.41	0.15	0.00	0.45	0.01	0.00	0.05
Trachurus declivis	0.87	0.00	2.93	0.13	0.00	0.39	0.15	0.00	0.45	0.02	0.00	0.11
Scomber australasicus	3.50	1.56	6.06	1.62	0.80	2.59	1.93	1.02	3.02	1.32	0.54	2.47
Apogonidae	0.12	0.00	0.37	0.13	0.00	0.40	0.15	0.00	0.46	0.01	0.00	0.02
Argentina elongata	0.06	0.00	0.18	0.25	0.00	0.65	0.30	0.00	0.74	0.01	0.00	0.05
Otariidae	0.79	0.00	2.67	0.12	0.00	0.38	0.14	0.00	0.45	0.02	0.00	0.10
Unid. Porifera	0.00	0.00	0.01	0.12	0.00	0.49	0.15	0.00	0.58	0.00	0.00	0.02
Unid. Hydrozoa	0.00	0.00	0.00	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01
Unid. Algae	0.01	0.00	0.04	0.12	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.01
Unid. Ophiuroidea	0.00	0.00	0.00	0.12	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.01

Appendix 4.a. Continued…

Ecological groups	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Benthic epifauna	4.02	5.25	2.87	41.15	46.80	35.61	29.41	32.78	26.12	30.70	35.62	25.72
Benthic infauna	1.24	1.99	0.65	5.86	7.71	4.22	7.56	9.69	5.62	1.24	1.78	0.80
Benthic	36.95	43.97	30.18	21.10	24.53	17.70	25.34	28.91	21.90	33.96	40.28	28.08
Demersal benthic	11.04	14.75	7.50	11.10	14.02	8.59	12.24	14.93	9.84	6.27	8.42	4.49
Demersal pelagic	40.25	48.22	32.30	16.41	19.51	13.62	20.25	23.54	17.26	26.52	32.34	21.17
Pelagic	6.49	10.00	3.64	4.38	6.08	2.85	5.19	7.21	3.54	1.31	2.08	0.79

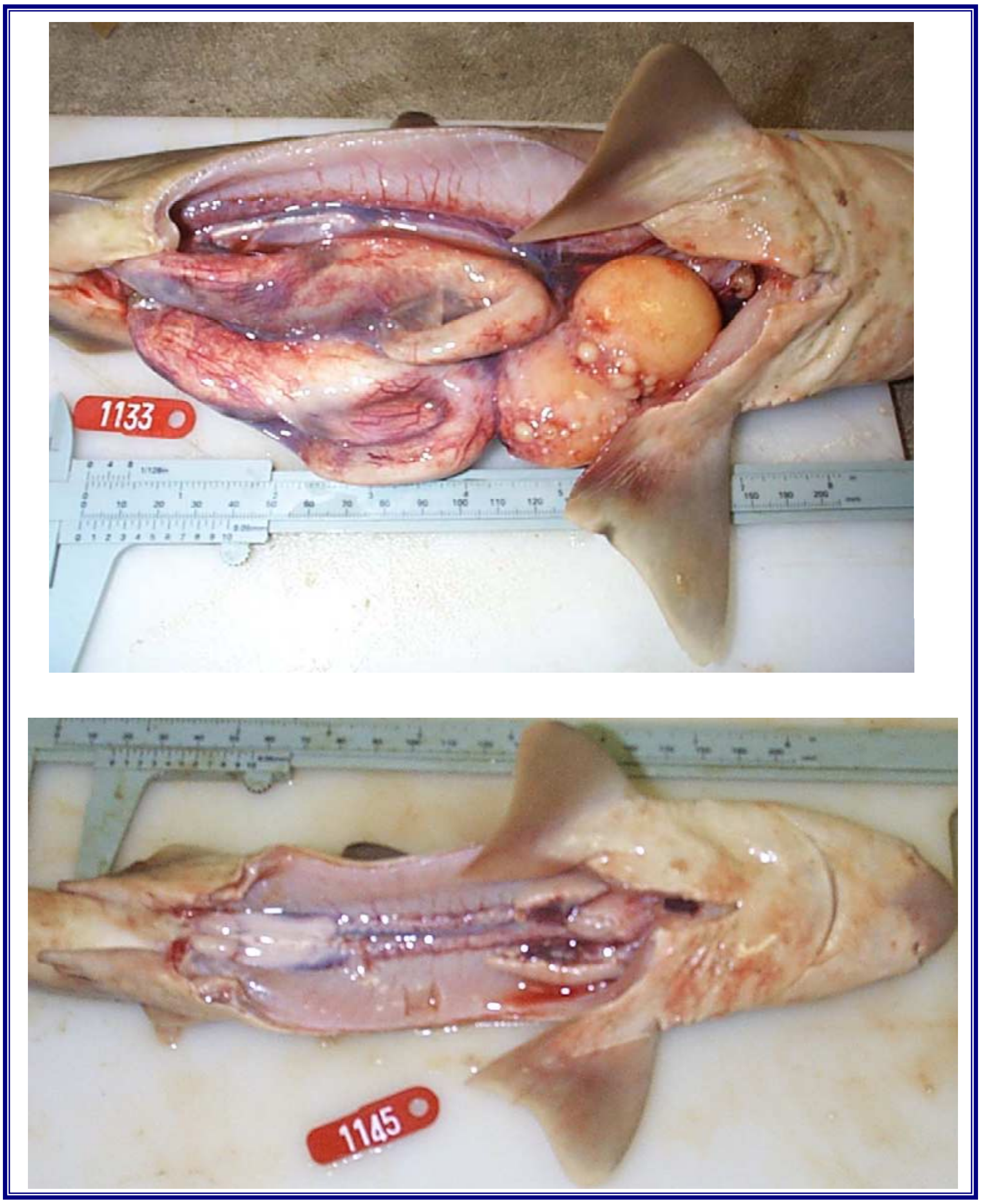

Photo of pregnant female and mature male (photos by the author).

CHAPTER 5

CHAPTER 5 PREAMBLE

Chapter 5 describes the reproductive biology of *Squalus megalops*, focusing on the reproductive parameters needed for quantitative population assessments. Given the uncertainty as to the best macroscopic descriptor of maturity, different indices are compared. Maturity, pregnancy and maternity ogives of females are also determined with a discussion on how recruitment rates will be over-estimated if maturity ogives are used in population assessments instead of maternity ogives. At the time this thesis was submitted (January 2006), this chapter was accepted for publication in the journal *Marine and Freshwater Research* (*in press*), with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide) and Terence I. Walker (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation. Permission from the publisher (CSIRO Publishing) to reproduce this manuscript has been granted (see Appendix A).

Contributions and signatures of authors

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CHAPTER 5

DETERMINING REPRODUCTIVE PARAMETERS FOR POPULATION ASSESSMENTS OF CHONDRICHTHYAN SPECIES WITH ASYNCHRONOUS OVULATION AND PARTURITION: PIKED SPURDOG (*SQUALUS MEGALOPS*) AS A CASE STUDY

5.1 ABSTRACT

Population assessments of chondrichthyan species require several key parameters of their reproductive biology, which were estimated for *Squalus megalops*. Length-at-maturity differed depending on the criterion adopted for defining maturity. In the case of males, length-at-maturity was smallest when condition of seminal vesicles was adopted as a maturity criterion. For females, length-at-maturity was smallest when the largest follicle diameter >3 mm was adopted as the criterion for maturity; this was appropriate only as an indicator of the onset of maturity. Mature males are capable of mating throughout the year. Females have a continuous asynchronous reproductive cycle. The sex ratio of embryos is 1:1 and litter size and near-term embryo length increase with maternal length. Females have an ovarian cycle and gestation period of two years. This was reflected in the differences found between the maturity and maternity ogives. Although all females are mature at 600 mm, only 50% of them contribute to annual recruitment each year. Hence, for chondrichthyan species with reproductive cycles of two, three or more years, if maturity ogives are used in population assessments instead of maternity ogives, the models will over-estimate recruitment rates.

5.2 INTRODUCTION

Depleted stocks of many teleost and invertebrate species have high potential for recovery but this is generally not the case for many species of Chondrichthyes (sharks, rays and chimaeras). Chondrichthyans have several biological characteristics that make them susceptible to fishing overexploitation. Chondrichthyans are mostly long-lived predators that have few offspring, producing close stock–recruitment relationships and slow stock recovery when overfished (FAO 2000*b*). In other words, chondrichthyan populations tend to have lower reproductive rates and lower natural mortality rates, and hence lower biological productivity, than teleost and invertebrate populations. Consequently, only a small proportion of chondrichthyan populations can be removed annually if catches and populations are to remain sustainable (Walker 1998). Fisheries targeting chondrichthyan species have been assessed by population models designed for teleosts, often resulting in inappropriate techniques being applied to these animals (Musick *et al.* 2000; Walker 2004). At present, assessment of chondrichthyan populations is limited by a lack of biological information (Cortés 1998*a*), especially for non-targeted-species.

Information on the reproductive biology of chondrichthyans is crucial for quantitative analysis of their populations. Measures of the biological productivity of chondrichthyan species, derived from reproductive and natural mortality rates, are required for stock assessments, demographic assessments and ecological risk assessments (Walker 2004). Furthermore, these measures are required in species assessments by wildlife conservation organizations such as the International Union for Conservation of Nature and Natural Resources (IUCN; Hilton-Taylor 2000). All these assessments use the same information for representing key parameters of reproduction: sex ratio at birth, the relationship between the number of offspring and maternal age or size of animals (litter size) and, sometimes useful for fisheries assessments, the relationship between the proportion of animals in mature condition at any time and the age or size of animals (maturity ogive). Essential for all types of assessment is the relationship between the proportion of the female population contributing to annual recruitment (i.e. females in maternal condition) and the age or size of animals (maternity ogive; Walker 2005).

Maternal condition is not usually considered or it is incorrectly equated to mature or pregnant conditions in most demographic studies. Maternity ogives of chondrichthyan species can be markedly different from maturity ogives and pregnancy ogives. For example, off southern Australia, the parturition frequency of school shark (*Galeorhinus galeus*) is triennial so at most one-third of the mature female population contributes to recruitment at the beginning of the following year. Also, length-at-maternity is much larger than length-at-maturity for this species (Walker 2005). Hence, although all females attain maturity at ~1600 mm total length, about one-third of them are in maternal condition in any year. Thus, for chondrichthyan species with complex breeding cycles exceeding one year of duration, if maternity ogives are ignored and only maturity curves are considered in the analysis, population models would over-estimate recruitment rates and bias assessments.

Methods for appropriate determination of maternity parameters needed for population assessments of chondrichthyans have only been established for viviparous species with synchronous reproductive cycles (Walker 2005). Although most viviparous chondrichthyans have synchronous mating, gestation and parturition (Hamlett and Koob 1999), in some species with complex breeding cycles, mating, gestation and parturition are asynchronous (Yano and Tanaka 1988; Yano 1993, 1995). For these species, a different approach is required for determining the parameters of maternity ogives for population assessments.

Complex asynchronous breeding cycles of several years duration have been reported for several squalid sharks (Squalidae) (Yano and Tanaka 1988; Yano 1995; Watson and Smale 1998). The piked spurdog (*Squalus megalops*) provides for a case study of the reproductive information needed for quantitative population studies as this species may have a long and complex ovarian cycle and gestation period (Watson and Smale 1998; Graham 2005). Hence, this shark may have different patterns of maturity condition and maternity condition. Furthermore, *S. megalops* has a high natural abundance in southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001) and, although this shark is among the most caught by-catch species (Walker *et al.* 2005), its abundance has remained stable off New South Wales since it was first surveyed (Graham *et al.* 2001).

The present paper is part of a broad-scale program for the assessment of ecological risk from the effects of fishing on the population status of *S. megalops* and other chondrichthyan species impacted by fishing in southern Australian fisheries. The specific objectives of the present study were to: (i) describe the reproductive biology of this species with emphasis on the information needed for quantitative population studies; (ii) analyse temporal variation in reproductive condition of mature males; (iii) determine sex ratio of embryos; (iv) evaluate litter and offspring size–maternal length relationships; (v) determine the periodicity of the ovarian cycle and gestation period of females; (vi) determine the maturity ogive as a function of length for each sex; and (vii) determine pregnancy and maternity ogives as a function of female length.

5.3 MATERIALS AND METHODS

Sampling

Specimens of *S. megalops* were obtained from the by-catch of the Australian Southern and Eastern Scalefish and Shark Fishery in waters off Robe, Lakes Entrance and Ulladulla, Australia (Fig. 5.1). Samples from Lakes Entrance and Ulladulla were caught by commercial bottom trawl fishing vessels, whereas samples from Robe were caught by commercial shark fishing vessels using gillnets of 6½-inch (165 mm) mesh-size. Samples were collected monthly between October 2002 and April 2004, with the exception of the August–September period, when *S. megalops* seemed to move off the fishing grounds and weather conditions hampered sampling operations. The specimens were sexed, measured (total length, TL, ±1 mm), weighed (body mass, TM) on an electronic balance (±1 g), and dissected to investigate their reproductive biology. Mass of liver (LM), gonads (GM) and seminal fluid in seminal vesicles (SFM) were also weighed (±0.1 g).

Analyses of males

For males, different criteria were used to investigate maturity condition. Length of the left clasper (CL) was recorded from the join in skin near the anus to the distal end (±1 mm). Macroscopic inspection of condition of clasper calcification (CI), testes (GI), seminal vesicles (VI), seminal fluid (VC), and vas deferens (VD) was undertaken to investigate further maturity by adopting four indices of maturity condition (using Walker's scale, modified for this species; Walker 2005) (Table 5.1).

Temporal variation in reproductive condition of mature males was investigated by recording the seminal vesicle fullness (VF) using a quarterly scale (0, empty to 4, full) and seminal fluid coloration and consistency (VC: 1, clear to 3, cloudy and thick). For each season, the gonadosomatic index ($GSI = 100\ GM\ TM^{-1}$), the hepatosomatic index ($HSI = 100\ LM\ TM^{-1}$) and the spermatosomatic index ($SSI = 100\ SFM\ TM^{-1}$) for males with VI = 2 were also calculated. Data were not analysed by month due to small sample sizes for some months. Winter samples of mature males were not considered due to small sample size ($n = 2$). Temporal variation in HSI, GSI and SSI was tested by ANOVA.

Reproductive cycle of females

For females, macroscopic inspection of condition of ovaries, oviducal glands and uteri was undertaken to investigate sex ratio of embryos, litter size, growth of embryos, periodicity of the ovarian cycle and gestation period, and mature, pregnant and maternal conditions. Indices were adopted for recording the condition of ovaries (GI), oviducal glands (OI) and uteri (UI) (using Walker's scale, modified for this species; Walker 2005) (Table 5.1). Maximum width of the left uterus was measured (±1 mm) to investigate the dynamics of the reproductive cycle. For pregnant females, number of *in utero* eggs or embryos and the sex, uterus (left or right), stage of development (*in utero* egg only, embryo with external yolk or embryo only), and total length (TLE, ±1 mm) of each embryo were recorded.

Sex ratio of embryos

Chi-square tests with Yates' continuity correction were applied to pregnant females (UI = 4 and 5) to test two hypotheses. (1) The number of *in utero* eggs and embryos in the left uterus equalled the number in the right uterus, and (2) the sex ratio of *in utero* embryos was 1:1.

Litter and offspring size–maternal length

The relationship between the number of *in utero* eggs or embryos (litter size) and maternal TL and the relationship between total length of near-term embryos (TLE) (offspring size) and maternal TL were represented by a linear regression model (Walker 2005). Embryos were considered near-term when the external yolk sac was completely absorbed. Females were collected from different regions (Fig. 5.1) and may exhibit geographic variation in their reproductive parameters (Wourms 1977). ANCOVA was used to test for the effects of region on the linear relationships between maternal TL and litter and offspring size.

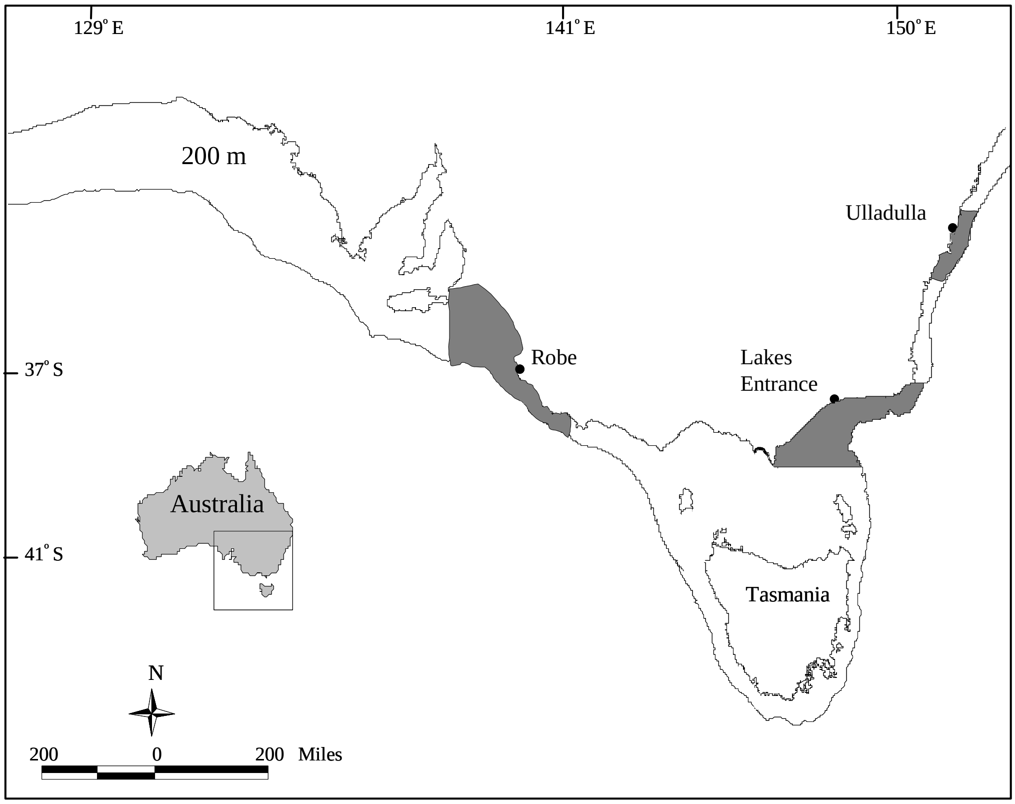

Figure 5.1. Map of sampling area showing the three regions compared (shaded) and ports.

Ovarian cycle

To determine the ovarian cycle, the diameter of the 20 largest follicles in each ovary was measured (±1 mm) to obtain the largest follicle diameter (LFD) for females caught throughout the year. Because the diameters of the largest follicles varied between individual animals and uterus condition, temporal variation of follicle growth was examined separately for each uterus condition defined in Table 5.1 (Walker 2005). Due to the asynchronous nature of the reproductive cycle (see "Results"), only pregnant females (UI = 4 and 5) were used to estimate the ovarian cycle. Pregnant females were arbitrarily classed in 5 categories based on the size of the embryo they carried: 0 for females carrying *in utero* eggs corresponding to 0 mm TLE, 1 for females carrying embryos <30 mm TLE, 2 for females carrying embryos 30–99 mm TLE, 3 for females carrying embryos 100–199 mm TLE, and 4 for females carrying embryos ≥200 mm TLE. Based on the assumption that LFD from different year classes have the same growth pattern, pregnant females in class 0 from late 2002, classes 1 and 2 from early 2003, class 3 from late 2003, and class 4 from early 2004 were used in a linear model to determine annual growth rate of follicles (Walker 2005). Data from different regions were pooled and no comparisons among regions were performed as no samples were collected from Robe and Ulladulla during May–November.

Gestation period

Gestation period was determined by plotting the percentage of females in uterus condition UI = 4–6 against month and TLE against Julian day. Based on the assumption that embryos from different year classes have the same growth pattern, TLE from the same subset of data selected for the ovarian cycle analysis was used in a growth model. The Gompertz curve is one of the best models of embryonic fish growth (Ricker 1979), hence, this model was fitted to the data subset, holding L_∞ at 230 mm, the average size at birth. Data from different regions were pooled and no comparisons among regions were conducted as no samples were collected from Robe and Ulladulla during May–November.

Maturity, pregnancy and maternity ogives

Logistic models were used to determine the proportion of mature males and females at any TL and, for females, the proportion in pregnant and maternal conditions (Punt and Walker 1998; Roa *et al.* 1999). Model parameters and the ogives with 95% confidence intervals (CI) were estimated by the method of maximum likelihood of the probit procedure using

Table 5.1. Indices used for staging reproductive condition. Maturity conditions corresponding to each index are also listed (modified from Walker 2005). Maturity condition: immature (I), mature (M), and uncertain (U).

Organ	Index	Description	Maturity
Male			
Clasper	CI = 0	Pliable with no calcification and without hooks	I
	CI = 1	Partly calcified with small hooks	I
	CI = 2	Rigid and fully calcified with evident hooks	M
Testis	GI = 1	Undifferentiated thin tissue strip	I
	GI = 2	Thickened tissue strip becoming lobular	I
	GI = 3	Enlarged with evident testicular lobules	M
Seminal vesicles	VI = 1	Thin translucent walls and seminal fluids absent	I
	VI = 2	Thickened opaque walls and seminal fluids present	M
	VI = 3	Thickened opaque walls and seminal fluids absent	M
Vas deferens	VD = 1	Thin line along dorsal surface of abdominal cavity	I
	VD = 2	Thickened line that begins to coil	I
	VD = 3	Enlarged and fully coiled	M
Female			
Ovary	GI = 1	Largest follicles hyaline and of diameter <3 mm	I
	GI = 2	Largest follicles white and of diameter 3–14 mm	I
	GI = 3	Largest follicles yellow with yolk and of diameter ≥15 mm	M
Oviducal gland	OI = 1	Indistinct from anterior uterus	I
	OI = 2	Distinct but only partly formed	I
	OI = 3	Enlarged and kidney-shaped	M
Uterus	UI = 1	Uniformly thin tubular structure	I
	UI = 2	Thin tubular structure partly enlarged posteriorly	I
	UI = 3	Enlarged tubular structure partly narrow anteriorly	U

Table 5.1. Continued…

Organ	Index	Description	Maturity
Uterus	UI = 4	*In utero* eggs present without macroscopically visible embryos present	M
	UI = 5	*In utero* embryos macroscopically visible	M
	UI = 6	Enlarged tubular structure distended (post-partum)	M

Clasper index (CI); gonad index (GI); seminal vesicle index (VI); vas deferens index (VD); oviducal gland index (OI); uterus index (UI).

the SAS statistical package (SAS Institute, Cary, North Carolina, USA) (Walker 2005). Given the uncertainty in determining maturity in males (Conrath 2004), indices for each of four separate methods were used and the results compared. A male was classed as in mature condition if CI = 2, GI = 3, VI = 2–3, or VD = 3; otherwise it was classed as immature. Logistic curves and associated parameters were determined for each maturity criterion. Females had a complex reproductive cycle (see “Results”), hence, as for males, different maturity criteria were adopted and the results compared. A female was classed as in mature condition if GI = 3, OI = 3, or UI = 4–6; otherwise it was classed as immature. In addition, the effect of adopting three alternative maturity criteria based on LFD was assessed: LFD >3 mm (Walker 2005) (for onset of maturity), LFD ≥15 mm (present study) and LFD ≥20 mm (Yano and Tanaka 1988; Watson and Smale 1998). Logistic curves and associated parameters were determined for each maturity criterion. Regional comparisons of samples from Lakes Entrance and Robe were undertaken using the logistic procedure of the SAS statistical package (SAS Institute, Cary, North Carolina, USA) (Walker 2005). Samples from Ulladulla were not included as all sharks were in mature condition and hence the maturity ogive was not calculated.

