

SHARKS AND THEIR RELATIVES II

BIODIVERSITY,
ADAPTIVE PHYSIOLOGY,
AND CONSERVATION



EDITED BY
JEFFREY C. CARRIER
JOHN A. MUSICK
MICHAEL R. HEITHAUS

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*To our students, past, present, and future, whose work has inspired our curiosity,
challenged us to continue to grow intellectually, and kept us forever young.*

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Preface

The publication of *The Biology of Sharks and Their Relatives* in 2004 provided a comprehensive review of research spanning the long interval since the publication of Perry Gilbert's classic works, *Sharks and Survival* and *Sharks, Skates, and Rays*. We were satisfied with our range of coverage and with the expertise provided by the authors who contributed to this work. Yet we realized that the volume would necessarily be incomplete because of the breadth of new research being undertaken, the rapid advances in technology that seemed to be opening new avenues for investigation, and the emergence of new investigators who were beginning to explore issues of biodiversity and distribution, physiology, and ecology in ways that have eluded more traditional studies.

To address subject areas and subdisciplines where our coverage was absent or superficial in volume one, we have assembled in the current volume a collection of works that reveal patterns of biodiversity, the physiological attributes that contribute to elasmobranchs' successful exploitation of oceanic and freshwater realms, and the unique issues associated with the interaction between elasmobranchs and humans, all of this with overarching attention to issues of conservation. We begin with chapters examining biodiversity. We have chosen to approach this discussion by presenting elasmobranchs as inhabitants of the range of zoogeographic provinces, realizing that significant overlap may occur for more pelagic species. This realization was reflected in the dialogue that occurred during preparation of the book between our chapter authors, and the recognition that many species simply cannot be confined to a specific habitat or range of habitats. We then continue by examining some of the unique physiological adaptations that allow these animals to exploit the range of habitats where they are found, from unique sensory modalities to compensatory mechanisms for physiological and environmental stress. Our concluding section presents some of the challenges faced by members of these groups. We have asked our authors to consider human interactions and anthropogenic effects on worldwide populations and the potential extinction risks posed from survival under increasing threats from changes in habitat, changes in water chemistry, and increasing commercial exploitation. Conservation of species under threat remains a theme throughout the book.

Our authors represent an international group of investigators including established scientists whose work has been widely published and respected, and emerging younger scientists who have exploited recent advances in technology to ask and answer new questions as well as offering new insights and interpretations to enduring problems in the fields of ecology and physiology. We have asked them to be speculative and challenging, and we have asked them to predict future areas for investigation in hopes that their work will both inspire and provoke additional studies of these fascinating animals.

The Editors

Jeffrey C. Carrier, Ph.D., is a professor of biology at Albion College, Albion, Michigan, where he has been a faculty member since 1979. He earned his B.S. in biology in 1970 from the University of Miami, and completed a Ph.D. in biology from the University of Miami in 1974. While at Albion College, Dr. Carrier has received multiple awards for teaching and scholarship and has held the A. Merton Chickering and W.W. Diehl Endowed Professorships in biology. His primary research interests have centered on various aspects of the physiology and ecology of nurse sharks in the Florida Keys. His most recent work has centered on the reproductive biology and mating behaviors of this species in a long-term study from an isolated region of the Florida Keys. Dr. Carrier has been a member of the American Elasmobranch Society, the American Society of Ichthyologists and Herpetologists, Sigma Xi, and the Council on Undergraduate Research. He served as secretary, editor, and two terms as president of the American Elasmobranch Society, and has received that society's Distinguished Service Award.

John A. (Jack) Musick, Ph.D., is the Marshall Acuff Professor Emeritus in Marine Science at the Virginia Institute of Marine Science (VIMS), College of William and Mary, where he has served on the faculty since 1967. He earned his B.A. in biology from Rutgers University in 1962 and his M.A. and Ph.D. in biology from Harvard University in 1964 and 1969, respectively. While at VIMS, he has successfully mentored 37 masters and 49 Ph.D. students. Dr. Musick has been awarded the Thomas Ashley Graves Award for Sustained Excellence in Teaching from the College of William and Mary, the Outstanding Faculty Award from the State Council on Higher Education in Virginia, and the Excellence in Fisheries Education Award from the American Fisheries Society. He has published more than 150 scientific papers and co-authored or edited 16 books focused on the ecology and conservation of sharks, other marine fishes, and sea turtles. In 1985, he was elected a fellow by the American Association for the Advancement of Science. He has received Distinguished Service Awards from both the American Fisheries Society and the American Elasmobranch Society, for which he has served as president, and been recognized as a distinguished fellow. Dr. Musick also has served as president of the Annual Sea Turtle Symposium (now the International Sea Turtle Society), and as a member of the World Conservation Union (IUCN) Marine Turtle Specialist Group. Dr. Musick served as co-chair of the IUCN Shark Specialist Group for nine years, and is currently the vice chair for science. He also has served on three national, five regional, and five state scientific advisory committees concerned with marine resource management and conservation. In 2008, Dr. Musick was awarded The Lifetime Achievement Award in Science by the State of Virginia.

Michael R. Heithaus, Ph.D., is an assistant professor of marine biology at Florida International University in Miami. He received his B.A. in biology from Oberlin College in Ohio and his Ph.D. from Simon Fraser University in British Columbia, Canada. He was a postdoctoral scientist and staff scientist at the Center for Shark Research at Mote Marine Laboratory in Sarasota, Florida (2001–2003) and also served as a research fellow at the National Geographic Society (2002–2003). Dr. Heithaus' main research interests are in predator–prey interactions and the factors influencing behavioral decisions, especially of large marine taxa including marine mammals, sharks and rays, and sea turtles. Currently,

he is investigating how behavioral decisions, especially anti-predator behavior, may influence behavioral decisions of other individuals and community dynamics. The majority of Dr. Heithaus' previous field work has focused on tiger sharks and their prey species in Western Australia. Dr. Heithaus is a member of the Ecological Society for America, Animal Behavior Society, International Society for Behavioral Ecology, Society for Marine Mammalogy, and Sigma Xi.

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Section I

Chondrichthyan Biodiversity: Ecosystems and Distribution of Fauna

1

Epipelagic Oceanic Elasmobranchs

John D. Stevens

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1.1 Introduction: The Epipelagic Oceanic Ecosystem

The oceanic zone is generally defined as those waters beyond the 200 m isobath at the edge of the continental shelf extending out and encompassing the ocean basins. This contrasts with the neritic zone that extends from the shore and is the water above the continental shelf. The pelagic zone includes all open waters that are not close to the bottom and is divided into the epipelagic, mesopelagic, bathypelagic, abyssopelagic, and hadopelagic zones that are distinguished by their depth and ecology (Bone, Marshall, and Blaxter 1995). The epipelagic zone extends from the surface down to 200 m and has an abundance of light that allows for photosynthesis. Nearly all primary production in the ocean occurs here and this is where most organisms are concentrated (Pinet 2006). About 80% of the ocean's surface is above water greater than 200 m in depth. In general, species diversity tends to decrease as one leaves the shore and the food web becomes supported by the planktonic production. Extending down from the epipelagic zone is the mesopelagic zone, or twilight zone, that reaches to a depth of 1000 m and has a little light but not enough for photosynthesis to occur. Together, the epipelagic and mesopelagic zones, where light penetrates the water, are known as the photic zone. The pelagic zone occupies about 1370 million cubic km (330 million cubic miles) and has a vertical range up to 11 km (6.8 miles). The diversity and abundance of pelagic life decrease with increasing depth. It is affected by light levels, pressure, temperature, salinity, the supply of dissolved oxygen and nutrients, and the submarine topography.

Epipelagic oceanic ecosystems occur in all major oceans, and in the context of this book there is some potential overlap with Chapters 2 (deepwater chondrichthyans), 3 (high latitude seas and chondrichthyans), and 4 (chondrichthyans of tropical marine ecosystems). While most epipelagic oceanic elasmobranchs migrate vertically into deeper zones, the distinction for this book is the zone in which they spend the majority of their time, although for some species this may not be well known. The majority of epipelagic oceanic elasmobranchs are tropical but, to avoid overlap, Chapter 9 will largely ignore these species. Some epipelagic oceanic elasmobranchs occur at high latitudes and these will be dealt with in this chapter. However, at the extremes of high latitude in the Arctic and Southern Oceans epipelagic elasmobranchs are absent.

1.2 Biodiversity and Biogeography

1.2.1 Biodiversity and Systematics

As with any division of species into specific ecosystems, the inclusion or exclusion of some will be debatable. Epipelagic is taken here to refer to highly mobile species that occur in the top 200 m of the water column; oceanic species primarily inhabit ocean basins away from the shelf edge of land masses. Some oceanic species may at times come into more coastal waters for a variety of reasons. Epipelagic oceanic elasmobranchs dealt with in this chapter are listed in Table 1.1 and comprise about 2% of the global extant chondrichthyan fauna (estimated at 1200 species). However, when examined by order about 73% of the Lamniformes are epipelagic and oceanic although the Carcharhiniformes probably dominate in terms of biomass. A number of other species that could be argued for inclusion (Table 1.2) have been omitted because either little is known about them (they may be based on only a few specimens), they are primarily associated with land masses and are only semi-oceanic, or if they have oceanic components to their populations it is not clear they are epipelagic. Including these species would take the total to about 33 or 3% of the extant chondrichthyan fauna. However, categorizing some species is still problematic. For example, it could be argued that the white shark (*Carcharodon carcharias*) is primarily coastal. However, recent tracking data have revealed a considerable oceanic life-history component that warrants its inclusion in this chapter. Of the 21 species in Table 1.1, 19 are sharks and two are batoids, with the most speciose family being the Lamnidae (five species) (Table 1.3). A further four families and six species are lamniform sharks. Four species are squaliform sharks (from two families). There is one epipelagic oceanic orectolobiform shark (family Rhincodontidae) and the two batoids are from the families Dasyatidae and Mobulidae (Table 1.3).

As noted by Compagno (2008), pelagic elasmobranchs exhibit three basic body plans or ecomorphotypes specialized for life in this environment, macrooceanic, microoceanic, and dorso-ventrally flattened. Compagno (1990) further examined sharks in terms of ecomorphotypes which can include diverse taxa that may or may not be related but which are grouped together by similarities in morphology, habitat, and behavior. He considered several oceanic ecomorphotypes: a high-speed or tachypelagic body form that parallels the tunas and is represented by the lamnids *Isurus oxyrinchus* (shortfin mako) and *Lamna* spp. (porbeagle and salmon sharks); the archipelagic (modified tachypelagic) superpredator represented by the white shark; the macrooceanic morphotype with long pectoral fins such as the blue shark (*Prionace glauca*), oceanic whitetip shark (*Carcharhinus longimanus*),

TABLE 1.1

Epipelagic Oceanic Elasmobranchs

Family	Species	Distribution/Depth	Size Range (TL)
Somniosidae	<i>Scymnodalatias albicauda</i>	Southern Ocean 150–510 m	>20–111 cm
Dalatiidae	<i>Euprotomicrops bispinatus</i>	Circumglobal 0–400 or 1800 m	8–27 cm
	<i>Isistius brasiliensis</i>	Circumglobal 0–>1000 m	14–50 cm
	<i>Squaliolus laticaudus</i>	Nearly circumglobal 200–500 m	Attains 28 cm
Rhincodontidae	<i>Rhincodon typus</i>	Circumglobal 0–1000 m	50–1200 cm
Pseudocarchariidae	<i>Pseudocarcharias kamoharai</i>	Circumglobal 0–600 m	40–118 cm
Megachasmidae	<i>Megachasma pelagios</i>	Circumglobal 150–1000 m	Attains 550 cm
Alopiidae	<i>Alopias pelagicus</i>	Indo-Pacific 0–150 m	130–390 cm
	<i>Alopias superciliosus</i>	Circumglobal 0–700 m	100–484 cm
	<i>Alopias vulpinus</i>	Circumglobal 0–650 m	115–570 cm
Cetorhinidae	<i>Cetorhinus maximus</i>	Atlantic and Pacific 0–1000 m	150–1000 cm
Lamnidae	<i>Carcharodon carcharias</i>	Circumglobal 0–1280 m	130–600 cm
	<i>Isurus oxyrinchus</i>	Circumglobal 0–650 m	60–394 cm
	<i>Isurus paucus</i>	Circumglobal Depth range uncertain	97–417 cm
	<i>Lamna nasus</i>	North and South Atlantic, South Pacific, and South Indian Oceans 0–370 m	70–324 cm
	<i>Lamna ditropis</i>	North Pacific 0–225 m	40–300 cm
Carcharhinidae	<i>Carcharhinus falciformis</i>	Circumglobal 0–500 m	70–330 cm
	<i>Carcharhinus longimanus</i>	Circumglobal 0–150 m	60–350 cm
	<i>Prionace glauca</i>	Circumglobal 0–1000 m	35–383 cm
Dasyatidae	<i>Pteroplatytrygon violacea</i>	Circumglobal 0–>100 m	16–80 cm disc width
Mobulidae	<i>Manta birostris</i>	Circumglobal Near surface (0–? m)	122–670 cm disc width

TABLE 1.2

Secondary* Epipelagic Oceanic Elasmobranchs

Family	Species
Squalidae	<i>Squalus acanthias</i>
Somniosidae	<i>Scymnodalatias oligodon</i>
	<i>Zameus squamulosus</i>
Etmopteridae	<i>Etmopterus pusillus</i>
	<i>Etmopterus bigelowi</i>
Dalatiidae	<i>Isistius plutodus</i>
	<i>Squaliolus aliae</i>
Triakidae	<i>Galeorhinus galeus</i>
Carcharhinidae	<i>Carcharhinus signatus</i>
Sphyrnidae	<i>Sphyrna lewini</i>
Mobulidae	<i>Mobula japonica</i>
	<i>Mobula thurstoni</i>

* Species that might be argued to be epipelagic and oceanic, but not included in this chapter.

TABLE 1.3

Number and Percentage of Oceanic Species Relative to All Species in That Order

Order	No. of Oceanic Species	% of Oceanic Species
Squaliformes	4	3.1
Orectolobiformes	1	3.0
Lamniformes	11	73.3
Carcharhiniformes	3	1.3
Myliobatiformes	2?	
Total	21	2.8

silky shark (*C. falciformis*), thresher sharks (*Alopias* spp.), longfin mako (*Isurus paucus*), and megamouth shark (*Megachasma pelagios*); the microoceanic morphotype of small- or moderate-sized sharks with long fusiform bodies and small pectoral fins such as dwarf members of the squaliformes and the crocodile shark (*Pseudocarcharias kamoharai*); the rhomboidal form of the pelagic stingray (*Pteroplatytrygon violacea*); and the aquilopelagic morphotype of the manta ray (*Mobula brevirostris*).

Compagno (2008) suggests that the relatively low diversity of extant pelagic chondrichthyans, as in freshwater, is evidence that the open ocean is a marginal habitat for this group when compared to the high diversity of oceanic teleosts and cephalopods. Pelagic sharks are best known from the epipelagic zone, which contains the highest known diversity of species and the largest biomass. Indeed, the cosmopolitan blue shark is (or was) arguably the most wide-ranging and abundant chondrichthyan.

1.2.2 Biogeography

All species in Table 1.1 are widespread, with most having circumglobal distributions. Nine species have primarily tropical distributions, eight are found in tropical and

temperate waters (five of these are more tropical and three are more temperate), and four have temperate distributions. In tropical reef fish, vagility or dispersal ability is lowest in small benthic species that lack pelagic eggs or larvae (Rosenblatt 1963; Rosenblatt and Waples 1986). Vagility is also inversely correlated with speciation, intrataxon diversity, and endemism. Musick, Harbin, and Compagno (2004), in their account of shark zoogeography, found that vagility increased with body size and was lowest in benthic species, higher in benthopelagic species, and highest in pelagic species. Coastal sharks also tend to have lower vagility than bathyal or oceanic species. These authors found a strong relationship between species diversity and body size, with about eight times the number of small species (<100 cm) than very large species (>300 cm). They also found that, regardless of size, benthic species had distributional ranges more than five times smaller than pelagic sharks. Musick, Harbin, and Compagno (2004) suggested that smaller benthic species that have reduced distributional ranges become more easily isolated, leading to higher rates of speciation and greater diversity than large, wide-ranging species. Of the species considered to be primarily epipelagic and oceanic in Table 1.1, 14 (67%) are very large (>300 cm). However, it is interesting that 19% are small (<100 cm), of which three are diminutive squaliform sharks in the family Dalatiidae. These species make diel migrations between near surface waters and depths of 500 to more than 1000 m and may be associated with specific water masses (Musick, Harbin, and Compagno 2004). It is possible they are able to take advantage of currents at different depths to aid in their dispersal.

The antitropical distributions of the porbeagle (*Lamna nasus*) and basking shark (*Cetorhinus maximus*) probably arose during glaciation periods when the tropical zone was more constricted, allowing these species to cross the tropics by remaining at depth in the equatorial zone. The salmon shark (*Lamna ditropis*) probably diverged from the porbeagle after closure of the Arctic seaway by an ice sheet in the late Cenozoic (Reif and Saure 1987). The absence of the pelagic thresher (*Alopias pelagicus*) from the Atlantic is more enigmatic. It is tempting to presume that this species evolved after the formation of the Isthmus of Panama and that Cape Horn and the Cape of Good Hope acted as barriers to the distribution of this tropical species into the Atlantic. However, this hypothesis is contradicted by the fossil record and it may be that the pelagic thresher was initially present in the Atlantic and subsequently died out (Musick, Harbin, and Compagno 2004).

1.3 Life-Histories

1.3.1 Reproductive Biology and Strategies

It is no great surprise that all epipelagic oceanic elasmobranchs considered in this chapter are viviparous. All known oviparous chondrichthyans lay, and usually attach, their eggs on the substrate that is not really an option for the species in question, and pelagic eggs do not appear to have evolved in this group (Musick and Ellis 2005). As discussed in Wourms, Grove, and Lombardi (1988), the relationship between viviparity and the ecology of viviparous species is poorly understood and attempts to explain viviparity using general life-history strategy models are inadequate. Viviparity confers a number of obvious advantages that facilitate protection and development of the young, dispersal and parental care with few of the constraints on mobility. Specializations for the transfer of nutrients

to the developing embryo may further enhance survival of the offspring. While viviparity is found in a range of different habitats in elasmobranchs, specific advantages for the epipelagic lifestyle would seem to be associated with freedom from the substrate (for egg laying) and production of well-advanced and self-sufficient young. Viviparous teleosts also have diverse lifestyles and occur in a range of habitats suggesting viviparity is a flexible reproductive strategy in teleosts (Wourms, Grove, and Lombardi 1988). However, the supply method of nutrients to the embryos in teleosts may be restricted by environmental conditions. In one group of teleosts (Poeciliidae), it has been suggested that lecithotrophy is successful in unpredictable environments but that matrotrophy requires a predictable food supply (Thibault and Schultz 1978). Lecithotrophic embryos are nourished by yolk reserves stored in the egg and are not dependent on food availability once vitellogenesis is complete. Conversely, the growth of embryos that rely on transfer of nutrients from the mother may be affected by changes in food availability. The epipelagic lifestyle does not appear to have restricted the methods of embryonic nutrition in elasmobranchs, with the dominant method, oophagy (52%), reflecting the dominance of lamnoid sharks in this habitat. Three (14%) of the species in Table 1.1 are placentotrophic and seven (33%) are either lecithotrophic or histotrophic. This dominance of matrotrophic methods would suggest, if the teleostean argument applied, that the oceanic epipelagic habitat provided a predictable food supply; however, this seems counterintuitive. The method of embryonic nutrition even varies among the four giant plankton feeders. The temperate basking shark and mainly tropical megamouth shark are oophagous, the tropical manta ray is histotrophic, and in the mainly tropical whale shark (*Rhincodon typus*) the method of nutrient transfer to the embryos is uncertain. Whale sharks were once thought to be oviparous, but they are now known to show a more primitive form of viviparity where the egg cases are retained inside the female until hatching.

Snelson et al. (2006) state that pelagic elasmobranchs have slightly larger litters of smaller young than coastal elasmobranchs and suggest this is due to the challenges of their respective habitats. These authors suggest that food and predators are more abundant in coastal habitats and that selective pressures have consequently produced larger, faster growing young to take advantage of more food and to combat higher predation. However, I suggest that this relationship is not clear and that, if anything, the reverse applies. Indeed, most authors have concluded that open waters are more dangerous than complex coastal habitats due to a lack of spatial refuges (Branstetter 1990; Heithaus 2001, 2007). So, it could be argued that large, well-developed young that are less vulnerable to predation might be selected for in the pelagic realm where protected nurseries or cryptic avoidance is less possible. Where information is available, birth size in the species from Table 1.1 varies from 3.8% (whale shark) to 38% (crocodile shark) of maximum size. However, the majority of species (60%) had a birth size between 15% and 25% of maximum size and 30% had a birth size greater than 25% of maximum size. In only 10% of species was the birth size less than 15% of maximum size. The only recorded litter size in the whale shark was 300 (Joung et al. 1996) while the blue shark, which has an average litter size of 30 to 40, can have up to 135 pups. In these two species it seems that a higher natural mortality associated with a small birth size (3.8% to 11.2% of maximum size) is traded off against larger litter sizes. Such trade-offs between offspring number and size are common in many taxa.

It is interesting that relatively few pregnant females of several of these epipelagic elasmobranchs have been recorded. While for some this is due to relatively few records for the species in general, for others like the basking shark, whale shark, white shark, short-fin mako, and manta ray this is not the case and they are common and frequently caught

(even targeted commercially) species. In the case of the white shark this may partly be explained by escapement of these large, powerful fish but it is also possible that pregnant females of these species are occupying a habitat or behaving in a way that makes them less likely to be captured. Epipelagic elasmobranchs show a diversity of gestation periods (4 to 18 months) and breeding frequencies that suggest this habitat does not impose any stringent restrictions on these parameters. The oceanic environment does, however, pose potential challenges, including encountering mates and a lack of protected nursery areas for neonates and small juveniles. Little is known about mechanisms associated with mating areas in these species; but in the relatively well-studied blue shark, females are able to store sperm for long periods after mating and there are complex movement patterns that bring the normally spatially segregated sexes together for mating (see Section 1.3.4). Again, little is known about nursery areas for most of these species but some (shortfin mako, thresher shark, silky shark) utilize coastal areas and others like the blue shark have spatially segregated areas in oceanic waters that are usually in more productive zones at higher latitudes. In salmon sharks, pupping and nursery grounds have been proposed both along the transition boundary of the subarctic and central Pacific currents (Nakano and Nagasawa 1996) and nearshore from the Alaska-Canada border to the northern end of Baja California, Mexico (Goldman and Musick 2008).

1.3.2 Age and Growth

It is not obvious that the epipelagic environment imposes any specific selective forces on growth rates or longevity of elasmobranchs. One probable exception is that the neonates of the whale shark and blue shark that are born at a relatively small size would need to grow quickly through the predation window. Of the 21 species listed in Table 1.1, age and growth are reasonably well studied in five species and there is some information for another eight. Age and growth parameters for these 13 species are shown in Table 1.4. Nothing is known about age and growth in eight species.