For the analysis of pregnant females, a female was classed as in pregnant condition if UI = 4–5; otherwise it was classed as non-pregnant. For the maternity analysis, a female was classed as in maternal condition if, had it survived, it would have given birth by the end of 2003 or early 2004; i.e. it contributed to annual recruitment at the beginning of 2004. Hence, for each pregnant female, parturition time was calculated using the embryo growth model. Pregnancy and maternity ogives were determined using logistic models. Model parameters and the ogives with 95% CI were estimated by the method of maximum likelihood of the probit procedure using the SAS statistical package (SAS Institute, Cary, North Carolina, USA) (Walker 2005). Given that parturition frequency is biennial (see “Results”), for SAS probit analysis of maternity condition, the parameter P_{max} (maximum proportion of animals in maternal condition) was altered from 1.0 to 0.5. The SAS output was then multiplied by 0.5 to obtain the parameters of the maternity ogive, with 95% CI (Walker 2005). Assuming that sampling was not biased for pregnant or non-pregnant females, pregnancy and maternity ogives were determined using pooled data from different regions; hence, no regional comparisons were made for these ogives.

5.4 RESULTS

Analyses of males

A total of 207 male *S. megalops* (274–470 mm TL) were collected for reproductive analyses. Male sharks were mostly sampled from Lakes Entrance (Fig. 5.1) so no regional comparisons were performed. Clasper length (CL) showed a sigmoid relationship with TL. Claspers grew gradually in animals <350 mm TL, followed by rapid growth until 385 mm TL and 27 mm CL (CI = 2), which several indicators suggest is the TL for the onset of maturity.

Maturity ogives differed depending on the maturity criterion adopted (Fig. 5.2e). The ogive based on maturity condition of seminal vesicles (VI = 2 or 3) showed a value of TL at which 50% of the population was mature (L_{50}) (with 95% CI) of 373 (368, 377) mm (Fig. 5.2a). This value was considerably smaller than those obtained using other maturity criteria. The ogives based on vas deferens (VD = 3), clasper (CI = 2) and gonad (GI = 3) conditions were in reasonable agreement and provided values of L_{50} of 392 (388, 396), 393 (390, 395) and 398 (395, 401) mm, respectively (Figs. 5.2b–d).

Irrespective of which maturity index was used, males classed as mature were found throughout the year (Fig. 5.3). Statistical testing of the frequency of males in different GI, CI, VI and VD conditions was not carried out due to the opportunistic nature of the sampling design and possible size and sex aggregation of the sharks; however, mature males (GI = 3, CI = 2, VI = 2–3 or VD = 3) were collected from each season (Figs. 5.3a–d). The frequency of vesicle fullness (VF) of mature males with VI = 2 was similar throughout the year; most mature males had full seminal vesicles (VF = 4) (Fig. 5.3e) containing cloudy and thick seminal fluids (VC = 3) (Fig. 5.3f). There were no seasonal differences in the maturity condition of mature males. Mature males had similar values of mean HSI throughout the sampling period (ANOVA: $F_{2,117}$= 2.19, P = 0.1164). Also, no seasonal variation was found in the mean GSI (ANOVA: $F_{2,114}$= 0.94, P = 0.3939) and mean SSI (ANOVA: $F_{2,112}$= 1.14, P = 0.3241). It appears that mature males are capable of mating throughout the year.

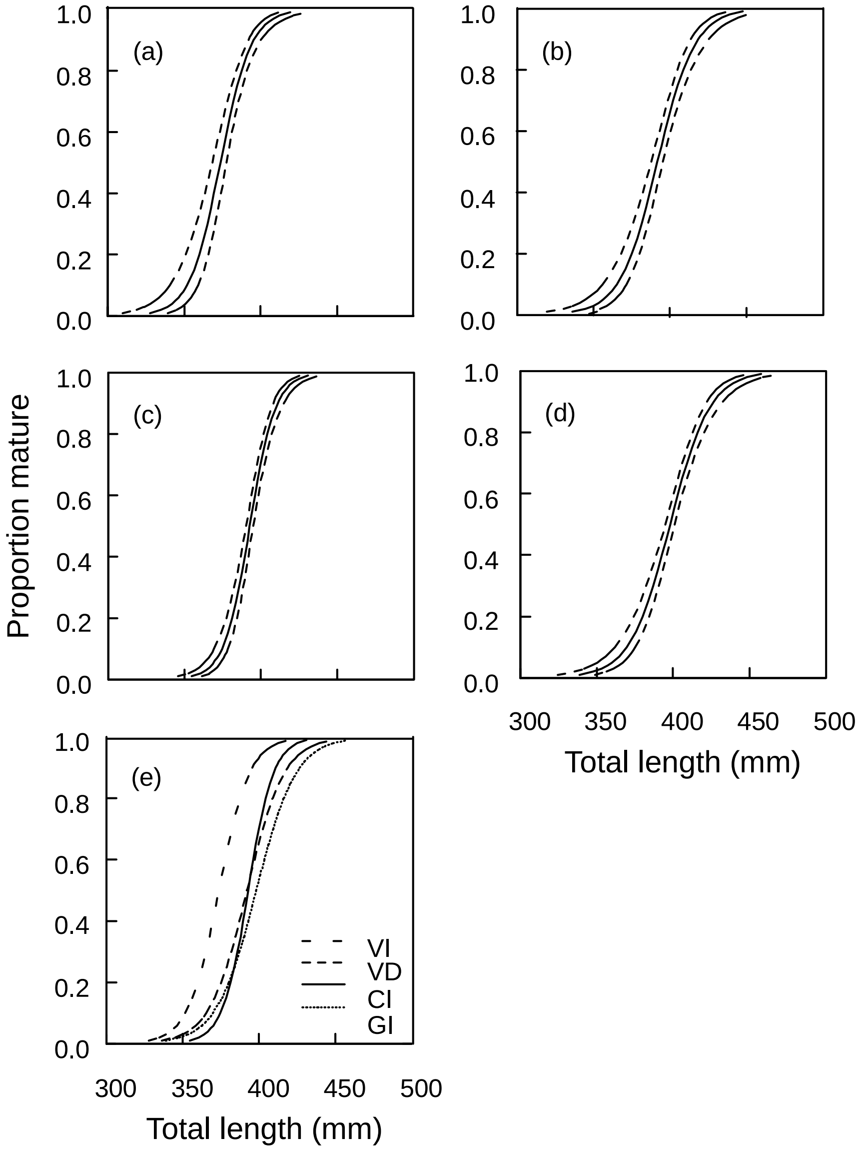

Figure 5.2. Male length-at-maturity ogives. Proportion of male population in mature condition versus total length with 95% confidence intervals (- - -) determined from (a) seminal vesicle condition (VI), (b) vas deferens condition (VD), (c) clasper condition (CI), (d) testis condition (GI), and (e) comparison of mean ogives for VI, VD, CI and GI. Values of parameters and statistical values for the equation $P = P_{max}\,(1 + e^{-\ln(19)((l - l_{50})/(l_{95} - l_{50}))})^{-1}$ used in the probit analysis are as follows:

Maturity criterion	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	*P*
Seminal vesicle condition	373 (368, 377)	403 (399, 409)	1	201	– 113.62	***
Vas deferens condition	392 (388, 396)	428 (422, 437)	1	172	– 141.71	***
Clasper condition	393 (390, 395)	417 (413, 422)	1	207	– 169.12	***
Testis condition	398 (395, 401)	436 (430, 444)	1	207	– 246.96	***

where l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and *P* is the probability of statistical significance ($^{***}P < 0.001$).

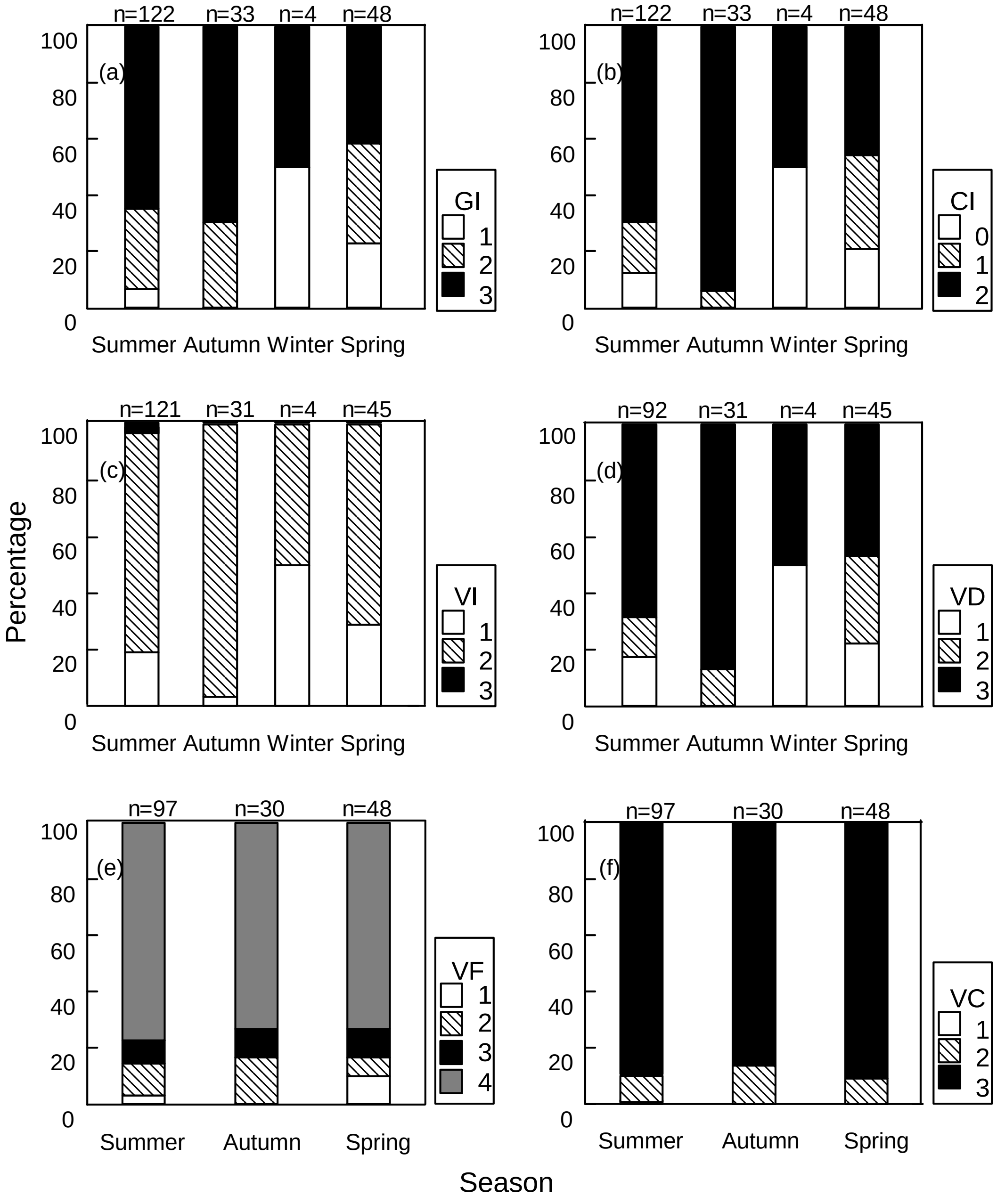

Figure 5.3. Percentage of male sharks at different maturity condition collected from different seasons. (a) Gonad index (GI), (b) clasper index (CI), (c) vesicle index (VI), (d) vas deferens index (VD), (e) vesicle fullness (VF) for males with VI = 2, and (f) seminal fluid coloration (VC) for males with VI = 2 and VF = 4. Sample sizes are shown above bars.

Reproductive cycle of females

Analyses of 722 female *S. megalops* (270–635 mm TL) suggested that females had a continuous asynchronous reproductive cycle. There was an increase in LFD with uterus width for females ovulating for the first time (UI = 1–3) (Fig. 5.4a). Ovulation occurred once LFD reached ~40 mm and uterus reached a width of ~18 mm. For pregnant females carrying *in utero* eggs (UI = 4) or embryos at an early-stage of development (UI = 5_1), LFD was small. The follicles enlarged throughout gestation synchronously with embryonic growth and were ready to be ovulated when embryos were near-term, indicating that fertilization and the gestation of a subsequent litter can occur immediately after parturition. This was supported by the significant correlation between LFD and TLE (r = 0.954, n = 544, P <0.0001) (Fig. 5.4b).

Sex ratio of embryos

Macroscopically visible *in utero* eggs and embryos were examined in 308 pregnant females (UI = 4–5). Most of these females (72.7%) carried only one egg or embryo per uterus and no female was observed to carry eggs and embryos at the same time. Significant differences were found in the number of *in utero* eggs and embryos between the left uterus and the right uterus (χ^2 = 15.882, d.f. = 1, P <0.001). Of a total of 668 eggs and embryos counted, 386 (57.8%) were present in the right uterus. However, when the analysis was performed on pregnant females carrying up to two *in utero* eggs or embryos, no significant differences were found between the left uterus and right uterus (χ^2 = 3.561, d.f. = 1, P = 0.059). A total of 450 embryos was sexed of which 154 (34.2%) were male, 145 (32.2%) were females, and 151 (33.6%) were classed as “unknown sex” due to their early stage of development. The sex ratio of embryos was not significantly different from 1:1 (χ^2 = 0.214, d.f. = 1, P = 0.644).

Litter and offspring size–maternal length

Litter size was recorded for 308 pregnant females. All females carrying only one embryo were excluded from the analysis because it was assumed that they had aborted embryo(s) due to stress of capture. This assumption was supported by the occasional presence of embryos on the deck of the vessels (J. M. Braccini, pers. obs.) and the fact that these females had empty uteri with stretched and vascularized walls, suggesting the loss of one or more embryos. Uteri containing one or two embryos had turgid walls, indicating that abortion had not occurred. Regional differences detected in the relationship between

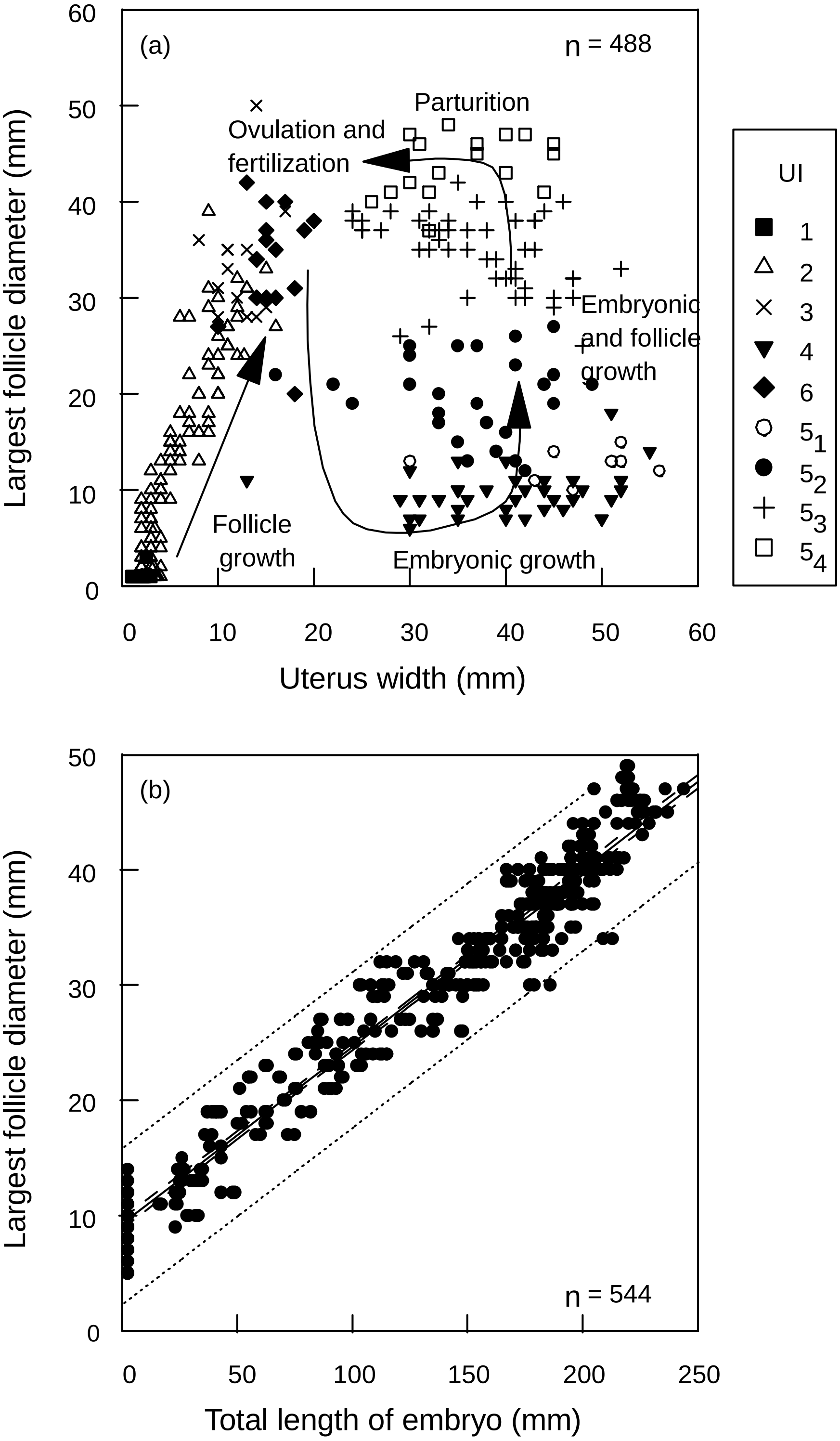

Figure 5.4. Relationships between largest follicle diameter (LFD) and (a) uterus width for females in different uterus condition (UI) and (b) total length of embryo (TLE) with 95% confidence intervals (- - -) and predicted intervals (·······) (see Table 5.1 for UI definition). LFD = 0.153 TLE + 9.303; $r^2 = 0.931$.

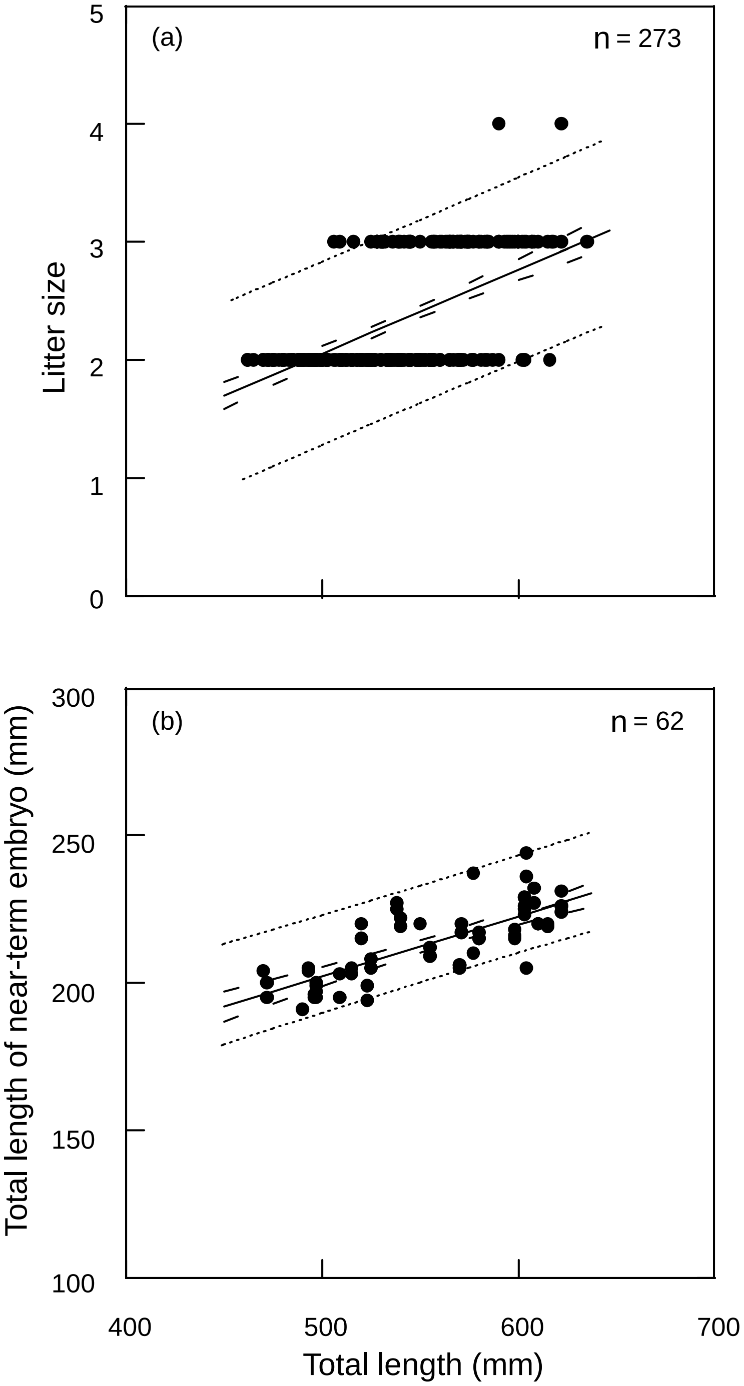

Figure 5.5. Relationship between maternal total length (TL) and (a) litter size and (b) total length of near-term embryos (TLE) with 95% confidence intervals (- - -) and predicted intervals (……). Litter size = 0.00711 TL – 1.503; $r^2 = 0.330$; TLE = 0.203 TL + 100.6; $r^2 = 0.587$.

litter size and maternal TL (ANCOVA: $F_{2, 274}$= 3.87, P = 0.022) were considered an artefact of the sampling method. Samples from Lakes Entrance and Ulladulla were collected by bottom trawl nets whereas those from Robe were collected by gillnets of 6½-inch (165 mm) mesh-size. For *S. megalops*, 6½-inch gillnets selected for large-sized females (J. M. Braccini, pers. obs.) and this is likely to have created apparent regional differences in the litter size–maternal TL relationship caused by sampling bias or length-selective fishing mortality. The results were therefore presented pooling the three regions. Litter size for most females was two (69.3%) or three (30.0%) and only a few of them carried four (0.7%) *in utero* eggs or embryos. Litter size showed a linear relationship with TL ($F_{1, 273}$ = 132.38, P <0.001) (Fig. 5.5a).

Embryo length (TLE) was recorded for 62 near-term embryos (191–244 mm TLE) and the mean relative length-at-birth (with 95% CI) was 38.5 (35.6, 42.4) % of maternal TL. No regional differences in the relationship between TLE and maternal TL (ANCOVA: $F_{2, 60}$= 0.67, P = 0.515) were detected, so samples collected from different regions were pooled for subsequent analyses. Near-term embryo length increased linearly with maternal TL ($F_{1, 60}$ = 85.40, P <0.001) (Fig. 5.5b).

Ovarian cycle

Largest follicle diameter (LFD) was recorded for 658 females and ranged from 1–49 mm. Females with uterus condition (UI) = 1 always had small follicles (Fig. 5.6a). Females with UI = 2 showed a wide range of LFD (1–39 mm) at any time (Fig. 5.6b), indicating that follicles can approach full size before the uteri were fully developed. Females with UI = 3 or 6 were observed carrying large follicles at all times of the year (Figs. 5.6c, d), suggesting that follicle enlargement and ovulation are not temporally synchronous between animals. For animals with UI = 4, LFD was relatively small indicating that ovulation was complete; no animals were observed in the process of ovulation (Fig. 5.6e). Wide variation of LFD (6–49 mm) was observed for pregnant females carrying embryos (UI = 5) (Fig. 5.6f). Females carrying small embryos had small follicles whereas females carrying near-term embryos had large follicles, suggesting that ovulation immediately follows parturition. Furthermore, only a small percentage of mature females (8.3%) were in UI = 6 condition and they all carried large follicles, indicating a short period between pregnancies. There was a linear relationship between LFD and Julian Day ($F_{1, 104}$ = 709.64, P <0.001)

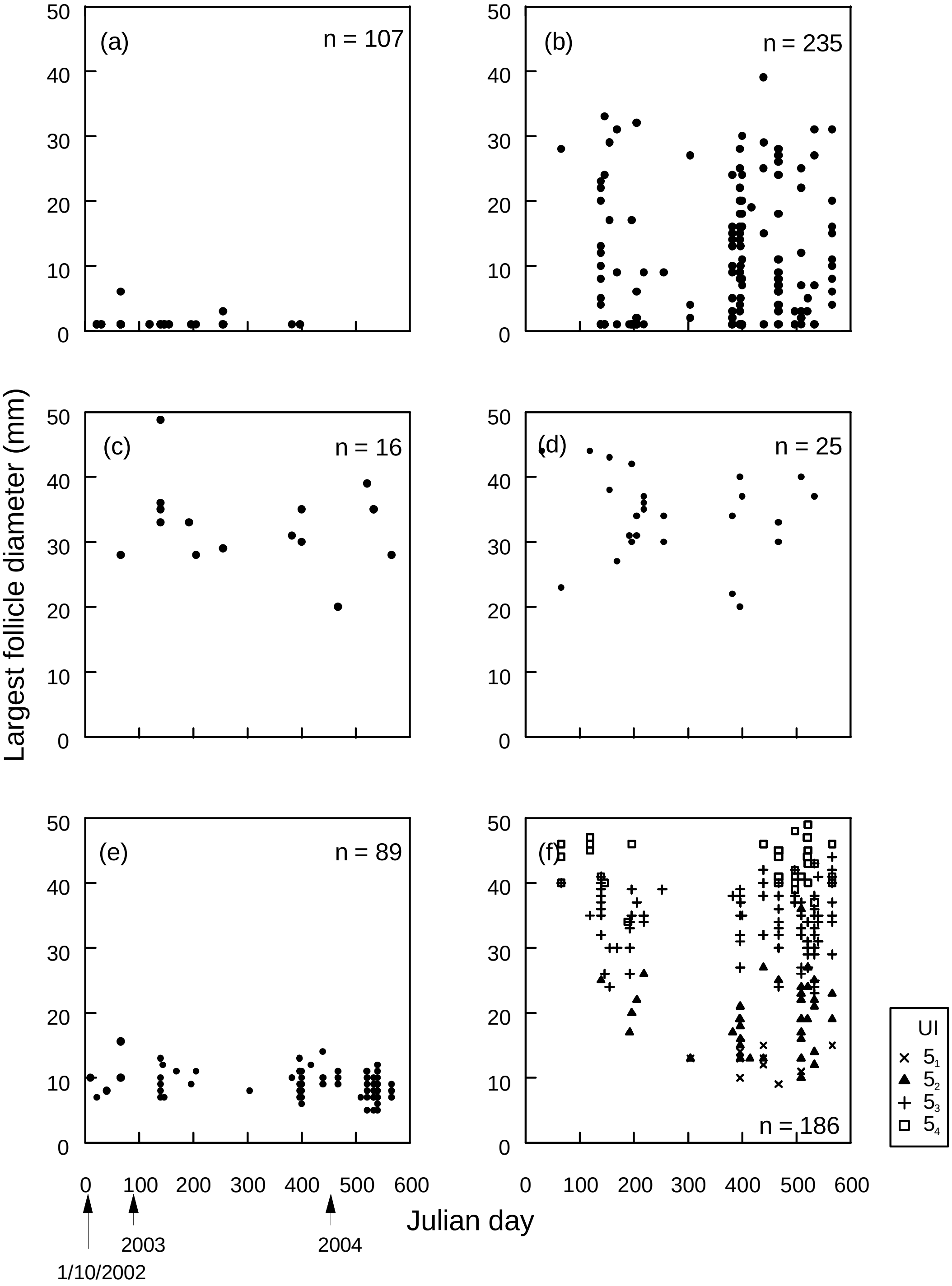

Figure 5.6. Ovarian cycle. Relationship between largest follicle diameter and Julian day for (a) uterus index (UI) = 1, (b) UI = 2, (c) UI = 3, (d) UI = 6, (e) UI = 4, and (f) UI = 5.

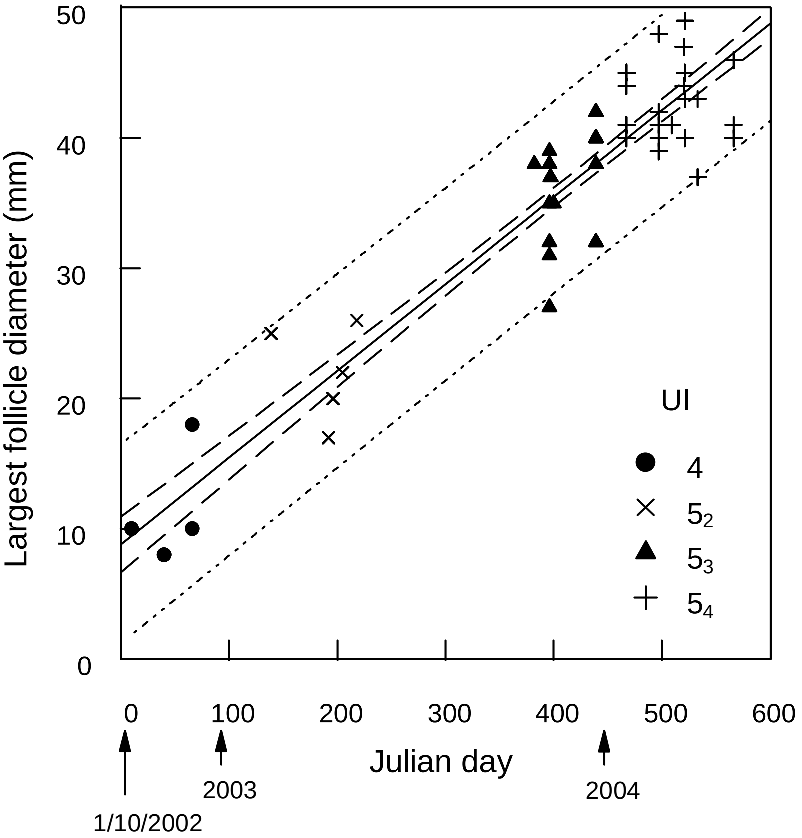

Figure 5.7. Hypothetical follicle development curve for females in uterus condition (UI) = 4 and 5. Linear model fitted to selected subset of data with 95% confidence intervals (- - -) and predicted intervals (·······). Largest follicle diameter = 0.07 Julian day + 8.797; r^2 = 0.874.

(Fig. 5.7), indicating linear follicular growth. Annual growth of LFD was 24 mm y^{-1}, suggesting an ovarian cycle of ~19 months.

Gestation period

A total of 423 embryos was measured and each of 152 *in utero* eggs was assigned a TLE value of 0 mm for determining gestation period. *S. megalops* was an asynchronous breeder in which ovulation, parturition and mating did not occur at any particular time of the year. Females carrying *in utero* eggs (UI = 4) or near-term embryos (UI = 5_4) were observed throughout the year, providing further evidence of no pattern of temporal periodicity in the reproductive cycle (Figs. 5.8a, b). Furthermore, embryos at different stages of development could be found at all times of the year. Based on the Gompertz growth model, annual growth of embryos was 170 mm y^{-1}, suggesting a gestation period of ~2 years (Fig. 5.8c).

Maturity, pregnancy and maternity ogives

Maturity ogives of females differed depending on the maturity criterion adopted (Fig. 5.9g). When the maturity criterion used was LFD >3 mm (onset of maturity), length at which 50% (L_{50}) of the animals were in mature condition (with 95% CI) was 459 (457, 461) mm (Fig. 5.9a). When LFD ≥15 mm and uteri condition (UI = 4, 5 or 6) were used, L_{50} was 484 (481, 487) mm and 486 (485, 488) mm, respectively (Figs. 5.9b, e). The ogives for LFD ≥20 mm and oviducal gland condition (OI = 3) were similar (Figs. 5.9c, f) and showed a larger value of L_{50} of 495 (492, 498) and 495 (491, 499) mm, respectively. Finally, L_{50} based on ovarian condition (GI = 3) was 477 (475, 479) (Fig. 5.9d).

The criterion used to test for the effects of region on the maturity ogives of females was LFD ≥15 mm. This criterion was preferred to other criteria because follicles of 15 mm diameter were yellow, indicating that vitellogenesis was well advanced and because the ogive and the value of L_{50} obtained were in reasonable agreement with most of the other criteria considered. Significant differences were found in the maturity ogives of females from Lakes Entrance and Robe (P <0.0001) (Fig. 5.9h). The value of L_{50} for females from Lakes Entrance was 478 (475, 482) mm, whereas the value of L_{50} for females from Robe was 514 (506, 523) mm. However, as in the case of the litter size–maternal TL relationship, there could be apparent differences due to the effects of length-selectivity of the 6½-inch gillnet used in Robe. Such length-selectivity might distort the maturity ogive by the effects of sampling bias and length-selective fishing mortality.

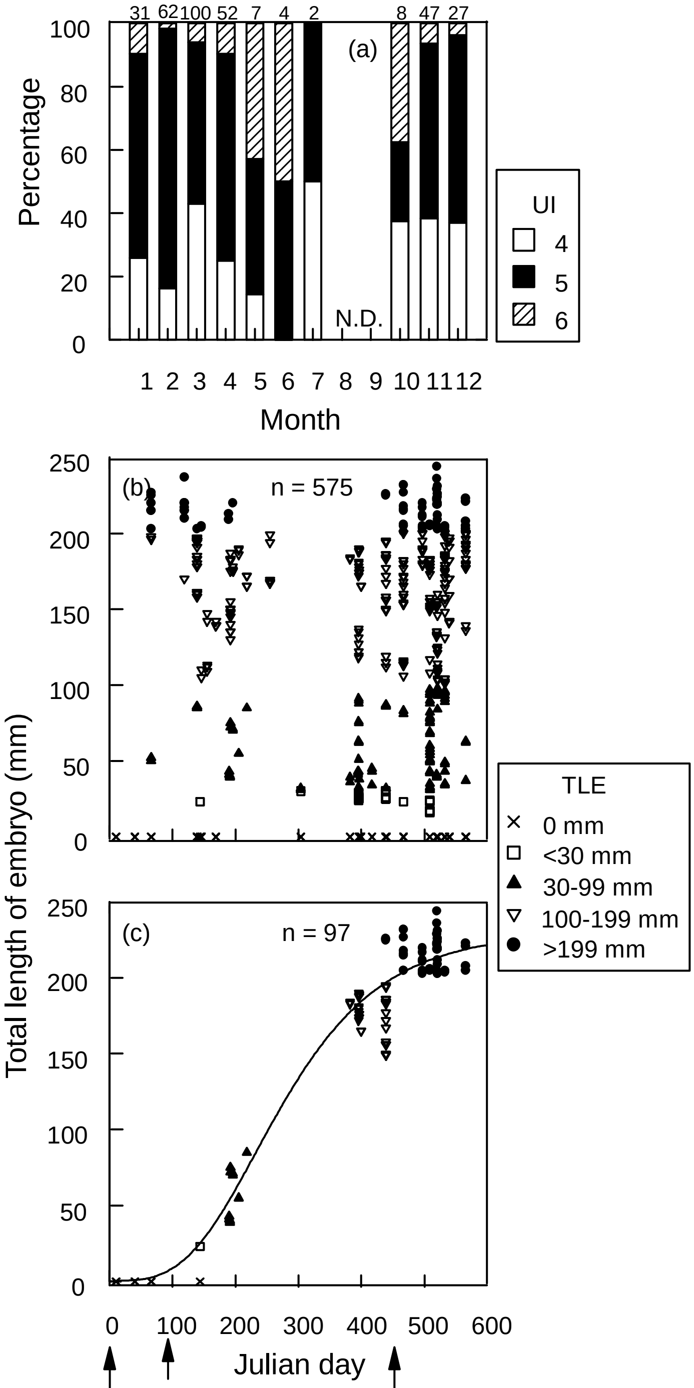

Figure 5.8. Gestation period. (a) Distribution of different stages of maturity of females in uterus condition (UI) = 4–6 during the year. (b) Length of embryos (TLE) collected during the sampling period. (c) Hypothetical growth curve with Gompertz model fitted to the selected subset of data. TLE = $230\,e^{(-8.068\,e^{(-0.009\,t)})}$; $r^2 = 0.9$. N.D.: no data. Sample sizes are shown above bars.

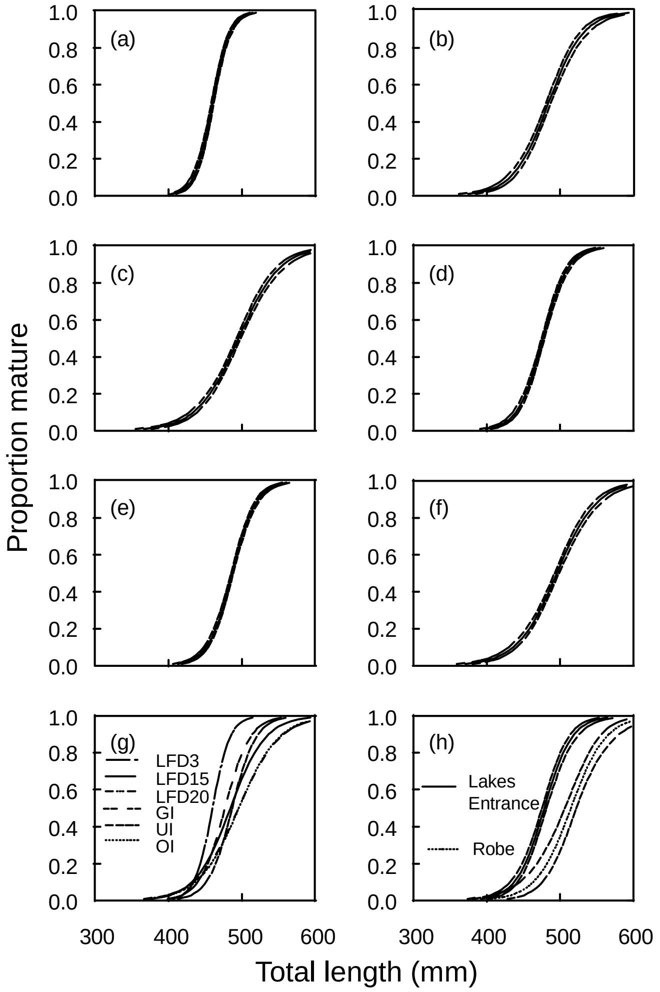

Figure 5.9. Female length-at-maturity ogives. Proportion of female population in mature condition against total length with 95% confidence intervals (- - -) determined from (a) largest ovarian follicle diameter (LFD) >3 mm (LFD3), (b) LFD ≥15 mm (LFD15), (c) LFD ≥20 mm (LFD20), (d) ovary condition (GI), (e) uteri condition (UI), and (f) oviducal gland condition (OI). (g) Comparison of mean ogives for LFD3, LFD15, LFD20, GI, UI, and OI, and (h) comparison between maturity ogives for females from Lakes Entrance and Robe with 95% confidence intervals (- - -) based on the maturity criterion LFD15. Values of parameters and statistical values for the equation $P = P_{max}\,(1 + e^{-\ln(19)((l - l_{50})/(l_{95} - l_{50}))})^{-1}$ used in the probit analysis are as follows:

Maturity criterion	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	*P*
LFD > 3 mm	459 (457, 461)	491 (488, 495)	1	706	– 390.86	***
LFD ≥ 15 mm	484 (481, 487)	554 (547, 563)	1	616	– 647.38	***
LFD ≥ 20 mm	495 (492, 498)	577 (570, 586)	1	615	– 1131.75	***
Ovaries condition	477 (475, 479)	527 (522, 531)	1	621	– 879.03	***
Uteri condition	486 (485, 488)	534 (530, 538)	1	719	– 1231.29	***
Oviducal gland condition	495 (491, 499)	573 (564, 584)	1	584	– 563.97	***

where l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and *P* is the probability of statistical significance ($^{***}P < 0.001$).

Length at which 50% of the female population was in pregnant condition was 495 (492, 497) mm (Fig. 5.10a); however, at any length, at most 50% of the female population was in maternal condition (Fig. 5.10b). The TL-at-maternity and TL-at-pregnancy were larger than TL-at-maturity (Fig. 5.10c). Although all females were mature at 600 mm, only half of the population was in maternal condition and hence contributing to annual recruitment.

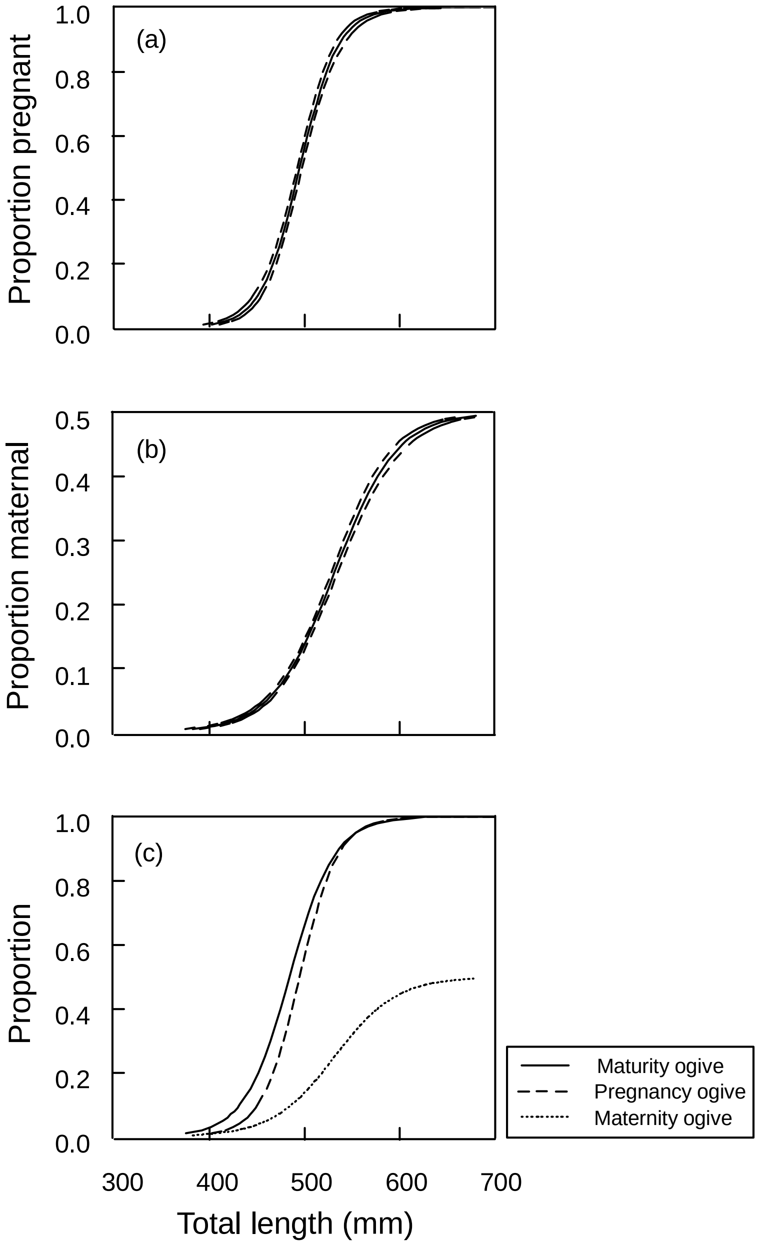

Figure 5.10. Female length-at-pregnancy and maternity ogives. Proportion of female population in (a) pregnancy and (b) maternal conditions against total length with 95% confidence intervals (- - -). (c) Comparisons between maturity, pregnancy and maternity ogives. Values of parameters and statistical values for the equation $P = P_{max} (1 + e^{-\ln(19)((l - l_{50})/(l_{95} - l_{50}))})^{-1}$ used in the probit analysis are as follows:

Condition	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	P
Pregnant	495 (492, 497)	554 (548, 560)	1	720	– 777.19	***
Maternal	531 (528, 534)	626 (618, 635)	0.5	522	– 1983.39	***

where l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and P is the probability of statistical significance ($^{***}P$ <0.001).

5.5 DISCUSSION

Given uncertainty as to the best descriptor of maturity of male sharks (Conrath 2004), the results for four indices were compared in the present study. When condition of seminal vesicles was used, L_{50} was considerably smaller than when conditions of gonads, vas deferens or clasper calcification were used. Walker (2005) also found a smaller value of L_{50} when comparing the condition of seminal vesicles with gonad condition or clasper calcification in *G. galeus*. These findings suggest that seminal vesicle condition might class some males as mature even though they may not be capable of mating as, for example, they may not have fully functional claspers. Watson and Smale (1998) and Graham (2005) found similar values of L_{50} to those obtained in the present study based on conditions of the gonads, vas deferens and clasper calcification. For male *S. megalops*, these criteria for maturity condition gave similar values of L_{50} and similar maturity ogives, suggesting that any of these criteria could be used to determine maturity.