1.3.3 Feeding Ecology and Behavior

Three main feeding strategies are employed by epipelagic oceanic elasmobranchs; there are the huge planktivorous species, vertically migrating diminutive dalatiids and a diverse group of mostly lamnid and carcharhinid species that feed mainly on fish and cephalopods. The plankton feeders (those considered here) comprise the whale, basking and megamouth shark, and the manta ray. These species exploit different temperature regimes and depth strata and have different morphological adaptations to capture their prey.

The whale shark occurs in tropical and warm temperate waters around the world, both in the open ocean but also close to the coast where it takes advantage of seasonal pulses of productivity. The prey taken varies considerably in size from coral and teleost spawn, krill, copepods, and jellyfish to small cephalopods and schooling fishes such as anchovies, mackerel, and even tuna (see reviews by Compagno 2001; Stevens 2007). Taylor, Compagno, and Struhsaker (1983) reviewed the feeding biology and filter apparatus of whale sharks in relation to the basking and megamouth shark. They concluded that the dense filter screens of whale sharks act as more efficient filters for short suction intakes and confer more versatile feeding behaviors, in contrast to the flow-through system of the other two species. The filter apparatus of the whale shark comprises parallel plates that transversely bridge the internal gill openings and connect adjacent holobranchs (Taylor,

TABLE 1.4
Age and Growth Parameters for Epipelagic Oceanic Elasmobranchs

Species	Area	L_{∞}	K	T_0	Age at Maturity	Maximum Age	References
<i>R. typus</i>	South Africa				F-22 M-20	F-19-27 M-20-31	Wintner 2000
<i>A. pelagicus</i>	Taiwan	F-197.2	F-0.085	F-7.67	F-9	F-16	Liu et al. 1999
		M-182.2	M-0.118	M-5.48	M-7-8	M-14	
<i>A. superciliosus</i>	Taiwan	F-224.6	F-0.092	F-4.21	F-12-13	F-20	Liu et al. 1998
		M-218.8	M-0.088	M-4.22	M-9-10	M-14	
<i>A. vulpinus</i>	California	F-464.3	F-0.124	F-3.35	F-5	F-22	Smith et al. 2008
		M-416.2	M-0.189	M-2.08	M-5	M-19	
<i>C. maximus</i>	Worldwide	Not currently possible to age from vertebrae					Natanson et al. 2008
<i>C. carcharias</i>	South Africa	544-PCL	0.065	-4.4	8-13	13(35?)	Wintner and Cliff 1999
<i>I. oxyrinchus</i>	NW Atlantic	366-FL	F-0.087		F-18	F-32	Natanson et al. 2006
		253-FL	M-0.125		M-8	M-29	
<i>L. nasus</i>	NW Atlantic	F-369.8	F-0.061	F-5.9	F-13	F-24	Natanson et al. 2002
		M-257.7	M-0.03	M-5.87	M-8	M-25	
<i>L. ditropis</i>	NW Pacific	F-203.8-PCL	F-0.136	F-3.95	F-8-10	F-17	Tanaka 1980
		M-180.3-PCL	M-0.171	M-3.63	M-5	M-25	
	NE Pacific	F-207.4-PCL	F-0.17	F-2.3	F-6-9	F-20	Goldman 2002
		M-182.8-PCL	M-0.23	M-1	M-3-5	M-17	

<i>C. falciiformis</i>	Gulf of Mexico	311.0	0.101	-2.72	F-12 M-10	F-22 M-20	Bonfil et al. 1993
	Taiwan	F-341.0 M-315.0	F-0.077 M-0.091	F-3.03 M-2.32	F-8-10 M-9	F-11 M-14	Joung et al. 2008
<i>C. longimanus</i>	Central Pacific	244.6-PCL	0.103	-2.70	4-5	11	Seki et al. 1998
	South Atlantic	284.9	0.100	-3.39	6-7	F-17 M-13	Lessa et al. 1999
<i>P. glauca</i>	North Pacific	F-304.0 M-369.0	F-0.16 M-0.1	F-1.01 M-1.38			Tanaka et al. 1990
	Central Pacific	F-243.3-PCL M-289.7-PCL	F-0.144 M-0.129	F-0.85 M-0.76	F-5-6 M-4-5	F-15-16 M-15-16	Nakano 1994
	NW Atlantic	F-310.0-FL M-282.0-FL	F-0.13 M-0.18	F-1.77 M-1.35	F-5 M-5	F-15 M-16	Skomal and Natanson 2003
<i>P. violacea</i>	California	F-103 M-67	F-0.32 M-0.8	F-8.2 M-5.6	3	8.6-12	Mollet et al. 2002

F = Female; M = Male; PCL = Precaudal Length; FL = Fork Length; L_{∞} is cm total length (unless otherwise noted); age is in years.

Compagno, and Struhsaker 1983). Whale sharks have been observed feeding on copepods by swimming through the patches, lifting their heads partly out of the water and gulping them in. They are also reported to feed almost vertically in the water, sucking in prey near the surface. Whale sharks can capture larger, more active nektonic prey such as small fishes and squid, but are not so well adapted for concentrating diffuse planktonic food, probably making them more dependent on dense aggregations of prey. Certainly, whale sharks arrive predictably at annual mass spawning events in various parts of the world, and individuals return in following years to the same site. Satellite tracking has revealed extensive oceanic movements (see review in Stevens 2007) and documented dives to at least 1000 m depth (Graham, Roberts, and Smart 2005; Wilson et al. 2006). Like most pelagic sharks and large teleosts, whale sharks show diel behavior, generally diving deeper during the day and remaining closer to the surface at night, probably associated with vertical migration of their prey. However, this pattern may vary when the sharks are feeding on dense prey concentrations when in coastal waters, probably due to differences in the behavior of their prey (Wilson et al. 2006).

The basking shark exploits the plankton-rich waters of the temperate zones, having an antitropical distribution. They feed on microscopic plankton such as copepods, trapping them on their unique gill rakers with the help of mucus secreted in the pharynx. The filter apparatus, with its enormous gill cavities and streamlined gill raker denticles, is adapted for high rates of water flow generated by swimming and is a more dynamic process than in the whale or megamouth sharks. When feeding they usually cruise near the surface with their mouth open and gill slits distended, occasionally closing their mouth to swallow their prey. Assuming a swimming speed of 3.7 km/h, an average adult basking shark may filter 2000 t of water per hour (Compagno 2001). Their large livers (up to 25% of body weight) are high in squalene oil, a low-density hydrocarbon, giving them near-neutral buoyancy. They actively locate plankton concentrations at the surface at tidal fronts or at boundaries of water masses, which they probably detect from chemical cues, and may occur in aggregations in coastal waters during spring and autumn plankton blooms. Basking sharks have been reported to lose their gill rakers in winter and along with the low plankton concentrations at this time of year it was hypothesized that they hibernated on the bottom. Certainly, these sharks have been caught in trawls near the bottom in winter in New Zealand (Francis and Duffy 2002). However, recent satellite tracking work in the North Atlantic has shown that they do not hibernate during winter but instead make extensive horizontal (up to 3400 km) and vertical (to more than 750 m depth) movements to take advantage of productive continental shelf and slope habitats during summer, autumn, and winter (Sims et al. 2003; Skomal, Wood, and Caloyianis 2004). Basking sharks probably also exploit the mesopelagic realm for plankton and usually show diel behavior, occurring deeper during the day than at night. However, when in productive shelf waters, like whale sharks, they may at times reverse this pattern in response to prey behavior (Sims et al. 2005).

The megamouth shark probably exploits both epipelagic and mesopelagic habitats where it feeds on euphausiid shrimps, copepods, and jellyfish in mainly tropical and subtropical waters. This rarely reported (it was only discovered in 1976) but probably widespread species has a soft, flabby body, heterocercal tail, small gill slits, and low-flow filter apparatus that suggests it is a less active species than the whale or basking shark. Taylor, Compagno, and Struhsaker (1983) suggested it might swim slowly through prey schools with its jaws wide open occasionally closing its mouth and contracting its pharynx to expel water and concentrate its prey before swallowing it. Tissue in the mouth may be bioluminescent, acting to attract prey (Taylor, Compagno, and Struhsaker 1983), and Compagno (2001) has

also suggested that it may use its mouth as a bellows to suck in prey. However, Nakaya, Matsumoto, and Suda (2008) consider that the megamouth shark has a unique feeding mechanism among sharks, which they call engulfment feeding, that is typically seen in balaenopterid whales. As noted by these authors, this species has a terminal mouth, large gape, small gill openings, long bucco-pharyngeal cavity, and unique elastic skin and loose connective tissue around the pharyngeal region. When feeding, the head is raised, opening the mouth and allowing water to flow in by suction. As the shark swims, it gulps water and the forward motion forces the jaws fully open and fills the fully expanded bucco-pharyngeal cavity stretching the skin around the pharyngeal region. The mouth is then closed forcing the water out through the gill slits, sieving the prey on the gill rakers. The weak body structure relative to whale and basking sharks may be an adaptation to a more nutrient-poor deepwater habitat, as seen in various mesopelagic teleosts (Taylor, Compagno, and Struhsaker 1983). However, Compagno (2001) noted that the coloration, liver oil composition, and catch records were more suggestive of an epipelagic rather than a deepwater habitat; he may also have been influenced by the two-day acoustic track of a megamouth shark that showed strong diel behavior, swimming at 12 to 25 m at night and descending to 120 to 166 m during the day. However, given that most epipelagic sharks regularly dive to at least 600 m, the usual depth preferences of the megamouth shark are still uncertain.

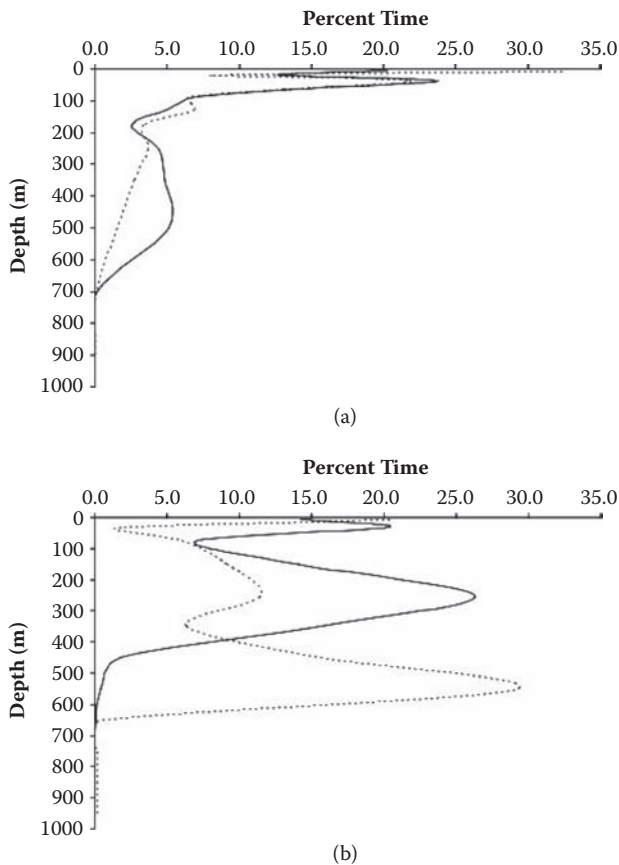
The manta ray has a similar, mainly tropical, distribution to the whale shark and probably exploits similar resources with the two species often found in the same area. They employ a dynamic filtering process, swimming slowly and channeling the plankton into their terminal mouths with their cephalic scoops. However, little is known about the depth behavior of manta rays or of the specific adaptations of their filtering plates or their preferred planktonic prey.