Irrespective of maturity criterion, mature males were observed in all seasons and none of GSI, HSI and SSI exhibited seasonal variation, indicating that males are in mating condition throughout the year. A similar pattern is reported for male *S. megalops* from South Africa (Watson and Smale 1998) and several other shark species (Parsons and Grier 1992). This would be advantageous for species that inhabit environments with little variation in environmental cues (e.g., deep sea and tropics) or where mate location may be difficult (e.g., deep sea and open ocean) or both (Wourms 1977; Parsons and Grier 1992). *Squalus megalops* inhabits waters of the continental shelf and upper continental slope to 510 m (Last and Stevens 1994) so it cannot be considered a deepwater shark. However, most squalid species occur in deeper waters on the continental slope (Last and Stevens 1994); hence, the apparent lack of seasonality in the reproductive cycle of male *S. megalops* may be an ancestral trait.

Females have a continuous reproductive cycle. Following ovulation, follicles begin to undergo vitellogenesis again concurrently with embryonic growth and are ready for ovulation and fertilization immediately after parturition. A similar pattern is reported for *S. megalops* from New South Wales, Australia (Graham 2005) and South Africa (Watson and Smale 1998) and for other species of *Squalus* (Kibesaki 1954; Jones and Geen 1977*b*; Chen *et al.* 1981) although some female spiny dogfish (*S. acanthias*) have a resting period between pregnancies (Jones and Geen 1977*b*; Hanchet 1988). The few observed mature female *S. megalops* in the present study that were not pregnant all carried enlarged follicles ready for ovulation, suggesting a very short period between pregnancies.

The sex ratio of embryos is 1:1. A 1:1 embryo sex ratio is also reported for *S. megalops* from South Africa (Watson and Smale 1998) and for other squalid species (Hanchet 1988; Yano 1995). A 1:1 embryo sex ratio is expected for a sexually balanced population, assuming that males and females have similar mortalities. Less straightforward is, however, the distribution of embryos between uteri. When all pregnant females were considered in the analysis, a larger proportion carried eggs or embryos in the right uterus than in the left uterus, but analysis of females carrying up to two eggs or embryos showed that eggs or embryos were carried in similar numbers between the two uteri. Space in the body cavity of viviparous sharks is important during embryonic development (Bass 1973), particularly for species carrying relatively large-sized embryos, like *S. megalops*. In this shark, the stomach is positioned on the left side of the body cavity; thus, when carrying more than two embryos, space would be maximized if females hold more embryos in the right uterus.

The litter size and embryo length of *S. megalops* increased with maternal TL. The pattern of increasing number of embryos (Hanchet 1988; Yano and Tanaka 1988; Taniuchi *et al.* 1993) and length of near-term embryos (Hanchet 1988; Guallart and Vicent 2001) with maternal TL is reported for other squalid species. This pattern is also observed in *S. megalops* from South Africa and it may be related to an increase in space in the body cavity (Watson and Smale 1998).

Ovulation and parturition in *S. megalops* exhibit no pattern of temporal periodicity, suggesting that this shark is an asynchronous breeder. Most viviparous chondrichthyans have synchronous mating (Hamlett and Koob 1999), although in a few species mating is asynchronous (Yano and Tanaka 1988; Yano 1993, 1995). For chondrichthyans with synchronous mating, the largest follicle diameter (LFD) and the size of the embryos are recorded through time to determine the ovarian cycle and gestation period. However, this method cannot be applied for species with asynchronous mating given that follicles or embryos at very different stages of development are found at all times of the year. The ovarian cycle of three deepwater squalid species could not be determined using this method (Yano and Tanaka 1988). Watson and Smale (1998) used a similar approach to estimate the gestation period of *S. megalops* without any success. In the present study, ovarian cycle and gestation period were determined using the linear and Gompertz growth models respectively, on a subset of data from different years. These models gave a good fit to the data and allowed an approximate determination of the ovarian cycle and gestation period. For other shark species, the linear (Walker 2005) and Gompertz (Hanchet 1988) models have been used successfully for determining periodicity of ovarian cycle and gestation period, respectively.

Squalus megalops has an ovarian cycle and gestation period of ~2 years. The periodicity of the ovarian cycle and gestation are crucial for defining maternal condition of female chondrichthyans; they need to be determined for population assessments of chondrichthyan species. Most viviparous sharks have gestation periods of approximately a year (Stevens and McLoughlin 1991; Hamlett and Koob 1999). However, for species producing large-sized follicles, such as most squalid species (Chen *et al.* 1981; Hanchet 1988; Guallart and Vicent 2001), ovarian cycle and gestation period are two, three or more years. Given that the ovarian cycle and gestation period in *S. megalops* are biennial and that development of follicles and embryos occurs concurrently, it is expected that parturition frequency for the population is also biennial.

The different criteria used to calculate the maturity ogive of females are in reasonable agreement in most cases. The condition of the reproductive tract and ovaries has been commonly recorded to determine maturity of female chondrichthyans (Jones and Geen 1977*b*; Hanchet 1988; Watson and Smale 1998) though Walker (2005) proposed measuring the diameter of the largest follicle (LFD) as an objective criterion of maturity condition least prone to observer bias. To determine the onset of maturity of *G. galeus*, he classed females as having reached the onset of maturity if LFD was >3 mm. In the present study, the smallest value of L_{50} was obtained using this criterion. For *S. megalops*, follicles <15 mm diameter were white, whereas follicles >15 mm were yellow, indicating that vitellogenesis began at about this size. Furthermore, the ogive and the value of L_{50} obtained using the criterion LFD ≥15 mm were in reasonable agreement with most of the other criteria considered, suggesting that vitellogenesis starts when other reproductive structures begin development. Thus, LFD ≥15 mm criterion was adopted for regional comparisons.

Differences in the maturity ogive of females from Lakes Entrance and Robe were found. Spatial differences in size-at-maturity could occur when different age or size classes from different locations are sampled or from length-selective fishing mortality (Walker 2005). In the present study, regional differences in size-at-maturity could be a result of length-selectivity of the 6½-inch gillnet used off Robe, selecting for the largest females and possibly distorting the maturity ogive. Graham (2005) reported similar values of length-at-maturity for females collected from New South Wales. In South Africa, female *S. megalops* also showed a similar length-at-maturity (Watson and Smale 1998) despite these authors collecting a larger range of sizes (the largest female being 782 mm TL). This suggests that females from New South Wales, South Africa and south-eastern Australia would have similar maturity parameters. Taniuchi *et al.* (1993) reported spatial variation in the length-at-maturity of female shortspine spurdogs (*S. mitsukurii*) from four different locations off Japan and attributed it to differences in local environmental conditions. However, they collected a different range of sizes from each location and their samples from each location were obtained from different depths and years. Given that females of squalid species can be segregated by stage of maturity and size (Yano and Tanaka 1988), the geographical differences reported by these authors may be apparent and another example of how using females of different size classes can distort maturity ogives.

The length at which 50% of the female population was pregnant was slightly larger than the length at which 50% was mature. This suggests that once females attain maturity most of them become pregnant soon after first ovulation and parturition there after. These findings further support the hypothesis of a continuous breeding cycle. However, for population assessment models it is important to distinguish the mature condition from pregnant and maternal conditions. For species with reproductive cycles of several years duration, a more critical relationship is the proportion of females in maternal condition.

Only half of the pregnant female population is in maternal condition in any year and contributes to annual recruitment. The size of a population depends on the rates of birth, death and migration. For viviparous chondrichthyans, birth rate can be calculated from the number of females in the population, its fecundity rate and the proportion of females contributing to annual recruitment (Walker 2005). Thus, for chondrichthyan species with one year continuous reproductive cycles, calculation of population size can be performed using maturity or maternity ogives as all mature females contribute to annual recruitment each year. However, for species with a reproductive cycle of more than one year, such as *S. megalops*, population size would differ depending on which ogive is used.

In conclusion, determining maternity ogives from information on the timing of ovulation, period of gestation and parturition frequency is more complex for asynchronous species than, as shown by Walker (2005), for synchronous species. Most squalid species are deepwater asynchronous breeders with reproductive cycles of several years duration. Also, many species are endemic and have restricted distributions. Given these biological and ecological attributes, they are particularly vulnerable to fishing overexploitation. Consequently, their populations require special management and a different approach to determine reproductive parameters for population assessments. Reproductive parameters of *S. megalops* were determined, despite this shark having an asynchronous reproductive cycle. Mature males and females are capable of mating throughout the year and females have a 2-year continuous cycle. Thus, although all females are mature at 600 mm TL, only 50% of them are in maternal condition, contributing to annual recruitment each year. Hence, for chondrichthyan species with reproductive cycles of two, three or more years, if maturity ogives are used in population assessments instead of maternity ogives, models will over-estimate recruitment rates.

Injecting live specimens with OTC (photo by the author).

CHAPTER 6

CHAPTER 6 PREAMBLE

Chapter 6 compares different deterministic growth models fitted to length-at-age data collected from first dorsal fin spines of *S. megalops* and discusses the implications of sampling bias, length-selective fishing mortality, length-selective migration, and bias in age estimation in the selection of the best growth model. At the time this thesis was submitted (January 2006), this chapter was under peer-review with the journal *Marine Ecology Progress Series*, with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide), Terence I. Walker (Primary Industries Research Victoria), and Javier Tovar-Avila (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation, and Javier Tovar-Avila read a sub-sample of 50 spines for evaluation of between-reader variability and between-reader bias and also helped in manuscript evaluation.

CHAPTER 6

COMPARISON OF DETERMINISTIC GROWTH MODELS FITTED TO LENGTH-AT-AGE DATA OF THE PIKED SPURDOG (*SQUALUS MEGALOPS*) IN SOUTH-EASTERN AUSTRALIA

6.1 ABSTRACT

Age and growth estimates of *Squalus megalops* were derived from the first dorsal fin spine of 452 sharks, ranging from 274–622 mm total length. Age bias plots and indices of precision indicated the ageing method was precise and unbiased. Edge analysis of the enameled surface of whole spines and similarities in the banding pattern laid in the enameled surface of spines and in spine sections support the hypothesis of annual band formation. Five growth models were fitted to length-at-age data from which a two-phase von Bertalanffy model produced the best fit. However, model selection cannot be based on quality of statistical fit only. Length-at-age data might not be representative of real growth due to a combination of sampling bias, length-selective fishing mortality and/or bias in age estimation. Regardless of the growth model used, growth rate of females (0.034–0.098 years^{-1}) was very low, making *S. megalops* highly susceptible to fishing overexploitation.

6.2 INTRODUCTION

The most commonly used model to describe growth of elasmobranchs has been the von Bertalanffy function (von Bertalanffy 1938) despite criticism (Knight 1968; Roff 1980). As indicated by Carlson and Baremore (2005), few studies on elasmobranch growth have examined alternative models and most studies simply fitted the von Bertalanffy function to the data without much concern about the quality of the fit or the biological meaning of the results. Hence, a range of growth models should be compared to determine the function that provides the best description of the growth process (Haddon 2001).

Age and growth rates have been mainly studied for commercially important elasmobranchs, such as spiny dogfish (*Squalus acanthias*), blue (*Prionace glauca*), gummy (*Mustelus antarcticus*), and school (*Galeorhinus galeus*) sharks; however, little is known about the age and growth of non-commercial squalid sharks (Squalidae). Although dogfish are amongst the most abundant demersal sharks of temperate seas (Compagno 1984), most of the ageing studies on this family have focused on *S. acanthias* (e.g. Holden and Meadows 1962; Ketchen 1975; Beamish and McFarlane 1985). For this species, maximum age varied widely, with a reported maximum age of up to 80 years (McFarlane and Beamish 1987*a*). For other species of *Squalus*, age and growth rate have been estimated for the shortspine spurdog (*S. mitsukurii*) in the North Pacific Ocean (Wilson and Seki 1994; Taniuchi and Tachikawa 1999) and the longnose spurdog (*S. blainvillei*) in the Mediterranean Sea (Cannizzaro *et al.* 1995). Age and growth rate information of the piked spurdog (*S. megalops*) were estimated for sharks from South African waters (Watson and Smale 1999). Males and females had different growth rates and maximum ages; the largest male was 572 mm total length (TL) and 29 years old whereas the largest female was 782 mm TL and 32 years old.

Squalus megalops is a demersal species that is distributed off southern and eastern Australia, from Carnarvon (Western Australia) to Townsville (Queensland), including Tasmania (Last and Stevens 1994). However, the distribution of this species needs further revision as it has also been reported off the coasts of Brazil (Vooren 1992) and South Africa (Bass *et al.* 1976) and there are unconfirmed reports off Indo China, New Caledonia and New Hebrides (Last and Stevens 1994). This species inhabits the continental shelf and upper continental slope (depths <510 m) in warm temperate and tropical areas (Last and Stevens 1994). *Squalus megalops* has a high natural abundance in southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001) and, although this shark is one of the major by-catch shark species in the area (Walker *et al.* 2005), its abundance has remained stable off New South Wales (southeast coast of Australia) since it was first surveyed in 1976–77 (Graham *et al.* 2001). At present, the lack of biological data hampers a classification of the conservation status of this species (Castro *et al.* 1999).

Until the present study, the age and growth rate of the Australian population(s) of *S. megalops* remained unknown. Given that age and growth parameters can vary among regions (e.g. Parsons 1993; Taniuchi and Tachikawa 1999) due to differences in environmental conditions (Francis 1988), age and growth information for *S. megalops* from Australian waters is required for population assessment of this species. Therefore, the purpose of the present study was to estimate the age of *S. megalops* captured in south-eastern Australia and compare different growth models to determine which model provides the best fit to the growth data.

6.3 MATERIALS AND METHODS

Sampling

Specimens of *S. megalops* were obtained from the by-catch of demersal trawl and shark gillnet vessels operating in the Southern and Eastern Scalefish and Shark Fishery in waters off south-eastern Australia. Samples were collected monthly between October 2002 and April 2004, with the exception of the August–September period, when *S. megalops* seemed to move off the fishing grounds and weather conditions restricted sampling. The specimens were sexed and measured (total length, TL, ±1 mm).

Spine and vertebrae preparation

Two portions of the spinal column (post cranial and thoracic vertebrae) and the first and second dorsal fin spines (DFS) were removed and stored frozen for age estimation. Spines were extracted by cutting horizontally just above the vertebral column to ensure that the spine base and stem were intact (Beamish and McFarlane 1985). Soft tissue was removed by immersing vertebrae and spines in hot water (55º C) for 0.5–1 minutes and trimming off the skin, flesh, and cartilage with a scalpel. Cleaned spines were then rubbed with a cloth to highlight the bands on the enameled surface. For vertebrae, the remaining tissue was removed by soaking them in 4% sodium hypochlorite solution. Soaking time varied with the size of the vertebrae between 10 and 20 minutes to avoid ‘over-bleaching’. Spines were air-dried and stored in paper envelopes, whereas vertebrae were stored in a freezer. Different measurements were recorded on the spines using electronic calipers to the nearest 0.01 mm following Ketchen (1975) (Fig. 6.1a).

Age estimation

A pilot study was carried out to determine which of the two structures—vertebrae or spines—was more appropriate for age estimation. Whole and cross-sectioned vertebrae (~300 µm) were used. The sections were obtained by embedding vertebrae in epoxy resin and sectioning with a Gemmasta^{TM} lapidary saw with a diamond-impregnated blade. Sections were cleaned using ethanol and water, air-dried and mounted on glass slides using epoxy resin. Sections were examined under transmitted light using a Leica IM 4.0 digital image system on a Leica DMLB compound microscope. Vertebrae of *S. megalops* are poorly calcified, with very fragile *intermedialia*, so, from sectioned vertebrae, only the *corpus calcareum* was used. No clear banding pattern was observed on whole or sections of vertebrae; hence, different stains (alizarin red S, silver nitrate, cobalt nitrate, ninhydrin) were used to enhance readability. However, no improvement in readability was observed, so only spines were used for further age estimation.

Bands laid on the external enameled surface of spines were counted using a dissecting microscope (10×) and reflected light (Fig. 6.1b). A band was defined as an alternating opaque and translucent zone or ridge or both, present on the enameled surface (McFarlane and Beamish 1987*a*; Watson and Smale 1999). Solid bands on the leading edge of the spine that were split on the trailing edge were counted as a single band (Watson and Smale 1999). Bands visible only as a dark mark on the leading edge but similar in thickness to neighbouring bands that did continue to the trailing edge were also counted as single bands (Watson and Smale 1999). A subjective readability score was assigned to each spine following Officer *et al.* (1996) (Table 6.1). After three readings, spines having a readability score of 4 (ambiguous band counts) or 5 (no band counts possible) were not used for further analysis (<9% of readings).

The spines of 10 full-term embryos were examined to determine pre-birth bands. No bands were observed and it was assumed that the first band was laid just prior to or after birth (birthmark) (e.g. Holden and Meadows 1962; Moulton *et al.* 1992). Thus, the total number of bands was calculated as the total number of bands counted minus one.

To determine whether the first or the second DFS was more appropriate for age estimation, a random sub-sample of first and second DFS from 61 animals was read two times separated by a minimum of one month without knowledge of length of animals. The readability scores of the first and second DFS were compared. The coefficient of variation (CV; Chang 1982; Campana *et al.* 1995) and the index of average percentage error (APE; Beamish and Fournier 1981) were calculated to evaluate precision between readings (first vs second reading) and between methods (first vs second DFS). Age bias plots (Campana *et al.* 1995) were used to detect count differences between the two methods. The first DFS showed better readability scores and higher precision between readings (see “Results”), hence, this spine was used for age estimation.

Table 6.1. Readability scores assigned to readings of spines (modified from Officer *et al.* 1996).

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

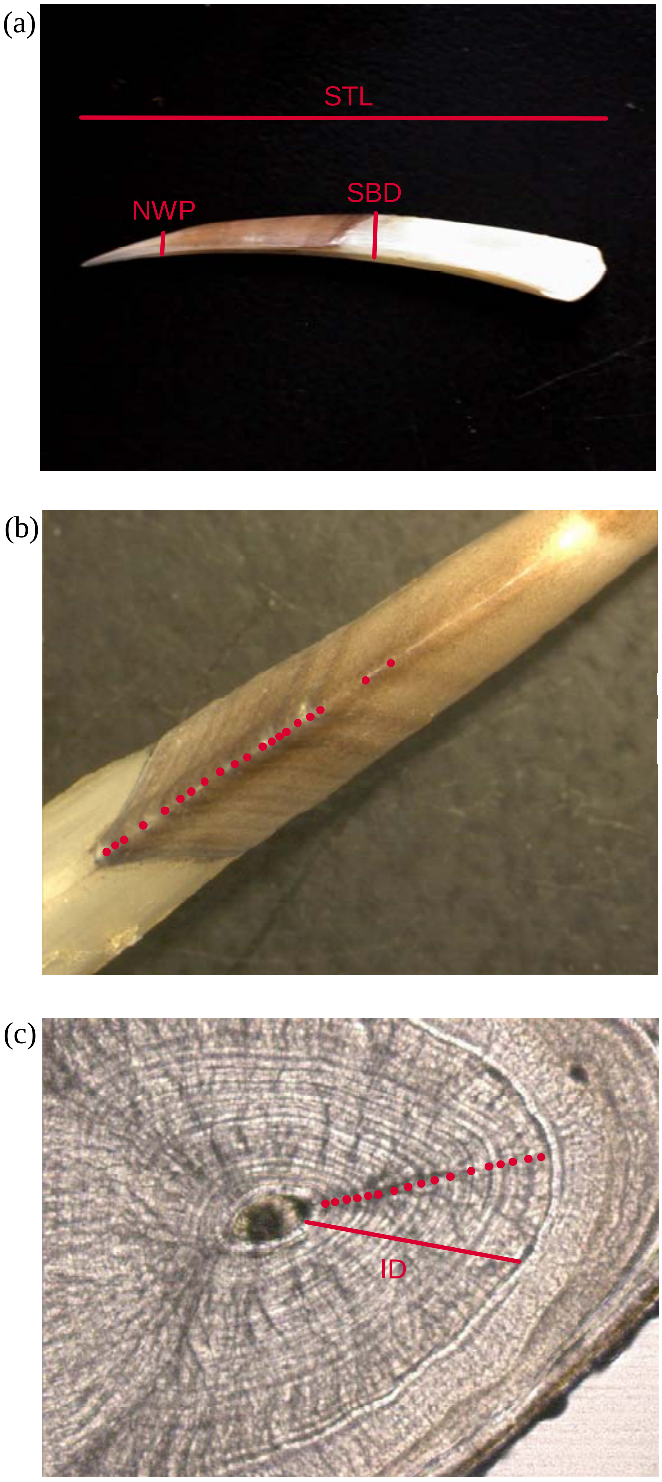

Figure 6.1. Dorsal fin spine of *Squalus megalops*. (a) Lateral view of worn second DFS showing the different measurements recorded following Ketchen (1975): spine total length (STL), spine base diameter (SBD) and no wear point (NWP). (b) Anterior view of first DFS (6×) showing 20 bands on the enameled surface. (c) Section of first DFS (100×) showing 17 bands on the inner dentine (ID) layer.

All first DFS were read three times by a single reader (first reader) separated by a minimum of one month between readings. A second reader read a random sub-sample of 50 spines for evaluation of between-reader variability and between-reader bias. To evaluate within- and between-reader precision, the CV and the APE index were calculated. Age bias plots were used to detect systematic count differences between the first and second reader. To accept a count for age estimation, the counts of at least two of three readings had to be identical. If counts from two of the three readings differed, spines were recounted a fourth time and the same procedure was applied. If the difference persisted, the spine was discarded (<9% of readings).

For worn spines, Ketchen's (1975) correction method was adopted to ensure that bands were not missing. The relationship between band counts and spine base diameter (SBD) was estimated for unworn spines from males (n = 45) and females (n = 46). For worn spines, the diameter of the spine at the most distal point of no wear (NWP) was then measured (Fig. 6.1a). From the band counts–SBD relationship, the number of bands corresponding to the diameter at the NWP of worn spines was calculated and added to the original count of bands (Ketchen 1975).

Verification and validation

A random sub-sample of spines from 10 female and 10 male sharks was sent to two international experts who agreed that the spines were appropriate to estimate the age of *S. megalops*. The annual periodicity of band deposition on whole spines was investigated by analysing the edge of their enameled surface (Holden and Meadows 1962; Nammack *et al.* 1985; Taniuchi and Tachikawa 1999). The edge of spines collected throughout the year was classified as dark, light or wide light following Holden and Meadows (1962) (Table 6.2).

For 89 sharks, counts on spine sections were compared with counts on the external enameled surface. Serial sections (~300 µm) were taken from the tip of each first DFS to determine the optimal position of sectioning. The same method for sectioning vertebrae was used to obtain spine sections. The inner dentine layer showed the clearest banding pattern and was hence used for counting (Fig 6.1c) (Maisey 1979; Clarke *et al.* 2002*a*). Maximum count of bands in the inner layer was found at the apex of the pulp cavity, representing the optimal position of sectioning. The sections were examined under

Table 6.2. Definition of edge type of whole spines for the edge analysis following Holden and Meadows (1962).

Edge type	Description
Dark	Dark band observed at the edge of the enamel.
Light	Dark band just formed and a light band of a width less than half the width of the light band between the last two dark bands observed at the edge of the enamel.
Wide light	Light band observed at the edge of the enamel equal to or more than half the width of the light band between the last two dark bands.

transmitted light using a Leica IM 4.0 digital image system on a Leica DMLB compound microscope. Within the internal dentine layer, a band was defined as a pair of dark (opaque) and light (translucent) concentric rings (Irvine 2004). Counting started at the pulp cavity (centre) and continued outwards to the junction between inner and outer dentine layers (Irvine 2004). Age bias plots (Campana *et al.* 1995) were used to detect count differences between external (enameled surface) and internal (sections) counts.

Validation of the periodicity of band deposition was attempted by injecting captive *S. megalops* with oxytetracycline (OTC). Twelve male and 12 female *S. megalops* of different sizes were measured, implanted with roto-tags for individual identification, injected with OTC at 25 mg per kg body mass (McFarlane and Beamish 1987*b*), and kept in a 27,000-L outdoor aquarium. Captive sharks were subjected to natural variation in water temperature and photoperiod and they were fed on a diet of squid and fish twice a week.

Growth estimation

Based on the assumption that external bands were formed annually, for each sex, several alternative growth models were fitted to the length-at-age data: the traditional von Bertalanffy growth model (VBGM; von Bertalanffy 1938), a two-parameter modified form of VBGM (2VBGM; Fabens 1965), a two-phase von Bertalanffy growth model (TPVBGM; Soriano *et al.* 1992), the Gompertz growth model (Ricker 1975), and a two-parameter modified form of the Gompertz growth model (2Gompertz; Mollet *et al.* 2002) (Table 6.3). Model parameters were estimated by least-squares non-linear regression. Akaike's Information Criterion (AIC) was used to determine the model that best fitted the length-at-age data (Buckland *et al.* 1997; Burnham and Anderson 2002).

$$\mathrm{AIC} = \mathrm{n} \ln(\hat{\sigma}^2) + 2\mathrm{p}$$

where n = sample size;

$\hat{\sigma} = \frac{\text{Residual sum of squares}}{\text{n}}$; and

p = number of parameters.

Comparisons among the AIC values of the different growth models enabled the best model for each sex to be selected, i.e. those models with the lowest AIC values. For model comparisons, the delta AIC (ΔAIC) and Akaike weights (w_i) were calculated. The ΔAIC is a measure of each model relative to the best model and is calculated as:

$$\Delta\text{AIC} = \text{AIC}_i - \text{minAIC}$$

where AIC_i = AIC value of model i; and

minAIC = AIC value of the best model.

Akaike weights represent the probability of choosing the correct model from the set of candidate models and are calculated as:

$$w_i = \frac{\exp(-\Delta\text{AIC}/2)}{\sum_{r=1}^{R} \exp(-\Delta\text{AIC}/2)}$$

where R = number of candidate models.

Once the best model was determined, the growth curves of males and females were compared by a Chi-square test on likelihood ratios (Kimura 1980; Cerrato 1990).

Table 6.3. Summary of growth models fitted to length-at-age data.

Model	Equation
VBGM	$L_t = L_\infty(1 - e^{-k\,(t - t_\circ)})$
2VBGM	$L_t = L_\infty(1 - be^{-k\,t})$, $b = (L_\infty - L_0)/ L_\infty$
TPVBGM	$L_t = L_\infty(1 - e^{-kA t\;(t - t_\circ)})$, $A_t = 1 - h/((t - t_h)^2 + 1)$
Gompertz	$L_t = L_\infty\, e^{-e(-k(t - t_\circ))}$
2Gompertz	$L_t = L_0(e^{G(1-e(-k\,t))})$, $G = \ln(L_\infty / L_0)$
Meaning of terms	L_t = mean length at time t
	L_∞ = theoretical asymptotic length
	k = growth coefficient
	t_0 = theoretical age at zero length
	h = magnitude of the maximum differences between VBGM and TPVBGM
	t_h = age at which transition between the two growth phases occurs
	L_0 = mean length at birth (214 mm for males and females)

6.4 RESULTS

Age estimation

The first dorsal fin spines (DFS) provided better readability scores and more precise readings than the second DFS. Most first DFS had a readability score of 2 (51.5%) or 3 (42.4%), whereas most of the second DFS had a readability score of 3 (62.1%) or more (Fig. 6.2a). Differences between the readings for first and second DFS varied by up to five bands, but differences were mostly ±1 count (Fig. 6.2b). Mean coefficient of variation (CV) and index of average percentage error (APE) among readings were 7.53% and 5.15%, respectively, for the first DFS and 9.03% and 6.39%, respectively, for the second DFS, indicating more precise counts were obtained when the first DFS was used. Mean CV and APE between the first and second DFS were 14.04% and 9.93%, respectively. Agreement between first and second DFS decreased with the number of bands counted, indicating the use of the second DFS systematically underestimates the number of bands (Fig. 6.2c). The first DFS was used for age estimation because it showed a clearer readability pattern, higher precision between readings, and an overall higher number of bands.

The relationship between the first DFS length and total length was linear (DFS length = 0.086 TL – 2.739; $r^2 = 0.9$) and there was no significant difference between males and females (t-test, $t = 1.77$, d.f. = 98, $P > 0.05$ for comparison of slopes, and $t = 1.07$, d.f. = 98, $P > 0.05$ for comparison of elevations). The increase in DFS length with total length shows that spines grow throughout life, indicating this structure is useful for age estimation.

A total of 493 first DFS was examined of which 41 (8.3%) were rejected because they did not conform to the selection criteria (i.e. readability score ≤3 and identical counts from at least two of three or four readings). Band counts from 163 males (274–470 mm TL) and 289 females (287–622 mm TL) were used for age estimation. Within-reader precision among readings was high; mean CV and APE were 6.99% and 5.25%, respectively. Overall, for each band class CV was low, showing the lowest values for mid-band classes (14–23 band class) (Fig. 6.3). A similar pattern was observed for APE. Mean CV and APE between readers were 11.35% and 8.03%, respectively. There were no appreciable systematic differences between readers (Fig. 6.4). Worn spines (4.9% males and 15.9% females) were corrected for missing bands using the equations derived from the

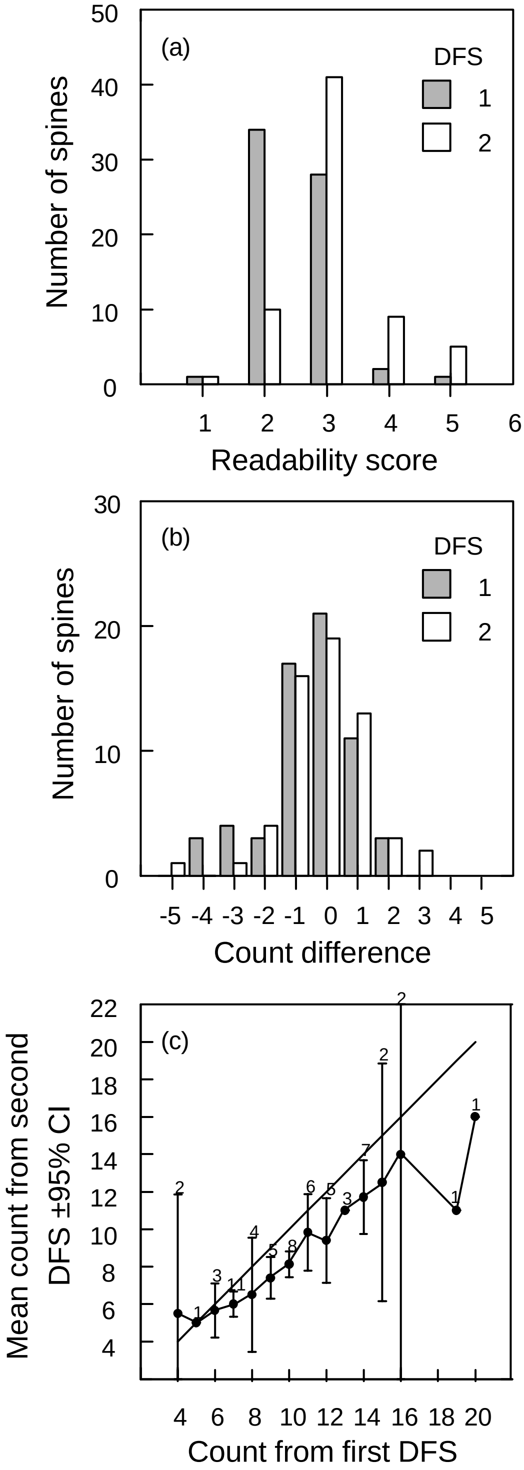

Figure 6.2. Comparison between first and second dorsal fin spines (DFS) for 61 sharks. (a) Distribution of readability scores assigned to readings of each spine. (b) Distribution of differences between two readings on first and second dorsal fin spines. (c) Age bias plots. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

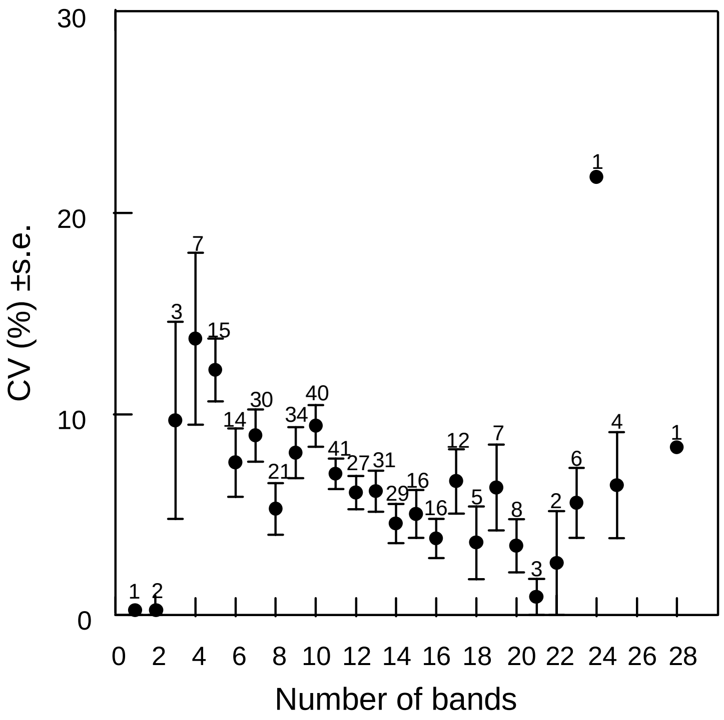

Figure 6.3. Mean values of coefficient of variation (CV) for each band class read by the principal reader. Sample sizes are given for each corresponding band class.

relationship between the number of bands and SBD of unworn spines (Counts $_{male}$ = 0.394 SBD $^{3.064}$; r^2 = 0.83; Counts $_{female}$ = 0.965 SBD $^{2.083}$; r^2 = 0.94).

Verification and validation

The nature of the enamel edge varied with month (Fig. 6.5). At no time of the year were the spines entirely of one edge type. Most sharks collected between May and July (autumn–winter) had dark edges, whereas the highest percentage of light edges occurred in sharks collected between October and December (spring–early summer). For spines with wide light edges, the highest percentage was found in sharks collected between January and April (summer–autumn). This annual edge pattern suggests that dark rings form during the cold period of the year. In addition, there was good agreement between counts on spine sections and counts on the external enameled surface (Fig. 6.4).

After a period of five months, captive sharks died due to a sudden increase in water temperature (from 12º C in late winter to 22º C in early summer). Also, the sharks showed signs of stress when approached, bumping the sides of the tank. Hence, validation of annual band deposition on spines of captive *S. megalops* was not achieved. Unlike other shallow-water sharks previously kept in similar conditions, *S. megalops* is a mid-water species (depths <510 m) which seems to be more sensitive to changes in water temperature than its shallow-water counterparts.

Growth estimation

Males ranged 1–15 years in age, whereas females reached a maximum age of 28 years. Most males were 11–12 years whereas most females were 13–14 (Fig. 6.6). The value of growth parameters of *S. megalops* were estimated separately from five models fitted to the length-at-age data (Table 6.4). Growth models fitted the data well, with females showing higher values of coefficient of determination (r^2 ≥0.88) than males (r^2 ≥0.72).

For males, the TPVBGM was the best of the five growth models fitted with an Akaike weight (w_i) of 0.54 (Table 6.4). However, VBGM and Gompertz growth model followed rather closely (w_i = 0.24 and 0.19, respectively), revealing a certain degree of uncertainty regarding the best model for fitting length-at-age data of males. Estimates of asymptotic length (L_∞) varied among models. Traditional VBGM and TPVBGM predicted a slightly

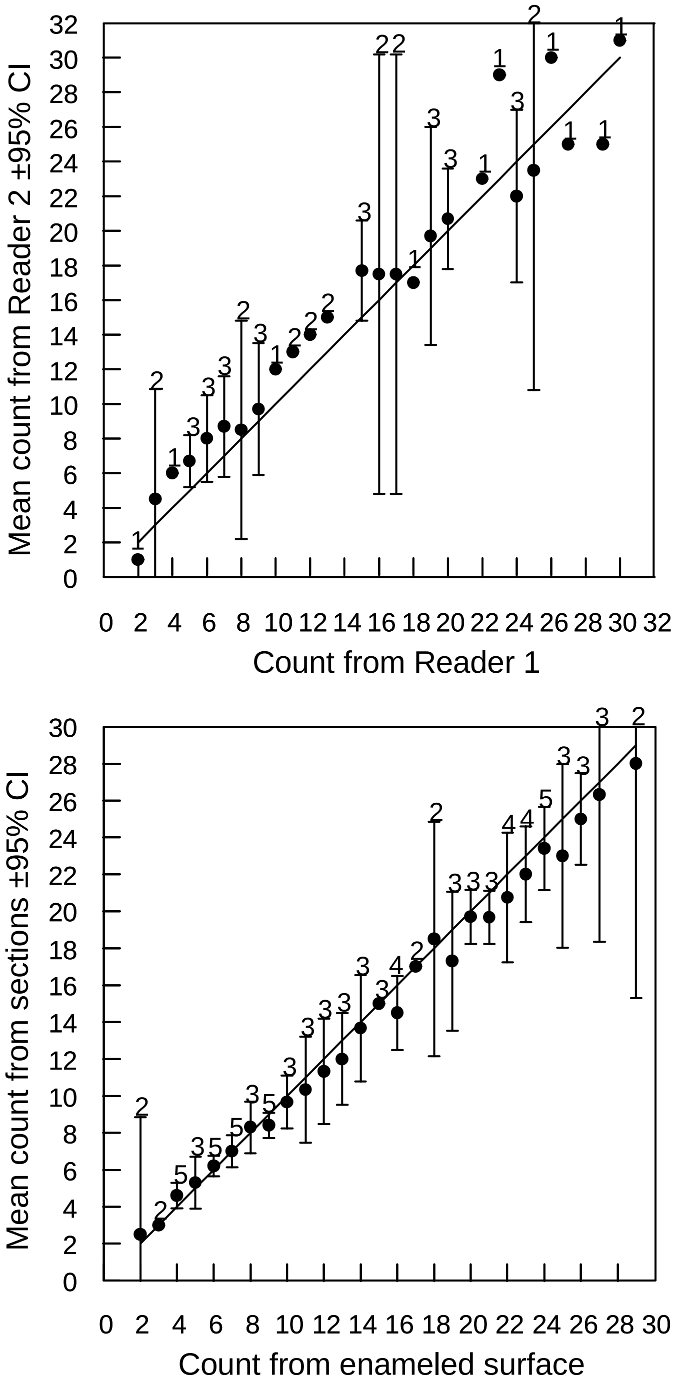

Figure 6.4. Age bias plot for the comparison of band counts between readers and band counts on spine sections and on the external enameled surface. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

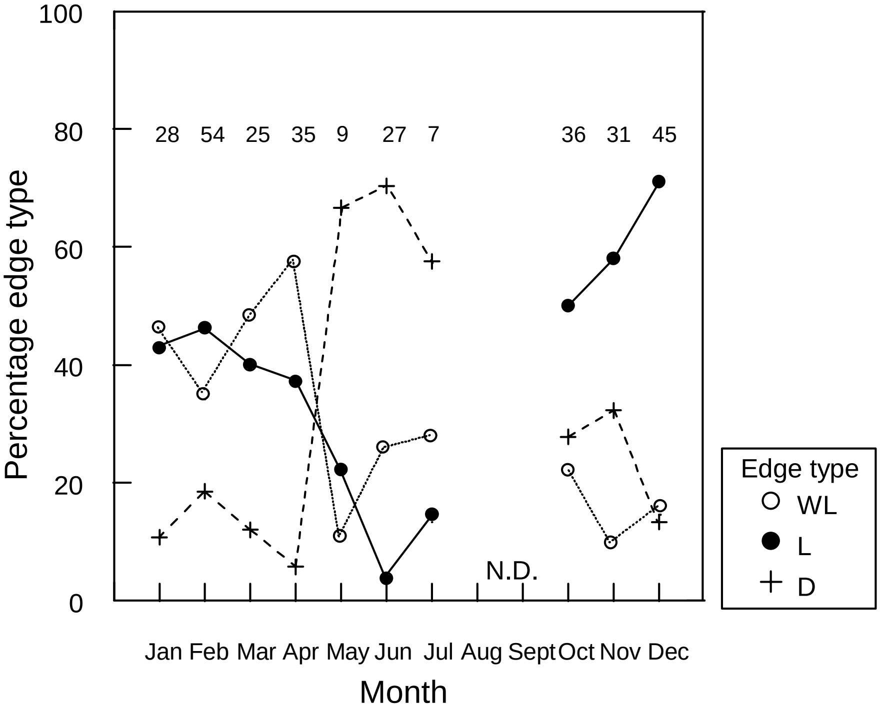

Figure 6.5. Monthly variation in the type of enamel edge; wide light (WL), light (L) and dark (D). Sample sizes are given for each corresponding month; N.D.: no data.

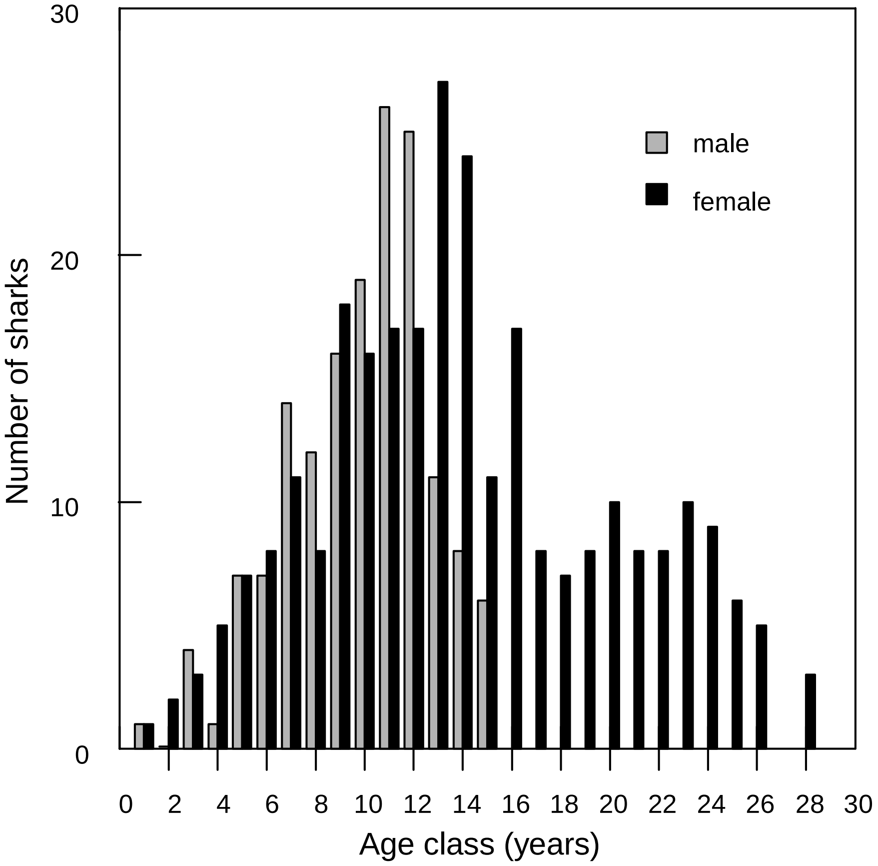

Figure 6.6. Age distribution for male and female *S. megalops*.

larger value of L_∞ (L_∞ = 455 mm TL) than Gompertz growth model, 2VBGM, and 2Gompertz growth model (L_∞ = 449, 440, and 433 mm TL, respectively). Estimates of growth coefficients (k) also varied among models, with 2Gompertz growth model and 2VBGM producing the highest values (k = 0.252 and 0.198 years^{-1}, respectively).

For females, the best fitting model was the TPVBGM as the probability of choosing this model as correct (w_i) was 0.95 (Table 6.4); other models showed lower values of w_i indicating they do not fit the length-at-age data as well. There was high variability in the estimates of L_∞ among models. The 2Gompertz growth model, 2VBGM, and Gompertz growth model predicted a lower value of L_∞ (L_∞ = 632, 699, and 717 mm TL, respectively) than the predicted value of TPVBGM (L_∞ = 756 mm TL) or VBGM (L_∞ = 829 mm TL). Estimates of k also varied widely among models, with 2Gompertz and traditional Gompertz growth models producing the highest values (k = 0.098 and 0.063 years^{-1}, respectively). Traditional VBGM produced the lowest growth coefficient value (k = 0.034 years^{-1}).

Given that the TPVBGM was the best fitting model, this function was used to draw the growth curves of males and females (Fig. 6.7). Likelihood ratio tests indicated significant differences between the growth curves (P <0.001) for the two sexes. Males (k = 0.158 years^{-1}) grew faster than females (k = 0.042 years^{-1}) (Table 6.4). Predicted length-at-age of males was initially higher but after they attained 8 years growth of males and females was similar up to ~10 years when transition between growth phases occurred (Fig. 6.7; Table 6.4). After age 10 growth of males slowed down whereas growth of females continued with length increasing steadily throughout their lifespan.

Table 6.4. Growth estimates (with 95% confidence intervals) and model selection criterion for male and female *S. megalops*. Akaike's information criterion (AIC); AIC differences between models (ΔAIC); Akaike weights (w_i); and sample size (n). Refer to Table 6.3 for meaning of parameters.