Of the pelagic and oceanic squaloids, the whitetail dogfish (*Symnodalutias albicauda*) is known from only a few specimens and nothing is known about its diet and feeding behavior. It is probably mainly mesopelagic or bathypelagic, migrating into the epipelagic zone at night, feeding mainly on small teleosts and cephalopods. The biology of the diminutive dalatiids the pygmy shark (*Euprotomicrus bispinatus*) and the spined pygmy shark (*Squaliolus laticaudus*) is also poorly known. Both are vertical migrators, ascending at night into the epipelagic zone from meso- or even bathypelagic depths. Both feed on small teleosts, cephalopods, and crustaceans. It is not known whether their luminous organs play any role in feeding behavior. The cookie-cutter shark (*Isistius brasiliensis*) is well known for its "cookie-cutting" behavior and is ectoparasitic on large fish and marine mammals to which it attaches itself with its suckorial lips and modified pharynx. It then spins, boring out a plug of flesh with its large lower teeth and leaving a crater-shaped wound on its victim. It has a large, oily liver that makes it neutrally buoyant and able to hang motionless in the water; victims may be lured by the shark's strong luminescence or by the patch of skin lacking luminescence that occurs under its head and that may resemble the silhouette of prey for the cookie-cutter sharks' hosts. It is probably bathypelagic during the day and rising to near the surface at night. These little sharks have even attacked nuclear submarines, leaving crater-marks on their rubber sonar domes. The diet also includes whole prey, particularly squid, some of which are nearly as large as their captors.

Within the lamnoid sharks, the medium-sized crocodile shark is poorly known. Its grasping dentition suggests it feeds mainly on small fish, cephalopods, and crustaceans and its large eyes imply that it is a visual hunter, living mainly in mesopelagic depths but migrating to and feeding in the epipelagic zone at night. Its squalene-rich liver oil is thought to aid in buoyancy control or vertical behavior.

The alopiid sharks have developed a highly specialized body form with their enormously elongated tails that are used to round up and then stun the small fishes on which they feed (Compagno 2001). In the thresher shark (*Alopias vulpinus*) (and maybe the two other species) the vertebrae near the tail-tip are broadened and strengthened to give it rigidity when striking their prey. While the three thresher shark species all appear to feed on similar prey, they exploit slightly different habitats. The pelagic thresher is predominantly tropical in the Indo-Pacific with a known depth distribution down to 150 m, although it probably goes deeper than that. The bigeye thresher (*Alopias superciliosus*) occurs in all tropical and warm temperate seas and satellite tracking of one individual in Australia (Figure 1.1) showed strong diel movements, with most of the day spent below the thermocline at 300 to 500 m (6°C to 12°C) and the night between 10 and 100 m (20°C to 26°C). Short-term tracking in the eastern Pacific showed similar movements from deeper (200 to 550 m) and cooler (6°C to 11°C) water during the day into the mixed layer (50 to 130 m) and warmer temperatures (15°C to 26°C) at night (H. Nakano reported in Smith et al. 2008). It may be able to maintain body temperatures above that of the surrounding sea water to conserve heat in its brain and eyes during its periods at depth (Carey et al. 1971). Its large eye suggests it is a visual predator, feeding in the mesopelagic layer during the day and in the epipelagic zone at night. Compagno (2001) suggested the keyhole-shaped orbits extending onto the dorsal surface of the head may help it to strike prey from below with its tail. Temperate waters of all oceans are the main habitat of the thresher shark, although it also occurs in tropical seas. Like the lamnids, this powerful swimmer (that often jumps clear of the water) has a well-developed heat-exchanging circulatory system, enabling it to maintain body temperatures higher than that of the surrounding water, which probably enables it to exploit cooler water than the other alopiids (Bone and Chubb 1983). Satellite tracking of one individual in Australia (Figure 1.1) showed daily vertical migrations, with most of the night spent in the top 50 m while during the day most time was spent at 300 to 400 m. The feeding behavior of all the thresher sharks results in them often being tail hooked in longline fisheries presumably as a result of them trying to stun the bait.

The lamnid sharks are highly specialized for a pelagic lifestyle and show parallel evolution in many of their morphological and physiological adaptations with the tunas. They have a thunniform body shape, cardiovascular and muscular systems that allow prolonged aerobic swimming speeds, and they are endothermic (Compagno 2001). Endothermy is best developed in the salmon shark and porbeagle, which have consequently been able to exploit subarctic and subantarctic waters where temperatures may be only a few degrees above zero. In the salmon shark, body temperatures may be as much as 15.6°C and stomach temperatures 21.2°C above the surrounding water, and increased amounts of certain proteins in the heart muscle allow it to maintain cardiac contractility in the cold (Goldman et al. 2004; Weng et al. 2005). This species occurs from the surface to about 370 m in subarctic waters in the Gulf of Alaska during winter, with 98% of the time of satellite-tracked individuals spent above 150 m. During this season they are probably feeding mainly on herring, while during the summer in the same area they feed on salmon. Some sharks migrated into subtropical waters during winter where they showed bimodal diving behavior, with one area of occupancy at 100 to 200 m and another below the thermocline at 300 to 500 m, going as deep as 830 m (Weng et al. 2005). Porbeagles tracked in the northeast Atlantic showed considerable plasticity in behavior, probably associated with feeding. In summer, they occupied shelf habitats utilizing the whole water column and probably feeding on both pelagic and demersal fish. In autumn, they occupied cooler shelf-edge habitats diving down to 550 m, possibly exploiting prey not available to ectothermic predators such as the blue shark (Pade et al. 2009).

**FIGURE 1.1**

Percentage time-at-depth recorded by pop-up satellite archival tags from four species of epipelagic oceanic sharks. (a) Solid line is blue shark, dotted line is shortfin mako. (b) Solid line is thresher shark, dotted line is bigeye thresher.

At the other extreme, the longfin mako is a tropical species and has a poorly developed heat-exchanger system. *Isurus* and *Lamna*, with their pointed, grasping teeth, feed predominantly on teleost fishes and cephalopods. In the shortfin mako, probably the fastest of all sharks, large individuals (over 3 m total length [TL]) have broader, cutting teeth and can take billfish and even small cetaceans. Satellite tracking of one individual in Australia showed that it spent 82% of its time at less than 100 m and 4% of its time at greater than 300 m, diving as deep as 620 m (Figure 1.1).

The white shark is described by Compagno (2008) as a superpredator and is one of the few sharks that, once it reaches a subadult size, regularly feeds on marine mammals. Its large cutting teeth and powerful jaws equip it for this purpose and it has a range of hunting strategies depending on the prey being targeted (Bruce, Stevens, and Malcolm 2006). Acoustic and satellite tracking studies have led to a great increase in our knowledge of the movements and behavior of this shark in the last 10 years. Around seal colonies, they patrol particularly the entry and exit points hunting mainly during the day, swimming close to the bottom and attacking their prey from underneath. When attacking large prey such as elephant seals they may first immobilize them, withdraw a safe distance, and then

only move in to feed once the seal is dead or severely weakened. Some seasonal movement patterns demonstrated from satellite tracking studies in Australasia and California have been linked to whale migrations (Weng et al. 2007) and it has been hypothesized that these sharks may prey upon the calves; however, this has yet to be substantiated. It is certainly intriguing why individuals would leave what appear to be productive feeding areas to travel into open ocean areas and oceanic island locations (see Section 1.3.4). When in open ocean areas they may dive regularly to >300 m and occasionally to >700 m and experience temperatures of 5°C to 26°C (Boustany et al. 2002). White sharks also prey on a variety of teleost and chondrichthyan fishes, as well as marine birds, turtles, cephalopods, and other molluscs and crustaceans.

The oceanic pelagic carcharhinids feed mainly on teleost fishes and cephalopods but the patchy nature of food resources leads to them opportunistically taking other prey. The blue shark, with its slender body and long pectoral fins, is well adapted to use ocean currents and is an inquisitive and persistent (if not immediately aggressive) predator that will also take birds and may consume cetaceans, although probably mainly through scavenging. Juvenile blue sharks will feed on aggregations of large planktonic crustaceans and have gill rakers that may aid in trapping these small prey items. Like most large pelagic predators, blue sharks show strong diel behavior, diving deeper during the day and remaining nearer the surface at night, probably following the deep-scattering layer and associated prey resources. Pop-off archival tag data from three sharks off the east coast of Australia showed that they spent between 35% and 58% of their time in depths of less than 50 m, between 52% and 78% of their time in less than 100 m, and between 10% and 16% in depths greater than 300 m (Figure 1.1). They dived as deep as 1000 m (the limit of the depth sensor). Blue sharks have been reported to show tropical submergence but there was little evidence of this in these data, with the sharks spending much time at or near the surface in 26°C to 27°C water. While most of their fish prey is pelagic, bottom fishes also feature in the diet in coastal waters. They are known to feed throughout the day and night but have been reported to be more active at night, with highest activity in the early evening (Sciarrotta and Nelson 1977).

The silky shark is often associated with tuna schools and will also follow groups of cetaceans; it is most likely these sharks are feeding on the same prey rather than on the tuna or cetaceans. It has been suggested that the mottled white tips on the fins of the oceanic whitetip shark may mimic a school of baitfish, attracting such prey as tunas and mackerels (Myrberg 1991). Compagno (1984) also reported an instance where several of these sharks cruised erratically among a school of small tuna that were feeding on baitfish. They did not chase the tuna but apparently just waited for them to swim into their jaws! Like the blue shark, the oceanic whitetip shark is a persistent predator, although it is more aggressive than the former species.

With the exception of the plankton-feeding mobulid rays, the pelagic stingray is the only batoid to exploit the epipelagic oceanic realm where its diet consists mainly of jellyfish, squid, crustaceans, and fishes. While it is relatively abundant and successful in this environment, little is known about the feeding behavior of this species.

1.3.4 Spatial Dynamics, Population Structure, and Migrations

The challenges of exploiting often patchy food resources and of finding mates and productive areas for giving birth in the oceanic environment have resulted in many of the species having complex population structures and migrations that we are still far from understanding. Our knowledge is greatest for a few of the species that are commonly taken

by fisheries and, in terms of movements, that have also been the subject of large tagging programs and recent studies using electronic tags. Without question we know most about the blue shark, which provides an excellent example of specialized adaptations to the oceanic lifestyle. While sex and size segregation is widespread among chondrichthyans, few species demonstrate it better than the blue shark. Recreational and commercial fisheries data provide a complex picture of sex and size structuring by both latitude and longitude in most oceans, although less is known from the Indian Ocean. Segregation is thought to reduce, through habitat partitioning, competition for food resources and to protect subadult females from the dangers associated with male mating behavior and pups from adult predation (Nakano 1994). Off the east coast of Australia, there is a decrease in body size and an increase in the proportion and abundance of females with increasing latitude so that at high latitudes (40°S) the population mainly comprises juvenile females (Stevens and Wayte 2008). Juveniles also predominate in higher latitudes of the North Pacific, North Atlantic, and Indian Ocean (Suda 1953; Gubanov and Grigor'yev 1975; Nakano 1994; Kohler and Turner 2008). The blue shark is highly migratory, with complex movement patterns related to water temperature, reproduction, and the distribution of prey. A seasonal shift in population abundance to higher latitudes is associated with high-productivity oceanic convergence or boundary zones. Tagging studies of blue sharks have demonstrated extensive movements in the North Atlantic, suggesting a single stock with numerous trans-Atlantic migrations (Kohler, Casey, and Turner 1998; Kohler and Turner 2008), which are probably accomplished by swimming slowly, but assisted by the major current systems (Stevens 1976, 1990; Casey 1985). More limited tagging in the Pacific has also shown extensive movements of up to 9200 km (P. Saul, NIWA, Wellington, personal communication).

A mainly tagging-based movement model has been developed for blue sharks in the North Atlantic (Casey 1985; Stevens 1990; Kohler and Turner 2008). In spring and summer the western Atlantic population consists mainly of juveniles, subadult females, and adult males that move inshore from the Gulf Stream. During summer, they extend northward in large numbers along the continental shelf from southern New England to the Grand Banks, where they feed and mate (Casey 1985). During late summer, autumn, and winter, subadult females and adult males move offshore into the Gulf Stream or south, with some traveling as far as the Caribbean and South America. Some subadult females, most of which have recently mated, move offshore and travel the current systems to the eastern Atlantic. During winter in the eastern Atlantic, adult females occur off the Canary Islands and African coast at about 27°N to 32°N (Muñoz-Chápuli 1984); many of these are pregnant (Casey 1985). Adult males are found farther north off Portugal, as are juvenile and subadult females that have moved south from northern Europe. Immature males are not caught in this region and may be offshore. Some mating of these subadult females probably occurs during winter. In spring and summer, adults of both sexes are found from 32°N to 35°N, where they mate. Immature males also occur in this area. Adult females seem to have a seasonal reproductive cycle, while males and subadult females are sexually active throughout the year (Pratt 1979; Stevens 1984). In summer, the immature females migrate north to northern Europe where they are common off the coast of southwestern England (Stevens 1976). Birth probably occurs in early spring. Nursery areas are found in the Mediterranean and off the Iberian peninsula, particularly off Portugal and near the Azores (Aires-da-Silva, Ferreira, and Pereira 2008), but extend as far north as the Bay of Biscay. Juvenile sharks remain in the nursery areas and do not take part in the extensive migrations of the adults until they reach a length of about 130 cm (Stevens 1976; Muñoz-Chápuli 1984). In the eastern Atlantic, mature females, pregnant sharks, and newborn young are common during certain seasons, and it seems that a large proportion of the

North Atlantic breeding population occurs in this region (Casey 1985). A similar movement cycle associated with reproduction appears to occur in the South Atlantic, although the picture is only slowly starting to be pieced together from fisheries data.

In the North Pacific, Nakano (1994) suggested that mating takes place in early summer at 20°N to 30°N, and that the pregnant females migrate north to the parturition grounds by the next summer. Birth occurs in early summer in pupping grounds that are located at 35°N to 45°N. The pupping and nursery areas are located in the subarctic boundary where there is a large prey biomass for the juveniles, who remain there for 5 to 6 years prior to maturity (Nakano and Nagasawa 1996). Adults occur mainly from equatorial waters to the south of the nursery grounds.

The picture is less clear for the shortfin mako. Although sex and size segregation occur, for example, small juveniles are found mainly in coastal waters, large males occur in the northeast Atlantic, and large females in the northwest Atlantic, there is no evident pattern of changes in sex ratio and size with latitude. Results from a large tagging study in the northwest Atlantic show that the shortfin mako makes extensive movements of up to 4543 km, with 36% of recaptures caught at greater than 556 km from their tagging site (Casey and Kohler 1992; Kohler, Casey, and Turner 1998). However, only one fish crossed the Mid-Atlantic Ridge, suggesting that trans-Atlantic migrations are not as common as in the blue shark. Casey and Kohler (1992) proposed the following hypothesis for migrations of the shortfin mako in the western North Atlantic. From January to April they are found along the western margin of the Gulf Stream north to Cape Hatteras. In April and May, as inshore shelf waters start to warm and the Gulf Stream strengthens, they move onto the shelf between Cape Hatteras and Georges Bank. From June to October they occur on the shelf between Cape Hatteras and the southern Gulf of Maine, as well as offshore to the Gulf Stream. They suggest that this area may be the main feeding grounds for a large part of the juvenile and subadult population in the western North Atlantic. During autumn and winter, they move offshore and south to the Gulf Stream and Sargasso Sea, with some also entering the Caribbean and Gulf of Mexico. The core distribution in the western North Atlantic seems to be between 20°N and 40°N and bordered by the Gulf Stream in the west and the Mid-Atlantic Ridge in the east (Casey and Kohler 1992). More limited data from the Pacific also show large movements of up to 5500 km, although most tag returns from New Zealand and southeast Australia are restricted to the southwest Pacific (see summary in Stevens 2008).

Tagging and genetic data suggest there is only one population of the blue shark in the North Atlantic, although there is some evidence that the Mediterranean stock may be separate; stock structure in other oceans is poorly understood although there is some exchange across ocean basins. Based on tagging and genetic data, northeast and northwest Atlantic populations of the shortfin mako appear to be separate, at least for management purposes, with little exchange between them. Several fisheries stocks of this species probably occur across the other oceans (Heist 2008).

In the salmon shark, the western side of the North Pacific is male dominated and the eastern side female dominated; dominance increases with latitude as does size (Goldman and Musick 2008). Satellite tracking of salmon sharks has demonstrated seasonal migrations from subarctic to temperate and subtropical regions of up to 18,220 km that are associated with feeding or reproduction. In the summer and autumn, the mainly female sharks were feeding in the Gulf of Alaska but in winter some sharks moved as far south as Hawaii and California, while others remained in Alaskan waters (Weng et al. 2005). Conventional tagging of the porbeagle in the North Atlantic has demonstrated movements from the English Channel to northern Norway (2370 km) and northern Spain and in the northwest

Atlantic from New England north to Newfoundland and offshore 1861 km into oceanic waters (Stevens 1990; Kohler, Casey, and Turner 1998). Tagging data suggest that northeast and northwest Atlantic stocks of porbeagle are essentially separate. There appears to be no exchange between northern and southern hemisphere populations, and the number of stocks in the southern hemisphere is unknown.

Observations on white sharks at some viewing sites such as the Neptune Islands off South Australia suggest relatively nomadic habits with only limited time spent at these sites, although they may be revisited periodically and in successive years. However, tagging at Guadalupe Island, Mexico, shows that at this site the sharks remain there for 5 to 8 months each year (Domeier and Nasby-Lucas 2008). The white shark makes seasonal movements and in Australia satellite-tracked juveniles and subadults move northward up both coasts in autumn as far as about 22°S where they spend the winter before returning to southern Australian waters in spring. Some of these small juveniles show site specificity to certain beaches on the New South Wales coast, where they appear to be feeding on schooling fishes (Bruce, Stevens, and Malcolm 2006). Subadults tracked in New Zealand have shown movements to the tropical waters of New Caledonia (M. Francis, NIWA, Wellington, personal communication). Trans-Tasman Sea migrations between Australia and New Zealand also occur. A shark tagged off South Africa traveled to northwest Australia in 99 days and returned to the tagging location in just under nine months (Bonfil et al. 2005). A tracking study off California showed that following periods of decreased pinniped abundance at the Farallon Island, offshore migrations of subadult and adult white sharks occurred during November to March. The sharks followed a migration corridor to a focal area 2500 km to the west in the eastern Pacific, with some sharks moving as far as Hawaii. The sharks remained in the eastern Pacific focal area for up to 167 days during spring and summer, occupying depths from the surface to more than 700 m (Boustany et al. 2002; Weng et al. 2007). Interestingly, sharks tagged off Guadalupe Island, Mexico, made annual migrations between December and May to the same area in the eastern Pacific visited by the Farallon Island sharks, and also as far as Hawaii. Both sexes travelled at the same time, but males returned to Guadalupe earlier than females. These long-distance movements are more likely to be associated with feeding than reproduction, but at this stage the targeted prey species are unknown (Domeier and Nasby-Lucas 2008). While some exchange between continents or across ocean basins is suggested by tagging and genetics data, global stock structure is still poorly known (Pardini et al. 2001; Bonfil et al. 2005).

The movements of some whale shark populations are linked to predictable seasonal food pulses in certain areas such as Ningaloo Reef in Western Australia, Gladden Spit in Belize, Holbox, Mexico and Donsol, Philippines, where ecotourism has developed around their presence. Satellite tracking has shown that after leaving Ningaloo Reef, the sharks move northward into the Indian Ocean and sometimes into the waters of Christmas Island and Indonesia (Wilson et al. 2006). Photo-identification studies have shown that individuals may return to Ningaloo in successive years (Meekan et al. 2006). Satellite tracking in other areas has shown both relatively localized and long-distance movements. However, because of difficulties with keeping tags attached to these animals, few regular migratory routes have been identified and interpretation of some long-distance movements is difficult because the tags have remained submerged (consequently giving no positions) for long periods. Sharks tagged in the Seychelles have moved toward the African coast and also to south of Sri Lanka (3380 km; Rowat and Gore 2007). Juveniles tagged off Taiwan moved offshore into the Taiwan Strait and northwestern Pacific to north off Okinawa (5900 km) where they appeared to be related to boundary currents (Hsu et al. 2007). Tagging in the Gulf of California showed mainly localized movements but one individual apparently

travelled 13,000 km into the Pacific Ocean (Eckert and Stewart 2001). Stock structure in the whale shark is poorly understood.

The basking shark appears to be highly migratory and as Compagno (2001) notes it is well known for its seasonal appearance during spring and autumn in large numbers in northern coastal waters of the North Atlantic and North Pacific and its subsequent disappearance in winter. These sharks have been seen in deep water above the continental slopes and in the ocean basins, and it is thought they move into coastal waters to take advantage of seasonal plankton blooms. Satellite tracking has shown long-distance movements (up to 3400 km) mainly associated with the shelf edge (Sims et al. 2003; Skomal, Wood, and Caloyianis 2004). However, one shark tagged off the British Isles migrated nearly 10,000 km across the North Atlantic to off Newfoundland (Gore et al. 2008), providing evidence that they use epi- and mesopelagic oceanic waters. The stock structure of basking sharks is poorly known.

For the remaining oceanic species considered in this chapter, we have very limited information on population structure or migration patterns. In most of the oceanic squalids we know that they make vertical migrations between the epipelagic and meso- or bathypelagic zones but the details of these movements are lacking. There are some limited tag-recapture data for the thresher sharks, longfin mako, silky and oceanic whitetip sharks from a large cooperative study that had most tagging effort on the Atlantic coast of the United States (Kohler, Casey, and Turner 1998). A few returns from the bigeye thresher showed movements from the New England or central Atlantic coast to Cuba, the Gulf of Mexico, and out into the central Atlantic (2767 km). Longfin mako returns ($n = 4$) showed some movement from shelf to oceanic waters (>1590 km) while the silky shark showed mainly coastal movements of up to 1339 km and the oceanic whitetip shark ($n = 6$) of up to 2270 km. Acoustic tagging studies show that the manta ray has strong site fidelity and limited movements in some areas such as Hawaii (Clark 2007). Little information is available on stock structure of any of these pelagic shark species.

1.4 Exploitation, Population Status, Management, and Conservation

1.4.1 Exploitation

Traditional subsistence fisheries for a variety of pelagic sharks have existed in undeveloped countries for hundreds of years. In the 1930s to 1980s, a number of target fisheries for the porbeagle and basking shark operated in Europe and the Americas for meat and liver oil. In more recent times, increasing demand and prices in the international shark fin trade have led to huge increases in catches of most pelagic species to supply this market. However, the only global database of reported catches maintained by the United Nations Food and Agriculture Organization (FAO) grossly underestimates the magnitude of catches (Camhi et al. 2008). An analysis of trade data from Hong Kong shark fin auctions estimated that pelagic sharks represented about a third of the fins traded (Clarke et al. 2006). A number of Regional Fishery Management Organisations (RFMOs) and tuna commissions are now improving their data collection of pelagic sharks (Camhi et al. 2008).