Model	Parameter	Males (n = 157)					Females (n = 274)				
		Estimate	r^2	AIC	ΔAIC	w_i	Estimate	r^2	AIC	ΔAIC	w_i
VBGM	L_∞ (mm)	455 (21)	0.74	851.85	1.68	0.24	829 (126)	0.89	1774.94	9.50	0.01
	k (years^{-1})	0.144 (0.05)					0.034 (0.01)				
	t_0 (years)	–5.72 (2.50)					–10.83 (2.82)				
2VBGM	L_∞ (mm)	440 (9)	0.73	856.19	6.02	0.03	699 (33)	0.88	1791.11	25.68	<0.01
	k (years^{-1})	0.198 (0.02)					0.056 (0.01)				
TPVBGM	L_∞ (mm)	455 (19)	0.75	850.17	0	0.54	756 (88)	0.89	1765.43	0	0.95
	k (years^{-1})	0.158 (0.05)					0.042 (0.01)				
	t_0 (years)	–4.86 (2.10)					–9.77 (2.60)				
	h	0.094 (0.08)					0.087 (0.05)				
	t_h (years)	10.5 (0.60)					10.2 (0.60)				
Gompertz	L_∞ (mm)	449 (17)	0.74	852.27	2.10	0.19	717 (59)	0.89	1771.92	6.49	0.04
	k (years^{-1})	0.172 (0.05)					0.063 (0.01)				
	t_0 (years)	–3.54 (1.68)					0.026 (0.81)				
2Gompertz	L_∞ (mm)	433 (7)	0.72	861.11	10.94	<0.01	632 (18)	0.88	1804.37	38.90	<0.01
	k (years^{-1})	0.252 (0.02)					0.098 (0.01)				

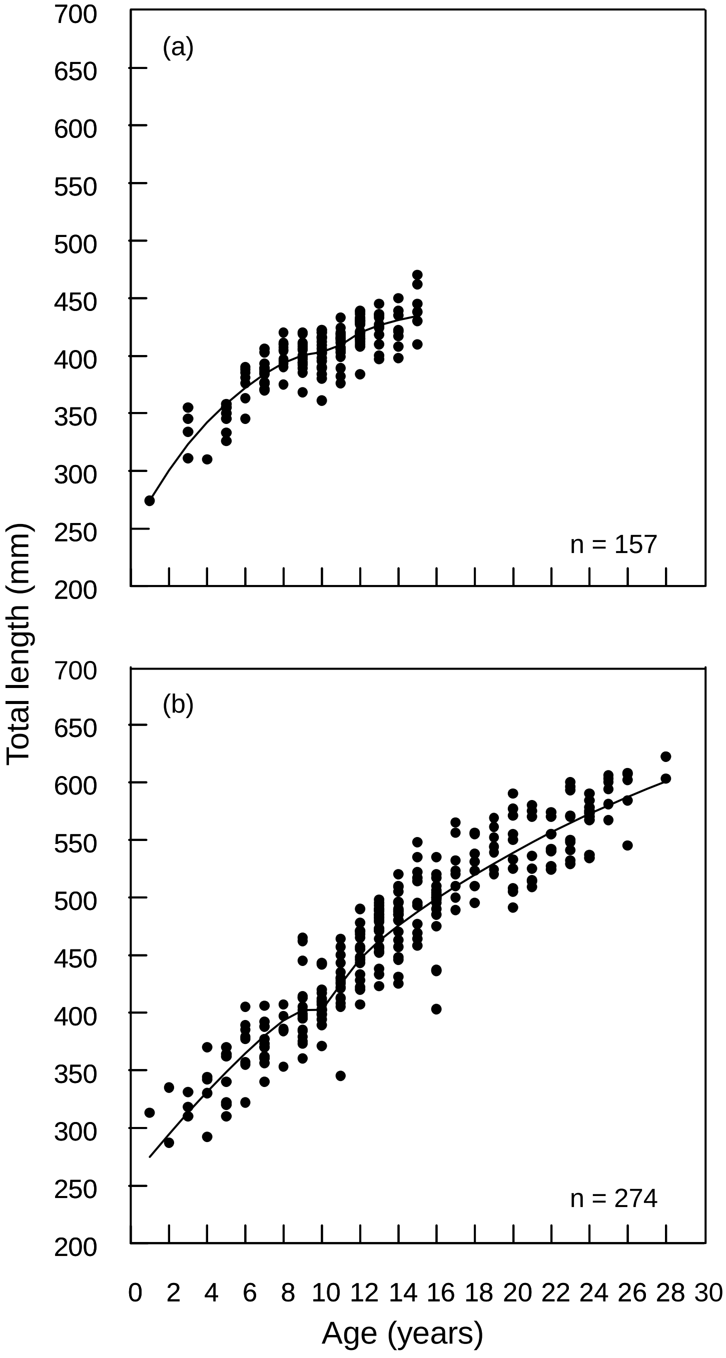

Figure 6.7. Two-phase von Bertalanffy growth model fitted to length-at-age data derived from counts on the first dorsal fin spine of (a) male and (b) female S. *megalops*. Estimates of model parameters are given in Table 6.4.

6.5 DISCUSSION

The first DFS of *S. megalops* showed clearer readability, higher precision between readings and an overall higher number of bands than the second DFS. Most ageing studies on squalid sharks use whole second DFS because it is larger and the tip of the first DFS tends to be worn down (Cailliet and Goldman 2004). Although some studies have used the first DFS as a check (e.g. Nammack *et al.* 1985), few have compared the suitability of the first and second DFS for ageing (but see Holden and Meadows 1962; Irvine 2004). Given the structure of the first and second DFS is similar (e.g. Holden and Meadows 1962; Clarke *et al.* 2002*a*), preference for first or second DFS for age estimation should be a question of readability. Sections of the first DFS of the birdbeak dogfish (*Deania calcea*) (Clarke *et al.* 2002*a*) and the gulper shark (*Centrophorus squamosus*) (Clarke *et al.* 2002*b*) provided better readability than sections from the second DFS. For *S. megalops* off South Africa, Watson and Smale (1999) only used the second DFS, rejecting, after several readings, 12% of the spines for age estimation whereas in the present study only 8% of the spines used were rejected, probably reflecting the better readability of first DFS. Therefore, for *S. megalops*, the clearer pattern of bands observed in the first DFS made this structure easier to read and hence more suitable for age analyses than the second DFS.

The low values of the CV and the APE index for the within- and between-reader analyses suggest high precision for the age assessment of *S. megalops*. These two indices assume that variability among observations of individual fish can be averaged over all age classes, obscuring differences in precision (Hoenig *et al.* 1995). However, when calculations were made for each age class (within-reader only), between-age-class variability was low. A trend for an increase in within-reader precision was observed for the mid-range age classes, suggesting these classes are easier to read. The age bias plot indicated no bias in the age estimation of Reader 1 (principal reader). Few studies on the age and growth of squalid sharks provide estimates of precision and bias, despite their importance for any ageing studies (Campana 2001). However, when such estimates are produced (Holden and Meadows 1962; Ketchen 1975; Nammack *et al.* 1985; Clarke *et al.* 2002*a, b*; Irvine 2004), most studies report high reproducibility of age estimates, further supporting the use of spines as a precise approach for ageing squalid sharks.

The analysis of the enamel edge of whole spines supports the hypothesis of annual band formation in *S. megalops*. The peak in dark bands observed during late autumn–winter

(May–July), followed by the peak in light bands during spring–early summer (October–December), and by the peak in wide light bands during early autumn (March–April) is the expected pattern for annual band deposition. A similar pattern is reported for *S. acanthias* off north and west Scotland (Holden and Meadows 1962) and off north-eastern USA (Nammack *et al.* 1985). For *S. acanthias*, the timing of light and dark band formation on the enamel edge of spines was validated using mark-recapture oxytetracycline (OTC)-tagged sharks (Tucker 1985).

Band counts on the inner dentine layer (spine sections) of first DFS of *S. megalops* were in good agreement with counts on the enameled surface, verifying the age estimates obtained from counts on the enameled surface of spines. Counts of bands on the inner dentine have been used for age estimation of other squalid sharks (e.g. Clarke *et al.* 2002*a*, *b*; Irvine 2004). For *S. acanthias*, comparisons of internal (sections) and external (enameled surface) counts agreed within ±2 bands (Holden and Meadows 1962). However, for the deepwater velvet dogfish (*Centroscymnus crepidater*), Portuguese dogfish (*C. coelolepis*), and New Zealand lantern shark (*Etmopterus baxteri*), the number of external bands exceeded the number of internal bands in sharks older than 3–5 years (Irvine 2004). As for *S. acanthias*, sections of first DFS of *S. megalops* confirmed the use of the enameled surface of whole spines as a method of age estimation as both methods yielded similar counts.

Several authors (e.g. Beamish and McFarlane 1983; Cailliet 1990; Campana 2001) have stressed the need for validation of the temporal periodicity of band deposition and of the absolute age for accurate age estimation. Captive rearing of OTC-tagged *S. megalops* was conducted as an attempt to validate the periodicity of band deposition. However, as with a similar study in South Africa (Watson and Smale 1999), holding the sharks in captivity was of limited success. More rigorous methods of age validation, such as the bomb radiocarbon method (Druffel and Linick 1978), is not applicable for *S. megalops* as samples of sharks born during the period of ^{14}C increase (1955–1970) are not available. Annual deposition of bands on spines of squalid sharks has been validated for *S. acanthias* and this was on both sections and the enameled surface of whole spines (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987*a*). Although it does not necessarily follow that these bands are annual in other squalid sharks (Clarke *et al.* 2002*b*), for *S. megalops,* the most parsimonious interpretation of available evidence (edge analysis and comparisons of internal and external bands) points to annual formation of bands.

However, further research is needed to confirm the annual pattern of band deposition and absolute age of *S. megalops*. A pilot tagging study showed promising results (9 sharks recaptured out of 617 tagged; Brown *et al.* 2000); hence, a large-scale release-recapture program of known age and marked sharks or OTC-tagged sharks (Beamish and McFarlane 1985; Campana 2001) would provide information on periodicity of band deposition.

Growth model selection is not a straightforward process. Based on the goodness-of-fit criterion used (AIC), the best model for both sexes was the TPVBGM. The use of a TPVBM allows dividing growth into two phases, such as changes in habitat (e.g. from coastal to off-shore waters), feeding habits (e.g. from a planktivorous to a piscivorous diet) or energy allocation (e.g. from energy allocated to growth, as in juveniles, to energy allocated to growth and reproduction, as in adults). For male *S. megalops* the change in growth rate (~10 years) corresponded with size at maturity whereas for females, the change (~10 years) was slightly before the size females start to mature (Braccini *et al.* 2006; Chapter 5). However, model selection is a matter beyond the quality of statistical fit (Haddon 2001). Proper description of the growth process also requires biological realism.

In addition to determining the best goodness-of-fit, the quality of the data used in the fitting process and the shape of the growth curve are of similar importance in the description of the growth process, particularly when samples are collected from commercial fishing operations. When growth models are fitted to these type of data the resulting parameters may be different from those obtained from a more representative sample (Haddon 2001). Most studies on age and growth of elasmobranchs obtain samples from commercial fisheries and assume that data are unbiased. However, the length–age scattergram and the growth curve of *S. megalops*, particularly females (see Fig. 6.7 present study; Watson and Smale 1999), and other shark species (e.g. Moulton *et al.* 1992; Cannizzaro *et al.* 1995) does not asymptote suggesting that either samples are not representative of the entire population or those species do not exhibit an asymptotic maximum length and hence asymptotic models are not adequate to describe growth. Linear growth for long-lived species, such as sharks, has only been reported for juveniles (e.g. Simpfendorfer 2000) or when sampling is not representative of all size classes (e.g. Wintner 2000). Hence, it is more likely that the observed scattergram and the subsequent growth curve derived are a result of unrepresentative data due to a combination of several factors. Length-selective sampling bias and length-selective fishing mortality of gillnets can cause distortions to growth curves (Moulton *et al.* 1992; Walker *et al.* 1998). In the present study, most of the samples were collected from demersal otter trawl and Danish seine vessels. Although the selectivity of the mesh of the trawl-codend is not adequately understood, length-selective sampling bias and fishing mortality might contribute to explaining the shape of the growth curve and the scatter of data points for *S. megalops*. Parturition is likely to occur outside the fishing grounds (Graham 2005). Larger neonates and juveniles are thought to move to the fishing areas to feed on trawl discards or prey exposed by trawl operations disturbing sediments, as *S. megalops* is an opportunistic predator that consumes a wide range of prey items (Braccini *et al.* 2005; Chapter 4). Hence, the larger neonates and juveniles would then become available to sampling by the trawling gear and thereby create a bias in the size distribution of neonates and juveniles sampled due to a higher probability of collecting large fast-growing individuals rather than small slow-growing individuals. For intermediate-aged sharks, the large fast-growing individuals of an age class may have been selectively removed from the population by fishing (Walker *et al.* 1998; Haddon 2001). This length-selective removal of the largest sharks of the available age classes by fishing has a biasing effect when sampling these age classes. Alternatively, due to the strong size segregation exhibited by *S. megalops* (Graham 2005; Chapter 2), if certain size class or size classes, for example the largest females of each age class, occurred outside the trawling areas only the smallest individuals would be available for sampling and the size-at-age frequency distribution of the age classes would be biased. Finally, age underestimation of older fish due to difficulties in band counting and/or poor representation of older fish in the sample due to their low natural abundance would also explain the lack of an asymptote in the growth curve (McFarlane and Beamish 1987*a*; Watson and Smale 1999). Hence, even when growth of *S. megalops* follows a VBGM or other growth model, the collected length-at-age data may be variously affected by sampling bias, length-selective fishing mortality, length-selective migration, and bias in age estimation.

Precision estimates, the relationship between spine total length and TL, edge analysis, and agreement between counts on the inner dentine layer and the enameled surface support the use of the first DFS for the age estimation of *S. megalops*. Based on goodness-of-fit criterion, the best growth model for males and females was the TPVBGM. However, model selection cannot be based on quality of statistical fit only and given that length-at-age data might not be representative of real growth, results should be interpreted with caution. Regardless of the model used, the growth rate of *S. megalops*, particularly of females, is very low, even within the range of growth rates reported for shark species (0.03–1.337 years^{-1}; Cailliet and Goldman 2004). The reproductive output of this species is also low as litter size is at most four and the reproductive cycle is almost two years (Braccini *et al.* 2006, Chapter 5). These characteristics indicate *S. megalops* has low biological productivity and therefore higher risk to the effects of fishing than species with higher biological productivity.

Lakes Entrance, some of the fishing vessels that operate in the mighty waters of the Southern Ocean (photo by the author).

CHAPTER 7

CHAPTER 7 PREAMBLE

In Chapter 7 I applied a hierarchical framework for the assessment of the effects of fishing on *Squalus megalops* by integrating qualitative and quantitative modelling tools. This is the first study to use expert judgement, the precautionary approach and stochastic matrix modelling to determine fishing effects on a chondrichthyan species. At the time this thesis was submitted (January 2006), this chapter was under peer-review with the *Canadian Journal of Fisheries and Aquatic Sciences*, with myself as senior author, and Bronwyn M. Gillanders (The University of Adelaide) and Terence I. Walker (Primary Industries Research Victoria) as co-authors.

I was responsible for sampling, analysing and interpreting the data, and for writing the manuscript. Bronwyn M. Gillanders and Terence I. Walker supervised development of research, data interpretation and manuscript evaluation.

CHAPTER 7

HIERARCHICAL APPROACH TO THE ASSESSMENT OF FISHING EFFECTS ON NON-TARGET CHONDRICHTHYANS: CASE STUDY OF *SQUALUS MEGALOPS* IN SOUTH-EASTERN AUSTRALIA

7.1 ABSTRACT

A three-levelled hierarchical risk assessment approach was trialed using piked spurdog (*Squalus megalops*) to evaluate the suitability of the approach for chondrichthyan species. At level 1, a qualitative assessment indicated that the only fishing-related activity to have moderate or high impact on *S. megalops* was ‘capture fishing’ by otter trawl, Danish seine, gillnet and automatic longline methods. At level 2, a semi-quantitative assessment ranked *S. megalops* at risk because of its low biological productivity and, possibly, its catch susceptibility from cumulative effects across the separate fishing methods. Finally, at level 3, a quantitative assessment showed that population growth is slow even under the assumption of density-dependent compensation where the fishing mortality rate equals the natural mortality rate. Although published information indicates relative abundance has been stable in several regions of southern Australia, it is concluded that given its low biological productivity, changed fishing practices leading to increased fishing mortality could quickly put *S. megalops* at high risk. The hierarchical approach appears particularly useful for assessment of chondrichthyan species in data-limited fisheries. This approach allows for a management response at any level, optimising research and management efforts by identifying and excluding low-risk species from data intensive assessments.

7.2 INTRODUCTION

Globally only limited attempts have been made to manage populations of chondrichthyan species impacted by the effects of fishing (Anderson 1990; Bonfil 1994). The few exceptions have focused on target species, such as gummy shark (*Mustelus antarcticus*) (Walker 1998) and dusky shark (*Carcharhinus obscurus*) (Simpfendorfer 1999) in southern Australia. Whereas biological parameter estimates and time series of catch, fishing effort, and other monitoring data have been collected to enable stock assessment for sustainable use of the high valued species, there is a paucity of such information for non-target species (Bonfil 2004). Given the comparatively low biological productivity and often high catch susceptibility of chondrichthyan species (Stobutzki *et al.* 2002; Walker 2004), management initiatives are needed long before sufficient data can be collected for stock assessment (Walker 2004). Concerns about widespread depletion of chondrichthyan populations led the United Nations Food and Agricultural Organization to develop an International Plan of Action for the Conservation and Management of sharks (IPOA-sharks; FAO 2000*a*) that was implemented during 1999.

More recently, to address the concerns of uncertainty associated with the wider impacts of fishing on marine ecosystems, Australia is developing and implementing a broad process for ecological assessment in a risk framework. This process is referred to as ecological risk assessment and explicitly identifies five ecological components for analysis: target species, non-target species comprising by-product (predominantly retained) and by-catch (predominantly discarded), threatened species, fish habitats, and ecological communities. Within each component, for each type of fishing method separately, the approach involves a three-levelled hierarchical process of assessment, with increasing data requirements and complexity when progressing from level 1, through level 2, to level 3 assessment. Level 1 assessment involves expert judgement and determines whether or not there is a need to progress to level 2 or, alternatively, to implement a management response. Level 2 assessment is semi-quantitative and determines whether or not there is a need to progress to level 3 or, alternatively, to implement a management response. When progressing from one level to the next, depending on costs, there is the choice of either immediately initiating a management response to ameliorate risk of adverse effects or, alternatively, proceeding to invest in research and monitoring to enable a higher level of assessment (Hobday *et al.* 2004). This approach to ecological risk assessment would be exhaustive if all components were taken to level 3 and would require excessive costs in a multi-species fishery.

The purpose of the present study is to simply take a single chondrichthyan species—the piked spurdog (*Squalus megalops*)—for which sufficient data are available to undertake an assessment at each of the three levels and to evaluate the suitability of the approach for chondrichthyan species in general. *Squalus megalops* falls within the non-target component and is one of the most abundant and widespread chondrichthyan species impacted by Australia’s Southern and Eastern Scalefish and Shark Fishery (SESSF). The species is mostly taken as by-catch by demersal trawl on the continental shelf and upper slope (~600 T/year) (Walker and Gason 2006). Small quantities are also taken on the upper slope by automatic longline targeted at teleost species and on the continental shelf by gillnets deployed in the targeted shark fishery for *M. antarcticus* (Walker *et al.* 2005; Walker and Gason 2006). Following long-term declines in abundance of shark and chimaera populations off New South Wales, southeast coast of Australia (Graham *et al.* 2001), quota reductions on target and by-product shark and chimaera species, and growing consumer demand for shark meat, some large individuals of *S. megalops* are beginning to be retained for marketing (Walker and Gason 2005).

7.3 MATERIALS AND METHODS

Squalus megalops was assessed using the Australian process for ecological risk assessment as part of the non-target component at each of the three hierarchical levels. Progressing through the three levels, level 1 involved qualitative assessment based on expert judgement, level 2 involved semi-quantitative assessment, and level 3 involved fully quantitative assessment based on available data. The approaches to level 1 and level 2 assessments are explicitly described (Hobday *et al.* 2004) and Australia has extensive experience with stock assessment of target and by-product species in a risk framework (level 3 assessment). However, the process is not presently explicit for level 3 assessment of non-target species where catches are not known precisely. The present study applies an approach which assumes no knowledge of catches and catch rates.

Level 1 assessment

Level 1 assessment was a qualitative analysis for each fishing method that may impact *S. megalops* based on expert knowledge. Adopting the precautionary approach, the species was assigned the highest risk value if there was uncertainty about risk judgement (Hobday *et al.* 2004). The fishing methods in the SESSF that may have an effect on *S. megalops* in southern Australia are otter trawl and Danish seine nets, demersal shark gillnets, demersal shark longlines, automatic longlines, droplines, and traps and pots. Within these fishing methods, seven associated activities, explained in Table 7.1, may impact *S. megalops*. Each fishing-related activity within the non-target component was assessed using spatial and temporal scale, intensity and consequence analysis (Hobday *et al.* 2004). This approach involved assigning a score to each of spatial and temporal scale, intensity and consequence of the fishing activity (explained in Table 7.2). Fishing methods with fishing activities with a consequence score ≤2 were eliminated from further assessments, whereas methods with higher scores were assessed more in-depth at level 2.

Table 7.1. Description of the potential impacts of different fishing activities on *Squalus megalops*. Direct impacts are impacts causing damage or mortality, whereas indirect impacts are impacts altering the habitat of the species (adapted from Hobday *et al.* 2004).

Impact	Fishing activity
Direct	Capture (damage or mortality due to gear deployment, including discards)
	Cryptic mortality (unaccounted damage or mortality due to interactions with fishing gear)
	Gear loss (damage or mortality without capture due to interactions with gear lost from the fishing vessel)
Indirect	Species translocation (introduction of species to the habitat of the assessed species)
	On board processing and catch discarding (discard of unwanted parts of target species or unwanted organisms from the catch)
	Provisioning (use of bait or burley)
	Pollution (introduction of chemical and physical pollutants from fishing vessels, such as exhaust, oil spills, detergents, rubbish, lost gear, noise)

Table 7.2. Description of the score values for the spatial and temporal scale, intensity and consequence of the fishing activities (adapted from Hobday *et al.* 2004).

Score	Spatial scale (nm)	Temporal scale	Intensity	Consequence
1	<1	Decadal	Negligible (remote likelihood of detection)	Negligible (impact unlikely to be measured)
2	1–10	Every several years	Minor (seldom occurring and rare to detect)	Minor (minimal impact on stock size, structure or dynamics)
3	10–100	Annual	Moderate (moderate at broader scale, or severe but local)	Moderate (medium impact on stock size, structure or dynamics)
4	100–500	Quarterly	Severe (severe and occurring often at broad scale)	Major (wider and longer term impact on stock size, structure or dynamics)
5	500–1000	Weekly	Major (occasional but very severe and localized or frequent and widespread but less severe)	Extreme (serious impact on stock size, structure or dynamics with long time period to restore to acceptable levels)
6	>1000	Daily	Catastrophic (local to regional severity or continual and widespread)	Intolerable (widespread and irreversible impact on stock size, structure or dynamics)

Level 2 assessment

For level 2, the species was assessed based on its biological productivity and catch susceptibility. Biological productivity can be inferred from the reproductive rate or the natural mortality rate of a species assuming that, immigration and emigration being equal, there has to be a balance between reproductive rate and natural mortality rate for a population to remain in equilibrium (Walker 2004). Species with low reproductive rate and low natural mortality have low biological productivity and hence are at higher risk from the effects of fishing than species with high biological productivity. For *S. megalops*, natural mortality (M) was used as a proxy for biological productivity. Natural mortality was estimated by five indirect life-history methods described elsewhere (e.g. Cortés 2002) and the mean value was used. The indirect methods of Pauly (1980), Hoenig (1983), and Chen and Watanabe (1989), and two methods by Jensen (1996) use parameters estimated from the von Bertalanffy growth model (VBGM) and maximum age information which for *S. megalops* were obtained from Chapter 6. Pauly’s (1980) method also uses information on the mean value of water temperature (14.6º C) that was taken from http://www.marine.csiro.au. Based on empirical data, Walker (2004) devised a scale for M categorization where values of M ≤0.16, between 0.16 and 0.38, and ≥0.39 correspond to low, moderate, and high biological productivity, respectively. This scale was used for biological productivity categorization of *S. megalops*.

Catch susceptibility, a measure of the extent of the fishing impact of each fishing method, is the product of availability (proportion of the spatial distribution of the population that is fished by the fishing method), encounterability (proportion of the available population encountered by one unit of fishing effort), selectivity (proportion of the encountered population that is captured by the fishing gear) and post-capture mortality (proportion of captured animals that die) (Walker 2004). Each of these fishing parameters ranges from 0 to 1; hence, catch susceptibility also ranges from 0 to 1. Fishing parameters with assigned values of 0.33, 0.66, and 1.00 (upper value for each one-third range) are designated low, moderate, and high, respectively (Table 7.3) (Walker 2004). Based on expert judgement and the precautionary approach (i.e. high if unknown), the availability, encounterability, selectivity, post-capture mortality, and catch susceptibility of *S. megalops* were determined for each fishing method.

A species identified as having low biological productivity with moderate to high catch susceptibility would be considered to be at high risk and need to be assessed at level 3. A species with moderate to high biological productivity and low catch susceptibility would be considered to be at low risk and require no further assessment.

Level 3 assessment

Level 3 assessment involved a quantitative data-intensive analysis. Application of biomass dynamic models or more complex models requires time series of catch, fishing effort and relative abundance data, which are not available for most shark species, particularly by-catch species. Given that demographic analyses require only life-history parameters, which are commonly available for many species, this approach was used to make the assessment more compatible and applicable to a broader suite of fisheries. The assessment involved the quantitative estimation of population growth rate, elasticities, rebound potential and population doubling time.

Population growth rate ($\lambda = e^r$) and elasticities (effect of a proportional change in a vital rate on population growth rate) were estimated using a birth-flow Leslie matrix (Caswell 2001). Elasticities of fertility, juvenile survival, and adult survival, are normally obtained by summation of matrix element elasticities across relevant age classes (e.g. Caswell 2001; Carlson *et al.* 2003). However, in the present study, age-at-maturity of *S. megalops* was not assumed to be knife-edge, rather, it was determined from an ogive produced by Braccini *et al.* (2006) and Chapter 5. Hence, for each age class, the survival elasticity of juveniles and adults was the product of the elasticity and the proportion of juvenile and adult females within each class. The total juvenile and adult elasticity was then obtained by summing across the different age classes. Population rebound potential (r_z) and doubling time (T_D = ln (2) r_z^{-1}) were estimated by the method of Smith *et al.* (1998), which incorporates density dependent compensation of adult M through preadult survival. Rebound potential is calculated at the population level of maximum sustainable yield (Smith *et al.* 1998).

To account for uncertainty in life-history parameter values, a probability density function (pdf) was developed for each life-history parameter following the approach of Cortés (2002) and Carlson *et al.* (2003). The pdfs were then used in a Monte Carlo simulation (with 10,000 iterations) to incorporate stochasticity in the estimation of population parameters. Each iteration involved the random selection of a set of life-history parameter

Table 7.3. Description of the score values of fishing parameters for three arbitrary risk categories (adapted from Walker 2004). Catch susceptibility is the product of availability, encounterability, selectivity, and post-capture mortality.

Parameter	Risk category		
	Low	Moderate	High
Availability	0.33 (fishery ranges <one-third of species range)	0.66 (fishery ranges one-third–two-thirds of species range)	1.00 (fishery ranges >two-thirds of species range)
Encounterability	0.33 (0–0.33 probability of species encountering the gear, e.g. pelagic species encountering bottom trawl net)	0.66 (0.33–0.66 probability of species encountering the gear, e.g. pelagic species encountering mid water trawl net)	1.00 (0.67–1.00 probability of species encountering the gear, e.g. bottom-dwelling species encountering bottom trawl net)
Selectivity	0.33 (0–0.33 probability of species being caught by the gear, e.g. filter-feeder species taking a baited hook)	0.66 (0.33–0.66 probability of species being caught by the gear, e.g. fast-swimming species taken by bottom trawl net)	1.00 (0.67–1.00 probability of species being caught by the gear, e.g. species with protruding structures taken by gillnet)
Post-capture mortality	0.33 (0.67–1.00 probability of survival after capture, e.g. discarded bottom-dwelling species with spiracles and robust structure)	0.66 (0.33–0.66 probability of survival after capture, e.g. discarded species with a fragile structure and ram-jet ventilation)	1.00 (0–0.33 probability of survival after capture, e.g. retained target and by-product species)
Catch susceptibility	0–0.33	0.33–0.66	0.67–1.00

values and the calculation of λ, elasticities, r_z, and T_D. In this way, prediction intervals (2.5th and 97.5th percentiles) were obtained from the probability density distribution for each of the estimated population parameters. Simulations were run using Microsoft Excel spreadsheets equipped with the add-in PopTools (http://www.cse.csiro.au/poptools/) and a risk assessment software (Crystal Ball; Decisioneering Inc.) lent by E. Cortés (NOAA, Southeast Fisheries Science Centre, Panama City, Florida, USA).

Life-history parameters needed for the estimation of population parameters were obtained from the literature. Average litter size, the relationship between fecundity and total length (TL) of female, embryo sex ratio, length-at-maturity, and length-at-maternity (relationship between the proportion of females in maternal condition, i.e. contributing to annual recruitment, and TL) were obtained from Braccini *et al.* (2006) and Chapter 5. Average litter size was assumed to follow a normal pdf with a mean (and s.d.) of 2.32 (0.48) and a lower and upper bounds of 2 and 4 reflecting the range of litter sizes reported. The fecundity–TL relationship was predicted from the linear equation: litter size = 0.0071 (0.001) TL – 1.503 (0.549) and was represented by a normal pdf. The embryo sex ratio reported for *S. megalops* was 1:1 so a 0.5 factor was used to half the litter size–TL function and obtain the number of female embryos per female. Length-at-maternity was predicted from the logistic equation, proportion maternal = $0.5\ (1 + e^{-\ln (19)\ ((\mathrm{TL} - 531\ (18))\ /\ (626\ (47) - 531\ (18)))})^{-1}$ and was represented by a normal pdf. Growth parameters and maximum age were obtained from Chapter 6. The growth equation for females was used to transform the relationships between the reproductive variables and TL to relationships between reproductive variables and age. Natality-at-age was calculated as the product of 0.5 (embryo sex ratio), the age-at-fecundity, and the age-at-maternity functions. Two extreme case scenarios were considered. The first is deemed as the worst-case scenario, whereas the second scenario is the more optimistic.

In the first scenario, growth parameters (and s.e.) $L_\infty = 756$ (45) mm, $k = 0.042$ (0.005) years^{-1} and $t_0 = -9.77$ (1.30) years produced by a two-phase VBGM were used as the most likely values in a normal pdf. Age at 50% maturity was represented by a triangular pdf with 15 as the likeliest value and ±2 years as the lower and upper bounds. These values were derived from a length-at-maturity curve (Braccini *et al.* 2006; Chapter 5) and the growth curve produced by the two-phase VBGM. Maximum age was represented by a linearly decreasing pdf scaled to 1, with the likeliest value of 28 (oldest shark aged; Chapter 6) and the lower bound set by arbitrarily adding 30% to the likeliest value, i.e. 36 (Cortés 2002). Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.862 to 0.936, estimated by the Hoenig (1983) and Jensen (1996) methods, respectively. Adult M for the Smith *et al.* (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.149. Maximum sustainable yield for the Smith *et al.* (1998) method was assumed to occur at total mortality (Z) = 1. 5 M.

In the second scenario, growth parameters L_∞ = 699 (17) mm and k = 0.056 (0.005) years^{-1} produced by a two-parameter VBGM growth model were used as the most likely values in a normal pdf. Age at 50% maturity was represented by a triangular pdf with 14 as the likeliest value and ±2 years as the lower and upper bounds. These values were derived from the length-at-maturity curve and the growth curve produced by the two-parameter VBGM growth. Maximum age was represented as in the first scenario, with the difference that the maximum bound was set to 50% of the likeliest value, i.e. 42. Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.930 to 0.936, estimated by the Chen and Watanabe (1989) and Jensen (1996) methods, respectively. Adult M for the Smith *et al.* (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.072. Maximum sustainable yield for the Smith *et al.* (1998) method was assumed to occur at Z = 2 M.

A Spearman rank correlation (r_s) was used to measure possible correlation between life-history parameters and λ. For each scenario, the correlation between the simulated M, k, the slope of the fecundity curve, and TL at 50% maturity of the length-at-maternity relationship with the forecasted λ was determined.

7.4 RESULTS

Level 1 assessment

Level 1 assessment of the fishing methods indicated that the only fishing-related activity to have moderate or higher consequences on the sustainability of *S. megalops* was that associated with ‘capture fishing’ (Appendix 7.a). Other activities had either negligible or minor consequences. Among methods, ‘capture fishing’ of shark longlines, droplines, and traps and pots had a negligible effect on *S. megalops* due to their recent decline to ~0 effort in 2004 (Walker and Gason 2006). Hence these methods were not assessed at a second level. Conversely, ‘capture fishing’ for the otter trawl, Danish seine, shark gillnet, and automatic longline methods had a consequence score >2 so these fishing methods need to be assessed at level 2.

Level 2 assessment

Estimates of natural mortality (M) had a mean value of 0.085, ranging from 0.066, for one of Jensen’s (1996) methods, to 0.149 (Hoenig 1983), indicating that *S. megalops* had low biological productivity (i.e. $M \leq 0.16$). Catch susceptibility of *S. megalops* varied depending on the fishing method (Appendix 7.b). For the shark gillnet method, given the low selectivity, and moderate availability and post-capture mortality, catch susceptibility was low (catch susceptibility = $0.66 \times 1.00 \times 0.33 \times 0.66 = 0.14$). For the automatic longline method, catch susceptibility was also low, as availability was low (catch susceptibility = $0.33 \times 1.00 \times 1.00 \times 0.66 = 0.22$). For the otter trawl and Danish seine methods, there is uncertainty regarding the extent of their spatial overlap with *S. megalops* distribution. If availability for these fishing methods was designated low, catch susceptibility was also low (catch susceptibility = $0.33 \times 1.00 \times 1.00 \times 1.00 = 0.33$). However, if availability was considered moderate, catch susceptibility was also moderate due to high encounterability, selectivity and post-capture mortality (catch susceptibility = $0.66 \times 1.00 \times 1.00 \times 1.00 = 0.66$). In addition, cumulative effects across the four fishing methods may cause an underestimation of total catch susceptibility; hence, based on *S. megalops* low biological productivity, this species was classed as at high risk and needed to be assessed at level 3.

Level 3 assessment

For the first scenario (worst-case), population growth rate (λ) averaged 0.975 (median 0.974, 95% CI 0.974–0.976) (Fig. 7.1). Fertility elasticities averaged 0.046 (0.045, 0.046–0.046), elasticities of juvenile survival were 0.630 (0.629, 0.628–0.631) and those of adults were 0.325 (0.325, 0.323–0.326). Rebound potential (r_z) averaged 0.031 years^{-1} (0.029, 0.030–0.032) and population doubling time (T_D) was 28.2 years (23.5, 27.9–28.5) (Fig. 7.1). There was a negative correlation between M and λ ($r_s = -0.685$, $P < 0.001$) and a positive correlation between the growth coefficient (k) and λ ($r_s = 0.474$, $P < 0.001$) but

TL_{50} (TL at 50% maturity) and the fecundity slope showed no correlation with λ (r_s = – 0.139, P >0.001 and r_s = 0.284, P >0.001, respectively).

For the second scenario (more optimistic), λ averaged 1.018 (median 1.019, 95% CI 1.017–1.019) (Fig. 7.1). Fertility elasticities averaged 0.045 (0.045, 0.045–0.045), elasticities of juvenile survival were 0.397 (0.395, 0.396–0.398) and those of adults were 0.559 (0.560, 0.558–0.560). Rebound potential averaged 0.035 years^{-1} (0.032, 0.035–0.035) and T_D was 23.7 years (21.4, 23.5–23.9) (Fig. 7.1). There was a positive correlation between the fecundity slope and λ (r_s = 0.638, P <0.001) and between k and λ (r_s = 0.342, P <0.001) but TL_{50} and M showed no correlation with λ (r_s = – 0.314, P >0.001 and r_s = – 0.111, P >0.001, respectively).

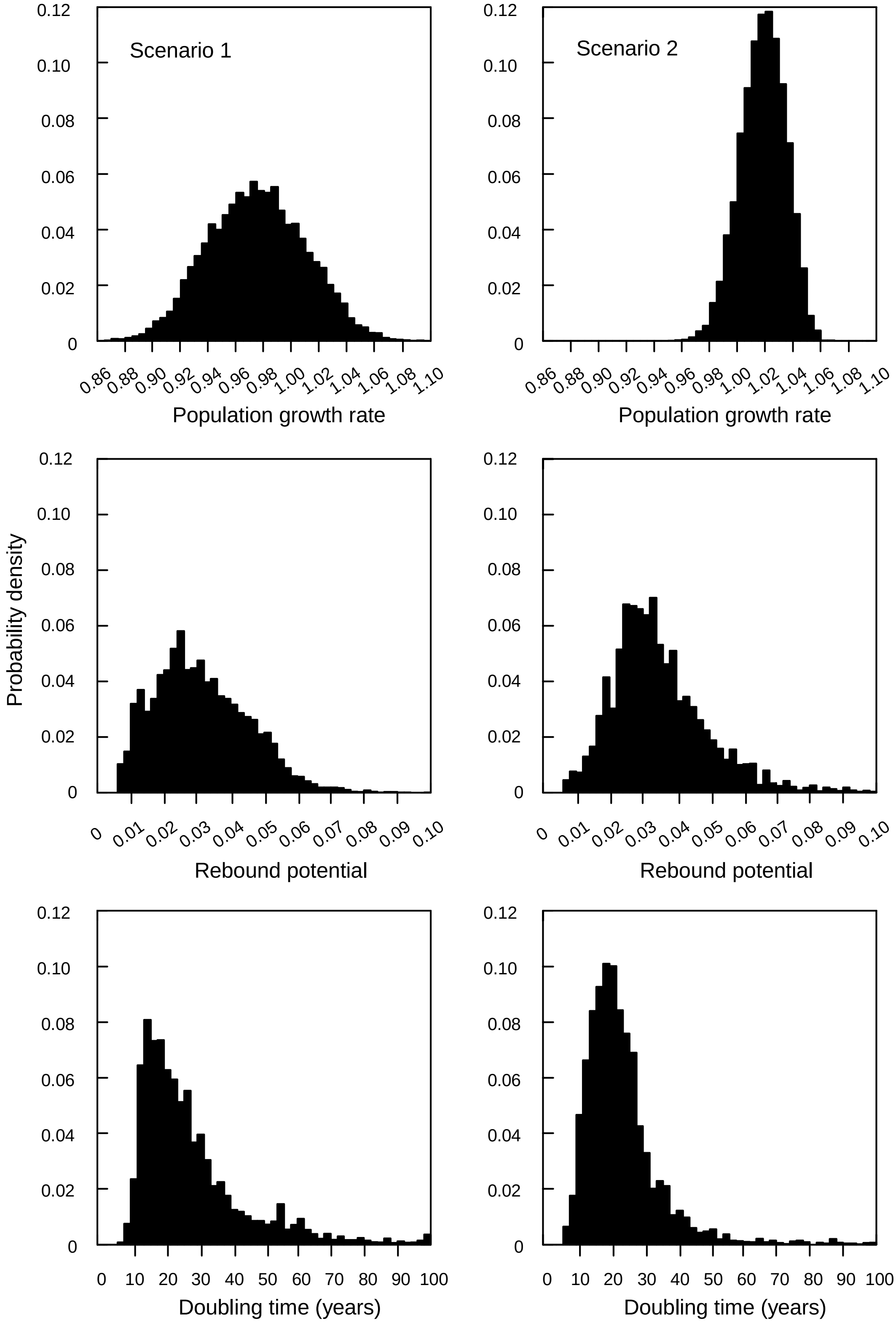

Figure 7.1. Probability density distribution of population growth rate, rebound potential and population doubling time for scenarios 1 and 2 (n = 10,000 simulations).

7.5 DISCUSSION

Protection and management of marine resources should be based on the integration of qualitative and quantitative methods (Cortés 2004) simply because management based solely on quantitative information is of limited application to data-poor fisheries (Johannes 1998). Qualitative, semi-quantitative, and quantitative data together in a hierarchical assessment framework showed that *S. megalops* is potentially highly susceptible to the effects of fishing. At a qualitative level (level 1), the hierarchical assessment allowed screening out of fishing methods and fishing-related activities considered to pose no risk to this species. This indicates that research effort should be allocated on those methods and fishing activities (‘capture fishing’) leading to moderate or higher impacts on *S. megalops*. Qualitative expert judgement, for example knowledge possessed by artisanal fishers, has been valuable for successful management of tropical fisheries in developing countries (Johannes 1998). Furthermore, expert knowledge is commonly used in Bayesian (e.g. Martin *et al.* 2005) and fuzzy logic (Cheung *et al.* 2005) modelling for conservation assessments. Hence, quantitative information need not be an exclusive condition for sound management; a qualitative assessment of chondrichthyans would allow ruling out of species ranked no risk allowing focus on those in risk. The value of this approach is twofold. First, it is usually not practical to undertake long-term studies on non-target chondrichthyan species due to an urgent need for their effective management. Second, the Australian ecological risk assessment process is valuable at making research more cost-effective and at prioritising research funding involving high costs associated with collecting quantitative fishing data (Dulvy *et al.* 2003); the process also provides the option for a management response at any level. In particular, this approach would be useful for developing countries where two-thirds of reported landings of chondrichthyans occurred (Bonfil 1994), resources for monitoring fishery impacts are limited (Johannes 1998) and plans of management have not been implemented.

A semi-quantitative assessment (level 2) ranked *S. megalops* at high risk given its low biological productivity and the cumulative catch susceptibility to the fishing methods. Shark gillnets and Danish seines are used on the continental shelf whereas otter trawlers operate on the upper slope throughout the SESSF and on the shelf off New South Wales, far eastern Victoria, and eastern Tasmania. When considered separately, each of the three fishing methods has low availability, but the three methods together have medium availability and therefore may increase the catch susceptibility of *S. megalops*. In addition, the availability to the otter trawl method would be high if the population is predominantly distributed on the upper continental slope. Demersal trawling may create a higher food supply by disturbing sediments and exposing prey, attracting *S. megalops* to the fishing grounds as this species of shark is an opportunistic predator that consumes a wide range of prey items (Braccini *et al.* 2005; Chapter 4). When applied to a large number of species, the advantage of this approach is to allow low-risk species to be excluded from the data-intensive quantitative analysis of level 3, such that research and management efforts can be directed where most needed (Stobutzki *et al.* 2002; Hobday *et al.* 2004). Even for data-poor fisheries, where species-specific information on biological productivity or catch susceptibility is not available, this level of analysis can be applied. Information can be used from studies from other areas or on closely related species (Walker 2004) with the caution that there may be some degree of geographical variation in life-history parameters (e.g. Parsons 1993) and catch susceptibility parameters.

A quantitative assessment (level 3) showed that population growth of *S. megalops* is slow even under the assumption of density-dependent compensation after a fishing exploitation rate equal to the natural mortality rate. For both the best- and worst-case scenarios, the stochastic estimations of rebound potential (r_z) and population doubling time (T_D) are low even within the range reported for shark species (0.017–0.136 years^{-1} and 5.1–41.5 years, respectively) and are similar to the values reported for the spiny dogfish (*S. acanthias*) from the north-western Atlantic (Smith *et al.* 1998). Stochastic population growth rate (λ) was also slow, placing *S. megalops* towards the “slow” end of the spectrum along a continuum of life-history traits of sharks (Cortés 2002). For the worst-case scenario, most simulated λ values fell below 1 suggesting population decrease even under no fishing mortality. *Squalus acanthias* and the shortspine spurdog (*S. mitsukurii*) also show λ values below 1 and would not possess the biological attributes to restore λ to its original level after moderate exploitation (Cortés 2002). For the worst-case scenario proposed for *S. megalops*, λ values below 1 would result from the negative correlation between λ and natural mortality (M) and the positive correlation between λ and growth coefficient (k). Within this scenario, some of the permutations of the combined M and k that can be obtained from their respective distributions (in this case high M and low k values) resulted in λ values below 1 (McAllister *et al.* 2001). Elasticities of juvenile and adult survival were higher than fertility elasticities indicating that λ is more sensitive to the survival of juveniles and adults. As for *S. acanthias* and *S. mitsukurii* (Cortés 2002), for the worst-case scenario, juvenile *S. megalops* had a higher elasticity than adults and management actions should focus on the protection of juveniles. For the best-case scenario, due to the simulated longer lifespan (42 years) and the larger number of adult age classes, elasticity of adults was higher for what management actions should focus on this latter group. In all, the estimated values of r_z, T_D and λ indicate that recovery time of *S. megalops* population after fishing overexploitation is expected to be very long. Although the relative abundance of *S. megalops* has remained stable off New South Wales (Graham *et al.* 2001), probably due to refuge areas where ground is untrawlable (Graham 2005), this is currently the most caught by-catch shark species taken by demersal trawlers in south-eastern Australia. Trends in catch per unit effort from onboard scientific observer data suggest the population has been stable during 1992–05 (Walker and Gason 2006). Nevertheless, the aggregating behaviour of *S. megalops* (Graham 2005; Chapter 2), in combination with its slow growth rate (Chapter 6) and low reproductive output (Braccini *et al.* 2006; Chapter 5), makes this species potentially vulnerable to the effects of fishing. For species with similar life-history traits, such as *S. acanthias*, stock depletions have been well documented (e.g. Holden 1977). Hence, any increase in catch susceptibility through targeting, increased retention of catch, or change in gear design such as reducing mesh-size of shark gillnets could quickly increase the risk of stock depletion for *S. megalops*. Conservation and management for sustainable use of *S. megalops* will require a close control of fishing mortality due to the low biological productivity of this species.