Targeted basking shark fisheries use nets to deliberately entangle the fish or harpoon guns to take basking sharks swimming or feeding on the surface. Targeted fisheries have been recorded from Norway, Ireland, Scotland, Iceland, California, China, Japan, Peru,

and Ecuador. There are a few well-documented fisheries for basking sharks, particularly in the northeast Atlantic, and these suggest stock reductions of 50% to 90% over a few decades or less. These declines have persisted into the long term, with no apparent recovery several decades after exploitation has ceased. However, factors other than exploitation, such as market and economic changes, food supply, and oceanographic changes may also be involved in these declines. The basking shark was traditionally targeted in the eighteenth to twentieth centuries for its liver oil, which was initially used for tanning leather, for lamp oil, and as a source of vitamin A; more recently it has been used as a rich source of squalene. The liver comprises 17% to 25% of the body weight and yields 60% to 75% oil. The meat and fins are also valuable products, while the cartilage and skin are of secondary importance. The meat has been used, either fresh or dried, for food or fishmeal since early fisheries. It was the secondary product of most traditional fisheries after oil, but is still valuable in some areas. Fins are recorded as a byproduct of the Monterey fishery in the 1940s, and were an important product of the Irish fishery by 1960. The increased value of fins during the past decade means they are probably the major incentive for continued directed basking shark fisheries in some areas. According to Compagno (2001), the huge pectoral and dorsal fins sold in 1999 for US\$10,000 to \$20,000 each. The cartilage has been used to produce fishmeal, and more recently for medical research and the health market. The thick skin can produce high quality leather. The high value of basking shark fins in international trade is reportedly the reason why the northeast Atlantic fishery for this species is still viable, now that liver oil prices have fallen.

Historically, targeted whale shark fisheries for meat, liver oil, and fins occurred in locations such as India, Pakistan, the Maldives, China, Taiwan, Japan, the Philippines, Indonesia, Malaysia, and Senegal using harpoons or gaffs, fish traps, and set nets. Liver oil was traditionally one of the most important products, being used to waterproof artisanal wooden fishing boats in the Maldives, India, and elsewhere. Flesh was traditionally utilized locally in fresh, dried, and salted form, and traded locally for food as in the Philippines where most other parts such as skin, gills, and intestines were used for food or medicinal purposes. Meat is the main traded product stimulated by increased demand in Taiwan over the past two decades. Rising prices and declining catches off Taiwan stimulated whale shark fishing in the Philippines and India turning incidental and traditional subsistence fisheries into targeted fisheries supplying the international market. Whale shark meat is reputed to be the world's most expensive shark meat. However, there is little good data in the primary literature from existing fisheries. From 1988 to 1991, some 647 whale sharks were caught off Vernal, India (Vivekanandan and Zala 1994). Joung et al. (1996) note that in the 1970s and early 1980s, 30 to 100 whale sharks were caught per season in southwest Taiwan, but by the late 1980s some seasons produced less than ten sharks. Chang, Leu, and Fang (1997) provide some fishery information that differs from that of Joung et al. (1996), stating that up to 100 sharks per year have been taken off the east coast and about 60 per year off the west coast of Taiwan. Alava et al. (2002) describe whale shark catches in the Philippines as ranging from about 20 to 150 individuals per year between 1990 and 1997. Chen, Liu, and Joung (2002) noted that the Taiwan whale shark fishery captured an annual average of 158 individuals from set nets and 114 individuals from harpoon fisheries. Catches were higher in the mid-1980s and lower in the mid-1990s. In addition to being a target species in certain areas, whale sharks are also taken as bycatch, notably in gillnet and purse seine fisheries (Silas 1986; Romanov 2002).

Manta rays are targeted in harpoon fisheries in parts of southeast Asia, where they are also a retained bycatch of gillnet fisheries. It has been estimated that 1575 mobulid rays are landed annually at one fishing port in Lombok, Indonesia, or about 320 t (White et al. 2006)

as drift gillnet bycatch in the skipjack tuna fishery. Five species of mobulids were recorded, including the manta ray (14% of the mobulid catch). The meat is consumed domestically and the skin is also deep-fried as *kerupuk* (similar to prawn crackers). However, the gill arches are traded internationally and are much more valuable. A buyer in Lombok was sold three adult manta rays for US\$545 and said he would receive US\$490 for the filter plates but only \$109 for skins and cartilage (White et al. 2006).

Porbeagles have been fished in the northeast Atlantic principally by Denmark, France, Norway, and Spain. Norway began a target longline fishery for this species in the 1920s. Landings reached their first peak of 3884 t in 1933; however, about 6000 t were taken in 1947, when the fishery restarted after the Second World War. From 1953 to 1960, there was a progressive drop in landings to between 1200 and 1900 t, which then fell to a 20 t mean over the past decade. Average Danish landings fell from above 1500 t in the early 1950s to a recent mean of ~50 t. Reported landings from the historically important UK and adjacent waters fishery have decreased to very low levels during the past 30 to 40 years. French and Spanish longliners have operated directed porbeagle fisheries since the 1970s, but in the last few years there have been only 8 to 11 French vessels targeting this species. In 2008, the quota was set at 580 t, but the European Commission has now recommended a zero take. Porbeagles have virtually disappeared from Mediterranean records.

Targeted porbeagle fishing started in the northwest Atlantic in 1961 when Norway switched its operations to the coast of New England and Newfoundland, following depletion of the northeast Atlantic stock. Catches increased from about 1900 t in 1961 to more than 9000 t in 1964. By 1965, many vessels had switched to other species or moved to other grounds because of depleted stocks. The fishery collapsed after only six years, landing less than 1000 t in 1970, and it took 25 years for only very limited recovery to occur. Norwegian and Faroese fleets were excluded from Canadian waters following the establishment of Canada's Exclusive Economic Zone (EEZ) in 1995. Three offshore and several inshore Canadian vessels entered the targeted northwest Atlantic fishery during the 1990s. Catches of 1000 to 2000 t/year throughout much of this decade reduced population levels to a new low in less than 10 years. Commercial catch rates are now only 10% to 30% of those in the early 1990s (Campana et al. 2008). Porbeagle landings from the southern hemisphere are poorly known, although the longline fleet of Uruguay and pelagic and bottom longliners and trawl fisheries in New Zealand are known to take this species. The porbeagle is also an important target species for recreational fishing in Ireland and the United Kingdom; the recreational fishery in Canada and the United States is very small.

Some small target fisheries for shortfin mako and thresher sharks exist, for example, in California and Spain. Although a relatively productive species, the U.S. west coast fishery for thresher shark showed signs of declining less than 10 years after a target fishery was initiated in the late 1970s (Smith et al. 2008). However, the majority of the catch of makos and threshers is taken incidentally by longlines and gillnets directed at tuna and billfish (Holts et al. 1998). Consequently the magnitude of the catch and mortality is not reflected in catch statistics. Stevens (2000) estimated that 12,500 metric tons (mt) of shortfin mako were caught by longline fleets in the Pacific in 1994, and Babcock and Nakano (2008) reported that about 10,000 mt were caught by tuna fleets in the Atlantic in 1995. Other annual catches from smaller areas or more specific fisheries are generally between 20 and 800 mt (Mejuto 1985; Muñoz-Chápuli et al. 1993; Bonfil 1994; Francis, Griggs, and Baird 2001; Stevens and Wayte 2008). In general, shortfin mako catches tend to be about 3% to 13% of blue shark catches in the same longline or gillnet fishery. For anglers, shortfin mako is the most desirable and commonly retained big-game shark because it puts up a good fight and has high-quality meat (Babcock 2008). Casey and Hoey (1985) stated that the recreational catch of shortfin

mako along the U.S. Atlantic Coast and in the Gulf of Mexico in 1978 was 17,973 fish weighing some 1223 mt. From 1987 to 1989, this annual catch was about 1000 mt (Casey and Kohler 1992). However, only 2882 makos (about 200 mt) were reported in 2001 (Babcock 2008).

Pelagic sharks are a major bycatch of longline and gillnet fisheries, particularly from nations with high-seas fleets such as Japan, Taiwan, South Korea, China, and Spain. Some species, notably the silky shark, are also a large bycatch of tuna purse seine fisheries. In the past, only a few species were targeted commercially, particularly porbeagle and short-fin mako, for their high-value meat. However, the increasing price of shark fins, rapidly growing Asian economies, and increasing management restrictions on coastal populations are leading to greater pressure on high-seas stocks of pelagic sharks. In the Pacific, high-seas fish catches from pelagic longlining are increasing. Because there is usually no requirement for these fisheries to record their shark catch, the magnitude of the catch is not reflected in catch statistics. Commercial catch data are poor because individuals are often finned and their carcasses discarded at sea. Of the species identified in the Hong Kong fin market, some 70% were pelagic sharks (Clarke et al. 2006). The median number and biomass of sharks entering the shark fin trade have been estimated at 38 million individuals and 1.7 million mt, respectively (Clarke et al. 2006). These figures suggest that official (reported) landings in the FAO database may underestimate real catches by three to four times (Clarke et al. 2006). In the light of international concern over shark stocks (FAO, International Union for Conservation of Nature [IUCN]) there are questions over the sustainability of this shark catch, and the resulting effects on the ecosystem (see Chapter 17).

The blue shark is the most frequently captured of the pelagic sharks in high-seas longline fisheries and is taken from the world's oceans in greater quantities than any other single species of chondrichthyan. It is also the most common pelagic shark taken by sport fishermen, particularly in the United States, Europe, and Australia (Babcock 2008). While reliable catch data for this species from longline and gillnet fishing are sparse, it is clear that very large quantities are being taken globally. The high-seas catch of blue sharks from North Pacific fisheries in 1988 was estimated at 5 million individuals, or 100,000 mt at an average weight of 20 kg (Nakano and Watanabe 1992), and the catch from longline fleets in the Pacific in 1994 was about 137,000 mt (Stevens 2000). Bonfil (1994) estimated that 6.2 to 6.5 million blue sharks were taken annually by high-seas fisheries around the world. Although these figures are only rough estimates, they give some idea of the magnitude of the exploitation. Blue shark fins are the most common in the Hong Kong fin market, comprising at least 17% of the total, and Clarke et al. (2006) estimated 10.7 million individuals (0.36 million tones) are killed for the global fin trade annually.

1.4.2 Demography and Population Status

Fishing is a major source of mortality for oceanic sharks and so it is important to understand their life-history traits and the constraints these impose on the species' ability to withstand exploitation. As with most other sharks and rays, epipelagic oceanic elasmobranchs have life-history traits that result in generally slow intrinsic rates of population increase. Au, Smith, and Show (2008) calculated rebound potentials (rates of population increase at maximum sustainable yield) for four pelagic sharks at 3.8% to 6.9% compared to 8.9% to 18.2% for large tunas and billfish. Within the oceanic elasmobranch group, however, there is considerable variation in demographic parameters, and this is illustrated in Table 1.5. However, these parameters are reliably known for few species. On average, these species mature at about 11 years (range 2 to 21 years) and live for between 8 and 65 years. Typically, they have gestation periods of 9 to 18 months and reproductive cycles of 1 to 3

TABLE 1.5

Demographic Parameters for Epipelagic Oceanic Elasmobranchs

Species	Population	Annual Survivorship	Generation Time (years)	Annual Rate of Increase	References
<i>A. pelagicus</i>	NW Pacific	0.77–0.90	13	0.033	Liu et al. 1999, 2006; Otake and Mizue 1981
<i>A. superciliosus</i>	NW Pacific	0.77–0.89	17	0.002	Chen et al. 1997; Liu et al. 1998
<i>A. vulpinus</i>	NE Pacific	0.56–0.93	8	0.254	Cailliet and Bedford 1983; Hixon 1979
<i>C. carcharias</i>	Global	0.71–0.96	22	0.051	Dulvy et al. 2008
<i>I. oxyrinchus</i>	NW Atlantic	0.79–0.94	24	0.047	Campana et al. 2005; Mollet et al. 2000; Natanson et al. 2006; Pratt and Casey 1983; Wood et al. 2007
	SW Pacific	0.79–0.93	23	0.034	Bishop et al. 2006; Francis 2007; Francis and Duffy 2005
<i>L. nasus</i>	North Atlantic	0.82–0.93	18	0.081	Campana et al. 2002; Natanson et al. 2002
	SW Pacific	0.78–0.94	26	0.086	Francis et al. 2007; Francis and Duffy 2005; Francis and Stevens 2000
	Central Pacific	0.64–0.90	10	0.058	Oshitani et al. 2003
<i>L. ditropis</i>	NE Pacific	0.67–0.91	13	0.081	Goldman 2007; Goldman and Musick 2006; Nagasawa 1998; Tanaka 1980
<i>C. falciformis</i>	Gulf of Mexico	0.75–0.90	16	0.067	Bonfil 1990; Bonfil et al. 1993; Branstetter 1987
<i>C. longimanus</i>	Pacific and Atlantic	0.72–0.92	11	0.110	Lessa et al. 1999; Seki et al. 1998
<i>P. glauca</i>	North Atlantic	0.65–0.91	10	0.287	Skomal and Natanson 2003
<i>P. violacea</i>	NE Pacific	0.68–0.88	6	0.311	Mollet et al. 2002; Mollet 2002; Neer 2008

years. Smith et al. (2008) calculated intrinsic rebound rates for 11 pelagic species and found they mostly fell in the middle range of the productivity spectrum. However, some species lay near both the low and high ends of the spectrum.

Of the species for which information is available, the pelagic stingray and the blue shark have the highest annual rates of population increase (31% and 29%, respectively), which is more than three times greater than the other species. In contrast, the bigeye thresher and pelagic thresher have annual rates of population increase of only 2% and 3.3%, respectively (Dulvy et al. 2008). The relatively productive pelagic stingray matures at 2 to 3 years, has a gestation period of 2 to 3 months, and a reproductive cycle of about 6 months, endowing the population with a fairly quick turnover rate. Toward the other end of the spectrum, in the shortfin mako females do not mature until 18 to 21 years, they have a gestation period of 15 to 18 months, a 3-year reproductive cycle, and an annual rate of population increase of 3.4% to 4.7%. Rates of population increase calculated by different authors can vary depending on the assumptions made, the life-history parameters chosen, and the degree to which uncertainty is incorporated. So, for example, estimated rates of population increase for the

pelagic stingray vary from 6% to 31% in the studies of Smith et al. (2008) and Dulvey et al. (2008). However, the relative ranking of species in these two studies is generally similar.

Cortés (2008) used principal component analysis to examine the difference in life-history traits between eight species of pelagic sharks. He noted that the early maturity and large litter size of the blue shark resulted in a high rate of population increase despite the small size of its pups, which would be subject to higher natural mortality rates. The silky shark, oceanic whitetip, and porbeagle formed a group that had moderate rates of population increase and shared similar-sized pups (70 to 76 cm TL), had similar annual fecundities (three to five pups per year), slow overall growth rates (k values of 0.06 to 0.10), and longevity of 17 to 25 years. The shortfin mako, bigeye and pelagic threshers formed a group that had very low productivities and shared large adult size, low annual fecundities of two to four, and low k values (0.08 to 0.09). As for sharks in general, the population growth rates of these pelagic species were more sensitive to survival of juveniles and adults than to survival of age 0 neonates or to fecundity (Cortés 2008). Cortés (2008) postulated that these pelagic species had maximum sustainable yields at or above 50% of their carrying capacity.

Comprehensive stock assessments for chondrichthyan fishes are very limited, and the situation is no different for oceanic elasmobranchs. A number of studies have attempted to assess the status of blue shark stocks, and to a lesser extent those of shortfin makos and porbeagles. A few studies have focused on other species such as the thresher and silky shark, and the pelagic stingray. West, Stevens, and Basson (2004) reviewed assessments carried out for blue sharks that included demographic methods, age structured models, and food web and ecosystem models, as well as various forms of catch rate analysis; they also used a yield analysis in the southwest Pacific. The International Commission for the Conservation of Atlantic Tunas (ICCAT) has also carried out assessments on this species (as well as on shortfin mako) and a fishery-independent approach using tag-recapture data has been carried out in the North Atlantic. These models have shown a conflicting picture of blue shark sustainability in the North Atlantic and central Pacific. Different catch rate analyses generate diverging trends even in the same ocean (Nakano 1998; Matsunaga, Nakano, and Minami 2001; Simpfendorfer et al. 2002; Baum et al. 2003; Aires-da-Silva, Ferreira, and Pereira 2008). The poor quality of catch data and problems of catch rate standardization have hampered analyses of both blue shark and shortfin mako population status by ICCAT. These data problems mean that any assessment will have high uncertainty.

For porbeagles, there is a recent stock assessment for the northwestern Atlantic (Campana et al. 2008). Based on tag-recapture and an age and sex structured population model, it is estimated that the total population biomass of this stock is 1572 to 7695 t (11% to 17% of virgin biomass) and 2612 to 13,847 mature females (4% to 14% of virgin abundance). Because of the very low numbers of mature females now present in the stock, it is unlikely that the strict quota management and area closures will allow quick rebuilding of the population (Campana et al. 2008). There is no stock assessment for the more heavily fished, unmanaged and possibly more seriously depleted northeast Atlantic and Mediterranean population, or for southern stocks.

For other species, evaluation of population status is limited to fisheries catch rate data, which show apparent declines in abundance of all three thresher sharks, white sharks, shortfin mako, silky, and oceanic whitetip. Salmon shark populations seem to be stable and few data are available for pelagic stingrays, although one study suggests numbers may be increasing in the Pacific (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005; Ferretti et al. 2008; Camhi et al. 2008).

Because of the paucity of data for many species (teleosts as well as chondrichthyans) another technique for assessing relative risk from fishing to population status is ecological

risk assessment (ERA). This can operate at different levels, from purely qualitative to fully quantitative depending on the amount of data available; the general methodology has been described by Hobday et al. (2007). Risk is considered on two axis, productivity (the ability of the species to withstand or recover from fishing) and susceptibility or the level at which a species is likely to be affected by fishing.

The global threatened status of oceanic epipelagic elasmobranchs has also been assessed using the IUCN Red List categories and criteria (Mace 1995; IUCN 2004). Dulvy et al. (2008) considered 21 species in their analysis, which showed strong overlap with the species considered in this chapter (Table 1.1). Eleven of the species they considered were assessed as globally threatened (one Endangered and ten Vulnerable), five as Near Threatened, two as Least Concern, and three were Data Deficient. The proportion of epipelagic oceanic elasmobranchs considered to be threatened, 52% from Dulvy et al. (2008) or 48% from Table 1.1 (Figure 1.2a) is considerably higher than the 22% of all chondrichthyans that are threatened (Figure 1.2b). The giant devilray (*Mobula mobular*) was the only globally Endangered oceanic pelagic elasmobranch considered by Dulvy et al. (2008), although this species was not included in Table 1.1 of this chapter.

An integrated approach to assessing the risk faced by Atlantic pelagic sharks to over-exploitation was used by Simpfendorfer et al. (2008). This incorporated ERA, the IUCN Red List assessments, and an approximation of the biomass at maximum sustainable yield

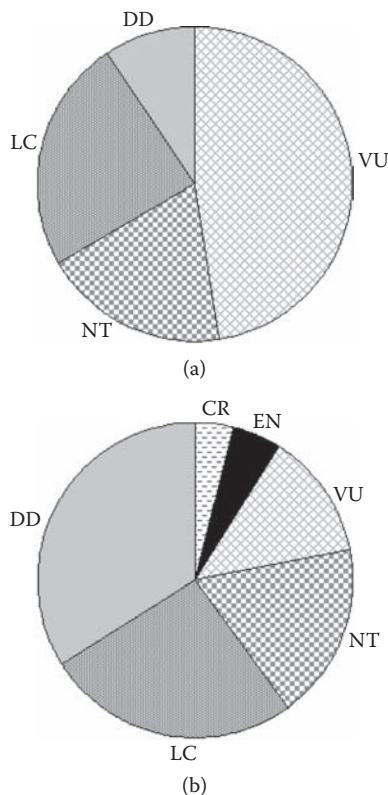


FIGURE 1.2

Percentage of (a) epipelagic oceanic elasmobranchs ($n = 21$ from Table 1.1) and (b) globally assessed chondrichthyan fishes ($n = 591$) within each IUCN Red List category. CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient.

(the inflection point on the population growth curve). Multivariate statistics were used to produce the integrated results. According to this analysis, the species at highest risk from longline fisheries were makos (both shortfin and longfin), bigeye thresher, and to a lesser extent silky sharks. The porbeagle, oceanic whitetip, and thresher shark formed a middle group and the pelagic stingray and blue shark had the lowest level of risk.

1.4.3 Management and Conservation

A growing concern over the global status of shark populations led to the FAO International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) in 1999. This requested all countries engaged in shark fishing, as well as RFMOs, to assess their shark resources and prepare National and Regional Shark Plans by 2001. However, IPOA-Sharks is voluntary and to date few countries and no RFMOs have produced Shark Plans. Few countries have comprehensive management plans for any of their chondrichthyan resources within their EEZs. For the high-seas component of pelagic elasmobranchs there is virtually no management because of the difficulty of establishing international agreements to take responsibility for these resources beyond national EEZs.

This lack of management, in particular of pelagic elasmobranchs, is due to the low priority afforded to them relative to high-value target species such as tunas. This is reflected in the poor quality of the data that is usually not species-specific and may not be reported accurately, if at all. While the larger RFMOs have now generally accepted that pelagic elasmobranchs fall under their mandate, few have attempted assessments for any of these species. Where they have, as in the case of ICCAT for blue shark and shortfin mako, the assessments are severely limited by the data quality and reporting problems. Even for the relatively data-rich blue shark, catch rate standardization, stock and population structure problems lead to major uncertainties in the assessment and to date there would be little confidence in the outputs of these models.

There is management of some pelagic elasmobranchs within national EEZs. Whale, basking, and white sharks are protected in a number of countries. In New Zealand, commercial target fishing for basking sharks was banned in 1991, although they are allowed to be taken as bycatch. Norway agreed to an annual quota on catches of 800 t liver weight in 1982. This was progressively reduced and has been at 100 mt (or about 200 to 300 sharks per year) since 1994. Porbeagles are managed by quota in parts of the North Atlantic and in New Zealand. Quota management based on stock assessment and scientific advice has been in place in the Canadian EEZ since 2002. This has maintained a relatively stable population, but with a slight decline in mature females; there is also a U.S. quota. Fisheries in the northeast Atlantic are effectively unrestricted (quotas greatly exceed landings). Scientific advice in 2005 that no fishery should be permitted in the northeast Atlantic was not adopted. New Zealand introduced quota management in 2004. A number of countries (and some RFMOs) have implemented finning bans that prohibit the retention of fins without the corresponding carcasses, or bycatch limits on pelagic sharks. However, in many cases these operate by allowing a certain ratio of fin to carcass weight. Some fleets argue for unrealistically high ratios based on cutting practices that may allow a loophole for finning (Dulvy et al. 2008). Better controls are achieved by requiring carcasses to be landed with fins attached, as in certain Australian fisheries. See Dulvy et al. (2008) for more details of countries and RFMOs that currently apply finning bans or other management measures.

On the high seas, no catch limits have yet been imposed by RFMOs. However, there are international treaties that include some pelagic sharks. White, basking, and whale sharks

are listed on both Appendix II of the Convention on International Trade in Endangered Species (CITES) and the Convention on Migratory Species (CMS). Shortfin makos are also included on Appendix II of CMS. Appendix II of CITES allows trade only if the take of that species can be demonstrated to be sustainable. Two regional treaties, the Barcelona and Bern Conventions, include some pelagic sharks (white and basking sharks, shortfin mako, porbeagle, and blue shark) that would give various levels of protection or permit certain levels of exploitation depending on stock status (Dulvy et al. 2008). However, the effectiveness of any of these listings has yet to be demonstrated.