In summary, the hierarchical ecological risk assessment approach adopted in Australia allows for the effective evaluation of the effects of fishing on non-target chondrichthyan species and the identification of species at risk. Under this approach, research and management effort can be prioritised and directed to where it is most needed. The hierarchical approach allows for management response at any level as an alternative to undertaking the research required to proceed to the next level of assessment. Hence, this approach is particularly useful for fishery management organizations for the assessment of data-limited fisheries. For example, the Australian Fisheries Management Authority (AFMA) is presently applying such a framework for the evaluation of 14 fisheries as the basis for determining priorities for research, fishery monitoring, and management (Hobday *et al.* 2004). There is no doubt about the need for management of chondrichthyans, particularly for those taken as by-catch in multispecies fisheries. The question is how to make research and management more cost-effective and priority-driven when chondrichthyan resources are being depleted and there are insufficient time or funding available for comprehensive data collection on all species.

Appendix 7.a.

Level 1 assessment of the fishing methods having a potential impact on *S. megalops*. Presence score: 1, present; 2, absent. Certainty score: 1 certain (data exist and considered sound); 2 uncertain (no data or considered poor or conflicting; see Table 7.2 for score value description). **a.1** Otter trawl and Danish seine methods, **a.2** shark gillnet method, and **a.3** automatic longline method.

a.1 Otter trawl and Danish seine methods

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Capture	1	6	6	4	3	1	*S. megalops* is captured by trawl nets throughout the range of the fishery. Moderate impact on stock as there has been no long-term decline in relative abundance in one region of the fishery (Graham *et al.* 2001); however, for the other regions there is no long-term relative abundance information.
Cryptic mortality	1	6	6	2	2	2	Cryptic mortality caused by escapement of animals injured from encounters with trawl nets may happen but it is considered to have a minor impact on the stock. Certainty low due to difficulties in measuring this impact.
Gear loss	1	6	6	1	1	1	Trawl net loss is a rare event due to their high price, which creates a high incentive not to loose and to retrieve them.

Appendix 7.a.1 Continued…

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Species translocation	1	6	6	1	1	1	Invertebrate and vertebrate species caught in trawl nets can be translocated up to several miles between shots but it is unlikely to have a measurable impact on the stock through habitat modification.
On board processing and catch discarding	1	6	6	3	3	2	Moderate to large quantities of organisms are discarded in trawling operations. This practice can attract opportunistic species, such as *S. megalops* (Braccini *et al.* 2005; Chapter 4), increasing the probability of being taken by the gear. However, the extent of this impact is uncertain due to lack of data.
Provisioning	0					1	Provisioning does not occur in this method.
Pollution	1	6	6	2	1	1	Chemical or physical pollutants might have minor risks as this hazard only affects a small area and *S. megalops* is a mobile species with an avoidance ability >scale of the hazard. Impact on stock is considered negligible.

a.2 Shark gillnet method

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Capture	1	6	6	3	4	1	Shark gillnets are 6–6½-inch mesh-size designed to target larger-sized species (e.g. *M. antarcticus*) so only large female *S. megalops* are taken throughout the range of the fishery (Walker *et al.* 2005). Selective removal of significant numbers of large females could have a major impact on the stock.
Cryptic mortality	1	6	6	2	2	2	Refer to Table a.1.
Gear loss	1	6	6	1	1	1	Refer to Table a.1.
Species translocation	1	6	6	1	1	1	Refer to Table a.1.
On board processing and catch discarding	1	6	6	3	3	2	Refer to Table a.1.
Provisioning	0					1	Refer to Table a.1.
Pollution	1	6	6	2	1	1	Refer to Table a.1.

a.3 Automatic longline method

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Capture	1	6	6	3	3	2	This fishing method is used across a broad spatial and temporal scale but only in deepwater (continental slope) where *S. megalops* is not very abundant; hence, the impact on the stock is considered moderate.
Cryptic mortality	1	6	6	2	2	2	Refer to Table a.1.
Gear loss	1	6	6	1	1	1	Refer to Table a.1.
Species translocation	1	6	6	1	1	1	Refer to Table a.1.
On board processing and catch discarding	1	6	6	2	2	1	Discards in this fishery are minimal, having a minor effect on the stock.

Appendix 7.a.3 Continued…

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Provisioning	1	6	6	2	2	1	The most commonly used bait is squid, which is harvested at low levels with minor consequence for the stock of squid and hence minor indirect effect on *S. megalops* stock.
Pollution	1	6	6	2	1	1	Refer to Table a.1.

Appendix 7.b.

Catch susceptibility for otter trawl and Danish seine method, shark gillnet method, and automatic longline method. Risk categories of availability (Av), encounterability (Ec), selectivity (Se), post-capture mortality (Pc), and catch susceptibility (Cs) are L (low, 0.33), Mo (moderate, 0.66), and H (high, 1.00).

Fishing method	Parameter					Rationale
	Av	Ec	Se	Pc	Cs	
Otter trawl & Danish seine	L–Mo	H	H	H	L–Mo	This method is confined to the continental shelf and upper slope overlapping in part with *S. megalops* spatial distribution. Encounterability is high due to depth distribution of gear and species. Selectivity is high given uncertainty in selectivity of trawl nets. Post-capture mortality is also high due to trauma caused inside the net.
Shark gillnet	Mo	H	L	Mo	L	This method is confined to the continental shelf, mostly inside the 120–150 isobath, with moderate overlap with *S. megalops* spatial distribution. Encounterability is high due to depth distribution of gear and species. Selectivity is low due to 6–6½-inch mesh-size of gillnet (see Table 6, Walker *et al.* 2005).
Automatic longline	L	H	H	Mo	L	This method is confined to the continental slope with very low overlap with *S. megalops* spatial distribution. Encounterability is high due to depth distribution of gear and species as *S. megalops* is likely to take the baited hook given its opportunistic feeding behaviour. Selectivity is high given hook size does not affect catch (Walker *et al.* 2005).

Sunset aboard the fishing vessel ‘*Ester-J*’ after a day of sampling (photo by the author).

CHAPTER 8

CHAPTER 8

GENERAL DISCUSSION

Due to increasing risk of depletion of shark species worldwide, the lack of long-term time-series of data, and urgent need for management actions, a different approach from that usually adopted for target species is required for the assessment of non-target species. This thesis applies the concept of hierarchical assessment for evaluating ecological risks to *Squalus megalops* by the main fisheries operating in south-eastern Australia. The thesis provides quantitative information that enables several key features of the life-history and population status of this species to be determined. This was achieved by studying *S. megalops* using different approaches: (i) analysing its population structure and morphological relationships (Chapters 2 and 3), (ii) quantifying its feeding ecology and the factors that contribute to variation in its diet (Chapter 4), (iii) determining the reproductive, and age and growth parameters needed for its population assessment (Chapters 5 and 6), and (iv) using the life-history information in a modelling framework for the assessment of ecological risks (Chapter 7).

The present chapter provides a summary of the key findings presented in this thesis. For expanded discussion of the points made here, and for further details that have been omitted, the reader should consult the relevant text in Chapters 2 through to 7.

8.1 POPULATION STRUCTURE AND MORPHOLOGICAL RELATIONSHIPS

Most dogfish species have complex population structures, exhibiting segregation by sex, size and mature condition (e.g. Hanchet 1988; Yano and Tanaka 1988; Yano 1995; Wetherbee 1996; Clarke 2000). It is, therefore, prudent to consider this pattern in the management of these species. Despite the opportunistic nature of the sampling design, individual analysis of selected fishing shots suggested that *S. megalops* also has a complex population structure, segregating by sex, size and breeding condition. In addition, given that females attain a larger maximum size than males, implementation of maximum legal sizes could result in a population dominated by females, affecting the biological productivity of the population. Finally, the sex ratio suggested that females may be more vulnerable to fishing than males probably due to an overlap between the distribution of females and of the various fisheries operating in south-eastern Australia. Hence, as for mammals with sexual segregation (Bowyer 2004), the strategies developed for the conservation of *S. megalops* should incorporate the segregation pattern in management plans, considering males and females as separate entities.

Commercial shark species are normally beheaded, eviscerated and landed with or without fins attached; hence, only partial lengths and partial masses can be recorded after landing (FAO 2000*b*). Furthermore, in many fisheries only the fins are retained, whereas the rest of the animal is discarded. Therefore, relationships between partial lengths and total length and between partial masses and total mass of sharks are needed to determine the length and mass composition of captured sharks. Although many studies provide total mass–total length relationships, few present conversion factors to allow calculating total mass or total length from partial mass or partial length measurements. However, these relationships and conversion factors are essential for fisheries monitoring programmes and population assessments. Given the depletion of many of the harvested species of sharks and a decline in abundance of most other shark species in southern Australia (Graham *et al.* 2001), *S. megalops* will inevitably become a more sought after species. Hence, the conversion factors from partial lengths to total length and from partial masses to total mass were determined. When measurements reflect only somatic growth, conversion factors to total length or total mass can be determined pooling sexes and sizes, but, for variables reflecting somatic and reproductive growth (total and liver masses), different outcomes can be expected when different ranges of size are compared. Due to the sexual size dimorphism of *S. megalops*, conversion factors should be determined for sexes and sizes separately.

8.2 DIETARY COMPOSITION AND SOURCES OF VARIATION

Several shark species play an important role in the structure of marine communities (Cortés and Gruber 1990; Ellis *et al.* 1996; Cortés 1999; Stevens *et al.* 2000) and the exchange of energy between upper trophic levels (Wetherbee *et al.* 1990); however, there are few quantitative studies on the feeding ecology of sharks and no studies account for the natural variability in the diet of marine predators. This thesis provides evidence of different sources of variation in the feeding ecology of *S. megalops*, an opportunistic predator with a diverse diet that consumes a wide range of prey items.

The use of multiple descriptors of dietary composition allowed a better representation of the overall diet of this opportunistic predator. When prey importance was inferred from the weight or frequency of occurrence of prey items, *S. megalops* preyed mainly on molluscs and teleosts. However, when number of prey was used, the most important prey items were crustaceans. Therefore, given that number, weight, and frequency of occurrence measures provide different information (MacDonald and Green 1983; Bigg and Perez 1985; Cortés 1998*b*), multiple measures should be used for the description of feeding habits, particularly when prey items differ in size (Ferry and Cailliet 1996).

There was a wide range of variability in the overall diet of *S. megalops*. The bootstrap analysis showed that importance of prey varied by up to 50% within the upper and lower 95% confidence intervals. Variability in the overall diet of shark species has not been previously reported. However, due to the combination of small sample sizes and opportunistic sampling by many diet studies, high proportion of empty stomachs, and the opportunistic predatory nature of many shark species, high variability in diet and hence in predator–prey interactions is expected. Predator–prey interactions are used as linkages between species in ecosystem modelling. However, model outputs may not be accurate when overall diet data do not account for the variability in the composition of diet.

The dietary composition of *S. megalops* varied in space and time, and exhibited differences among regions, seasons and size classes. When spatial and temporal effects in the diet of sharks have been tested (Simpfendorfer *et al.* 2001*b*; Vögler *et al.* 2003; White *et al.* 2004), region, season or ontogeny have been evaluated independently of each other and the interaction of these factors was not taken into account even though samples were collected across wide spatial and temporal scales. Apart from Cortés *et al.* (1996), no other study on the diet of shark has tested for the interaction of factors. This thesis showed an interaction between size and season where large and small *S. megalops* had different diets in summer and autumn, but consumed similar prey items in spring. Hence, large and small individuals would have, at least during part of the year, different ecological roles within the marine ecosystem. Therefore, the intrinsic natural variability in the dietary composition of *S. megalops* and its spatial and temporal variation in diet suggests that information on the ecological relationships among species is likely to be missed when predator–prey interactions are only inferred from overall diet.

8.3 REPRODUCTIVE AND GROWTH PARAMETERS

Reproductive and age and growth parameters were estimated for the quantitative population assessment of *S. megalops*. The reproductive and growth traits of *S. megalops* are typical of species with low resilience, making this shark species highly susceptible to the effects of fishing overexploitation.

Male and female *S. megalops* are capable of reproducing throughout the year, exhibiting no pattern of temporal periodicity in their reproductive cycle. Continuous asynchronous cycles have been reported for other dogfish species (Yano and Tanaka 1988; Yano 1995); however, gestation period and ovarian cycle of those species have not been determined. This thesis provides a method for the estimation of these parameters in asynchronous breeders, such as *S. megalops*. For this species, ovarian cycle and gestation period are ~2 years. Periodicity of ovarian cycle and gestation period are crucial for defining maternal condition of female chondrichthyans. Although most viviparous sharks have gestation periods of approximately a year (Stevens and McLoughlin 1991; Hamlett and Koob 1999), species producing large-sized follicles, such as most squalid species (Chen *et al.* 1981; Hanchet 1988; Guallart and Vicent 2001), have ovarian cycles and gestation periods of two, three or more years. Hence, for shark species with asynchronous breeding and reproductive cycles of several years duration, if maturity ogives (i.e. proportion of females in mature condition at any size) are used in population assessments instead of maternity ogives (i.e. proportion of females contributing to annual recruitment), models will over-estimate recruitment rates, leading to overly optimistic predictions.

Age and growth information needed for the population assessment of *S. megalops* was derived from bands laid on the first dorsal fin spine. Precision estimates, the relationship between spine total length and body length, edge analysis, and agreement between counts on the inner dentine layer and the enameled surface support the use of this structure for the age estimation of *S. megalops*. Most studies on age and growth of dogfish also use dorsal fin spines for age estimation (e.g. Holden and Meadows 1962; Ketchen 1975; Clarke *et al.* 2002*a*). Different growth functions were fitted to length-at-age data to determine the best growth model. From the examined models, a two-phase von Bertalanffy function provided the best goodness-of-fit. However, the results should be interpreted with caution and might not be representative of real growth because of the effects of sampling bias, length-selective fishing mortality and bias in age estimation on length-at-age data. Data quality is particularly relevant when samples are obtained from commercial fisheries, as in most studies on age and growth of sharks, because growth parameters may be different from those obtained from a more representative sample (Haddon 2001). Regardless of the model used, the growth rate of *S. megalops* (particularly of females) is very low even within the range of growth rates reported for shark species; hence, it is expected that population recovery will be slow following fishing overexploitation.

8.4 ECOLOGICAL RISK ASSESSMENT

A hierarchical framework was applied to *S. megalops* for the assessment of ecological risks from effects of fishing. By integrating qualitative and quantitative biological (reproduction, age and growth) and fishing impact data, this approach showed that *S. megalops* is potentially highly susceptible to the effects of fishing. A qualitative assessment indicated that the only fishing-related activity to have moderate or high impact on this species was that associated with 'capture fishing' of the otter trawl, Danish seine, gillnet and automatic longline methods. Hence, other fishing methods or fishing-related activities were screened out from further analyses. At the next assessment level, a semi-quantitative evaluation ranked *S. megalops* as at risk given its low biological productivity and, possibly, its catch susceptibility from cumulative effects across the separate fishing methods. The qualitative and semi-quantitative assessments make use of qualitative expert judgement for efficient risk identification (Hobday *et al.* 2004). Hence, quantitative data need not be an exclusive condition for sound management of sharks as qualitative and semi-quantitative assessments allow ruling out of species at low risk and focus on those at medium or high risk. This approach ensures that research is more cost-effective and priority-driven. In particular, such a method is useful for developing countries where two-thirds of reported landings of sharks occurs (Bonfil 1994), resources for monitoring fishery impacts are limited (Johannes 1998), and where plans of management have not been developed.

A quantitative assessment showed that population growth of *S. megalops* is slow even under the assumption of density-dependent compensation where the fishing mortality rate equals the natural mortality rate. The rebound potential and population doubling time are low and similar to the values reported for *S. acanthias* from the north-western Atlantic (Smith *et al.* 1998). For the worst-case scenario, most of the simulated population growth rates suggested population decrease even under no fishing mortality. In this case, *S. megalops* would not have the biological potential to restore population growth to its original level after exploitation (Cortés 2002). *Squalus megalops* is currently the most caught by-catch shark species taken by demersal trawlers in south-eastern Australia (Walker and Gason 2006). Therefore, its conservation and management for sustainable use will require a close monitoring and control of fishing mortality due to the low biological productivity of this species.

Application of the hierarchical framework presented in this thesis allows research and management efforts to be optimised by identifying and excluding low-risk species and low-risk fisheries from data intensive assessments. Under this scheme, research and management efforts can be prioritised and directed to where most needed. By making research more cost-effective and priority-driven, this approach is particularly useful for fishery management organizations for the assessment of data-limited fisheries.

8.5 MANAGEMENT

History has shown that marine resources are far from being unlimited and, in fact, are usually overexploited. To quote Ludwig *et al.* (1993), “Although there is considerable variation in detail, there is remarkable consistency in the history of resource exploitation: resources are inevitably overexploited, often to the point of collapse or extinction” (p. 17). Unfortunately, management of marine resources has commonly been implemented after overexploitation of resources.

Management of sharks has been no exception. Concerns over the worldwide decline in most harvested shark stocks led to the development of the International Plan of Action for the Conservation and Management of Sharks. The Plan of Action requires each signatory country to develop a national plan for the management of all chondrichthyan species taken in the local fisheries. Currently, only Australia, USA, New Zealand, South Africa, and Canada have developed management plans for some shark species (IUCN 2002). Management in most other countries has been hindered by the lack of biological and fishing information on most species, especially for fisheries in developing countries. It is within this context that hierarchical assessments of ecological risks are of significant relevance. As summarized in the words of Johannes (1998), “…the key management question should not be what data do we need to make sound management decisions but rather, what are the best management decisions to make when such data are unobtainable” (p. 245).

The apparent stable population structure and relative abundance of *S. megalops* off New South Wales after 20 years of commercial trawling suggests that this species inhabits untrawlable grounds that provide large refuge areas (Graham 2005). Also, commercial trawlers targeting more valuable species tend to avoid aggregation areas of undesirable species, such as *S. megalops*. Automatic longliners only operate on the continental slope, with very low spatial overlap with *S. megalops* distribution. Finally, only the largest animals are retained by gillnets of 6- and 6½-inch mesh-size used in the commercial shark gillnet method (pers. obs.) and most of the population is protected from this fishing method by the legal minimum mesh-size of 6 inches (since 1975) (Walker *et al.* 2005). Hence, current fishing mortality from these fishing methods is expected to be low and this would explain the high relative abundance of this shark. However, at the same time, *S. megalops* is the most commonly captured by-catch shark species by demersal trawlers in south-eastern Australia (Walker and Gason 2006) and has started to be landed by the GHATF at an increasing rate (from 5 T in 2002 to 16 T in 2004) (Walker and Gason 2005). In addition, due to long-term declines in abundance of shark and chimaera populations in southern Australia (Graham *et al.* 2001), quota reductions on target and by-product shark and chimaera species (Walker and Gason 2005), and growing consumer demand for shark meat, *S. megalops* will inevitably become a more sought after species. As previously shown, the life-history traits, population growth rate, and rebound potential of *S. megalops* only allow for low harvesting rate and any increase in fishing mortality should be closely monitored for this species to avoid depletion.

8.6 FUTURE RESEARCH

Several areas need further research.

- There is solid evidence for New South Wales (Graham 2005) and for south-eastern Australia, from selected fishing shots, of sexual and size segregation. Females in the first year of pregnancy seem to be segregated from females in the second year of pregnancy. Small individuals may have a pelagic phase and would not be collected by bottom trawl and gillnets. Given that *S. megalops* is the most commonly taken by-catch shark species by demersal trawlers in south-eastern Australia (Walker and Gason 2006), further information is needed on the location of parturition areas, and the spatial distribution of juveniles, males, and females in various breeding conditions. Therefore, a more rigorous sampling design would allow determining the extent of the segregation pattern of *S. megalops* in south-eastern Australia and testing the hypothesis proposed for the depth distribution of small sharks. Finally, the areas of large aggregations of individuals, particularly of large females, need to be determined and considered in management plans.

- In this thesis, I tested for different sources of variation in the feeding ecology of *S. megalops* (Chapter 4). However, regional effects could only be analysed for large females collected in autumn, and samples from only three seasons could be compared for the seasonal analysis. Future research will benefit from further collection of samples from the sexes, sizes and seasons missing. The use of captive sharks would allow estimates of feeding frequency and periodicity. Important for fisheries management would be to incorporate variability in dietary composition into ecosystem models to understand the implications of diet variability on model predictions.

- Age and growth parameters are vital for population assessment. I estimated the age and growth rate of *S. megalops*, but, perhaps in part due to sampling bias, length-at-age data might not be representative of natural growth. A more representative sample, obtained from fishery-independent sources, would allow determining an unbiased growth curve for the population. Also, band periodicity was only partly validated; hence, further research, on both validation of periodicity of band formation and absolute age, is essential. A large scale tagging program might allow for the age validation of this species and also the estimation of its natural mortality. In this thesis, I fitted different growth models to age data, from which a model other than the Von Bertalanffy growth model produced the best fit. My results encourage the use of a suite of growth functions to determine the model that best represents the data.

- The risk assessment provided a step towards the conservation and sustainable management of *S. megalops*. However, the population dynamics of this species are still uncertain due to several factors. Time series of catch and effort, and fishery-dependent estimates of relative abundance are only available for the otter trawl method for the past 13 years (1992–05), and there is little information for other fishing methods used in southern Australia. There are no accurate estimates of natural and fishing mortality and a poor understanding of the selectivity of the trawl and hook gears. This information is not only lacking for *S. megalops*, but also for most shark species, particularly non-target ones.

8.7 CONCLUSIONS

The data presented in this thesis and the applied risk assessment approach have shown that the life-history characteristics of *S. megalops* of aggregating behaviour, low reproductive output, slow growth rate, and high longevity make this species particularly vulnerable to the effects of fishing. Although published information indicates relative abundance has been stable in several regions of southern Australia, given the low biological productivity of *S. megalops*, changed fishing practices leading to increased fishing mortality could quickly put this species at high risk. Hence, effective management of *S. megalops* will require a close control of fishing mortality.

APPENDIX A

APPENDIX A

SUMMARY

Appendix A provides documentation from publishers that gives permission to reproduce chapters in this thesis that were published manuscripts (or accepted for publication) at the time of thesis submission (January 2006). This information applies to Chapters 3, 4, and 5. Chapters under peer-review with journals at the time of thesis submission do not require such information.

CHAPTER 3

Chapter 3 was accepted for publication in the journal *Fisheries Research* in 2006.

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