1.5 Summary

Epipelagic oceanic elasmobranchs show a wide range of morphological, physiological, and behavioral specializations for exploiting their environment. However, although this zone comprises over 70% of the oceans, the number of species regularly living there is relatively low. The adaptive diversity of these species encompasses the giant plankton feeders, diminutive squaloid sharks, bizarre body form of the alopiids, ectoparasitic feeding strategies of *Isistius*, and the highly active and powerful endothermic lamnids. Most of these species are widely distributed, highly migratory, and show complex spatial population structuring, all of which help them exploit the often patchy food resources and meet the challenges of reproduction over the vast distances of the open ocean. However, these oceanic elasmobranchs face an uncertain future. Growing Asian economies are fueling increases in the international shark fin trade, and high-seas exploitation from longlining, gillnetting, and purse-seining activities are resulting in unsustainable fishing pressure. Three-quarters of these species are listed as Threatened or Near Threatened on the IUCN Red List. Fisheries catch and effort data for most of these species is poor leading to high uncertainty in those few species where population assessments have been attempted.

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2

Deepwater Chondrichthyans

Peter M. Kyne and Colin A. Simpfendorfer

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2.1 Introduction

The deep sea is a relatively stable environment, characterized by cold temperatures and poor or absent light. Relative to inshore shelf habitats, the ocean's deepwater environments remain poorly known. The continued expansion of global fishing into the deep ocean has raised new concerns about the ability of deepwater organisms to sustain the pressures of exploitation (Morato et al. 2006). General knowledge on the deep sea lags behind the expansion of fisheries (Haedrich, Merrett, and O'Dea 2001) and as such management is often further behind. The intrinsic vulnerability of the chondrichthyan fishes given their life history characteristics (Hoenig and Gruber 1990; Cahmi et al. 1998; Musick 1999) is widely acknowledged and often cited. This vulnerability may be heightened in the deep sea, where conditions result in slower growth rates and reduced recruitment to populations. The vast majority of available life history data on the sharks, batoids, and chimaeras comes from the shallow water. Logistical, biological, and geographical difficulties with sampling (i.e., scattered distributions, deep occurrence, taxonomic uncertainty, and limited material) in the deep sea have limited the present state of knowledge. The amount of available information has, however, increased in recent years, and demonstrates that deepwater species are among the most unproductive of the chondrichthyans.

Here we review the present state of knowledge concerning this diverse group of chondrichthyans, which represents some 46% of the global shark, ray, and chimaera fauna. We focus mainly on their life history, the essential information required to effectively direct management. We define the deep sea to be that region of the ocean that lies beyond the 200 m isobath, the depth generally recognized as the continental and insular shelf edge (Merrett and Haedrich 1997). Hence, deepwater chondrichthyans are those sharks, rays, and holocephalans whose distribution is confined to (or predominantly at) depths below 200 m, or those that spend a considerable part of their lifecycle below this depth. This encompasses the continental and insular slopes and beyond, including the abyssal plains and oceanic seamounts. In the broadest sense, the deepwater fauna can be divided into pelagic species that occupy the water column and demersal species that occur on (benthic) or just above (epibenthic or benthopelagic) the ocean floor (Haedrich 1996). We discuss both of these groups, although the demersal species feature more prominently. With regards to the pelagic fauna we have limited our discussion of those species that occur in the mesopelagic (200 to 1000 m) and bathypelagic (1000 to 4000 m) zones if they also readily occupy the epipelagic (0 to 200 m) zone. Epipelagic species are treated in Chapter 1.

Excluded from our discussion are many chondrichthyans that have been recorded at depths of >200 m but that are predominantly species of the shelf. These species are recorded far less commonly or irregularly in the deep sea and include such examples as spiny dogfish *Squalus acanthias* (recorded exceptionally to 1446 m) and many skates whose distribution extends to the upper slope (including sandy skate *Leucoraja circularis*, blonde skate *Raja brachyura*, thornback skate *R. clavata*, clearnose skate *R. eglanteria*, brown skate *R. miraletus*, and rough skate *R. radula*). Other species that are abundant on the shelf in parts of their range are included here if they are also widely occurring on the slope. Examples include shortnose spurdog *Squalus megalops*, longnose skate *R. rhina*, big skate *R. binoculata*, barndoor skate *Dipturus laevis*, and spotted ratfish *Hydrolagus collii*, and for these species, much of the available information on life history comes from the shelf (where the species may be subject to strong seasonal light and temperature signals).

2.2 Biodiversity and Biogeography

2.2.1 Biodiversity and Systematics

The total number of extant, formally described chondrichthyan species currently stands at 1144; this comprises 482 sharks, 671 batoids, and 45 holocephalans (W.T. White, personal communication). Of the global fauna, 530 chondrichthyans can be considered to be deepwater species (according to our definition) representing 46.3% of the global total (Table 2.1). The deepwater fauna is divided between 254 sharks (52.7% of global), 236 batoids (38.2% of global), and 40 holocephalans (88.9% of global). All nine orders of elasmobranchs and the single holocephalan order are represented in the deep sea (see the appendix to this chapter).

In addition to the formally described species mentioned above, there are many more new or recently identified sharks, batoids, and chimaeras that are known to researchers, but have not yet been formally described. At present this includes about 70 deepwater species (calculated from the literature and available checklists), and more are sure to be discovered and described. The number of undescribed species not only highlights the overall lack of knowledge of the deep sea fauna at even the most basic (i.e., taxonomic) level, but also that the deep sea chondrichthyan fauna is far from fully documented and species will continue to be added as deepwater surveys continue (e.g., the 2003 NORFANZ cruise surveying the seamounts and abyssal plains around the Lord Howe and Norfolk Ridges in the Western Pacific; Last 2007). In addition, the systematics and interrelationships of several groups of deep sea chondrichthyans remain unresolved, and much work is still needed on such groups as the spurdogs (*Squalus*), gulper sharks (*Centrophorus*), catsharks of the genus *Apristurus*, and some of the skate assemblages.

The bulk of the deepwater chondrichthyan fauna is attributable to four main groups: (1) squaloid dogfishes (order Squaliformes), which represent 46.1% of the deepwater shark fauna; (2) scyliorhinid catsharks (order Carcharhiniformes, family Scyliorhinidae) (40.2% of the deepwater shark fauna); (3) skates (order Rajiformes, families Arhynchobatidae, Rajidae and Anacanthobatidae) (89.8% of the deepwater batoid fauna); and (4) holocephalans (order Chimaeriformes, families Rhinochimaeridae and Chimaeridae).

The squaloid dogfishes are mostly benthic or benthopelagic, although the kitefin sharks (Dalatiidae) are primarily pelagic and include many species that undergo daily vertical migrations (there are also a few pelagic species within the Somniosidae; Compagno, Dando, and Fowler 2005). This group includes what is probably the world's smallest shark, the smalleye pygmy shark *Squaliolus aliae*, which reaches a maximum size of 22 cm total length (TL) (Last and Stevens 2009), and some of the largest shark species, that is, sleeper sharks (*Somniosus*), some of which can reach >600 cm TL (Compagno, Dando, and Fowler 2005). The lanternsharks (Etmopteridae) and some kitefin sharks possess photophores that produce a bioluminescence, aiding in counter-illumination (emitted light eliminates the silhouette of the fish formed when it is illuminated from above; Claes and Mallefet 2008).

The catsharks are the largest shark family, with about two-thirds of the known fauna occurring in the deep sea. These are generally small species (<100 cm TL), which are benthic and relatively poor swimmers (Compagno, Dando, and Fowler 2005). The skates are a morphologically conservative, yet highly diverse group of benthic batoids (McEachran and Dunn 1998). Species range from small (<0.3 m TL) to some of the largest batoids (>2.5 m TL) and diversity is greatest on the outer continental shelves and upper slopes (Ebert and Bizzarro 2007). The holocephalans—among the most poorly known cartilaginous

TABLE 2.1

Diversity of Deepwater Chondrichthyan Fishes by Order and Family

Order	Family	Common Name	No. of Species
<i>Sharks</i>			
Hexanchiformes	Chlamydoselachidae	Frilled sharks	1
	Hexanchidae	Sixgill and sevengill sharks	3
Squaliformes	Echinorhinidae	Bramble sharks	2
	Squalidae	Dogfish sharks	25
	Centrophoridae	Gulper sharks	18
	Etmopteridae	Lanternsharks	42
	Somniosidae	Sleeper sharks	16
	Oxynotidae	Roughsharks	5
	Dalatiidae	Kitefin sharks	9
	Squatiniiformes	Squatinae	Angelsharks
Pristiophoriformes	Pristiophoridae	Sawsharks	3
Heterodontiformes	Heterodontidae	Bullhead sharks	1
Orectolobiformes	Parascylliidae	Collared carpetsharks	2
Lamniformes	Odontaspidae	Sand tiger sharks	2
	Pseudocarchariidae	Crocodile sharks	1
	Mitsukurinidae	Goblin sharks	1
	Alopiidae	Thresher sharks	1
	Cetorhinidae	Basking sharks	1
	Carcharhiniformes	Scyliorhinidae	Catsharks
Proscylliidae		Finback catsharks	3
Pseudotriakidae		False catsharks	2
Triakidae		Houndsharks	6
Carcharhinidae		Requiem sharks	1
		<i>Subtotal sharks</i>	254
<i>Batooids</i>			
Rajiformes	Rhinobatidae	Guitarfishes	1
	Narcinidae	Numbfishes	7
	Narkidae	Sleeper rays	4
	Torpedinidae	Torpedo rays	7
	Arhynchobatidae	Softnose skates	75
	Rajidae	Hardnose skates	116
	Anacanthobatidae	Legskates	21
	Plesiobatidae	Giant stingarees	1
	Urolophidae	Stingarees	2
	Hexatrygonidae	Sixgill stingrays	1
	Dasyatidae	Whiptail stingrays	1
		<i>Subtotal batooids</i>	236
<i>Holocephalans</i>			
Chimaeriformes	Rhinochimaeridae	Longnose chimaeras	8
	Chimaeridae	Shortnose chimaeras	32
	<i>Subtotal holocephalans</i>	40	
	Total	530	

fishes—are a group of mostly deepwater benthic soft-bodied chondrichthyans with body lengths reaching >1.5 m.

2.2.2 Biogeography and Bathymetry

The deepwater chondrichthyan fauna reaches its highest diversity in the Indo-West Pacific (Table 2.2). The Western and Eastern Atlantic have similar numbers of species, but diversity is lower in the Eastern Pacific. The Arctic and Antarctic regions are depauperate in terms of deep sea fauna. These biogeographical patterns follow general trends of chondrichthyan biogeography and diversity (Musick, Harbin, and Compagno 2004). The Indo-West Pacific is a large ocean region with a high level of endemism and thus it is not surprising that the highest diversity is recorded there. Lower diversity in the Eastern Pacific is attributable to a general lack of squaloid sharks (Musick, Harbin, and Compagno 2004). In contrast to sharks and holocephalans, skate diversity is great at high latitudes (Ebert and Bizzarro 2007; see Chapter 3 in this volume).

Deepwater chondrichthyans include some very wide-ranging species, for example the smooth lanternshark *Etmopterus pusillus* and the longnose velvet dogfish *Centroselachus crepidater*, which both occur widely in the Atlantic and Indo-West Pacific. However, the vast majority of deepwater chondrichthyans are geographically and bathymetrically restricted. Levels of endemism are high in the lanternsharks, catsharks, and the skates, and many species have localized regional distributions (Ebert and Bizzarro 2007). Endemism is often associated with seamounts and deep sea ridges. Localized species are often poorly known; many species are known from only one specimen (e.g., pocket shark *Mollisquama parini* and Aguja skate *Bathyraja aguja* from the Southeast Pacific).

The deepest recorded chondrichthyan fishes are great lanternshark *Etmopterus princeps* (to 4500 m; Compagno, Dando, and Fowler 2005) and Bigelow's skate *Rajella bigelowi* (to 4156 m; Stehmann 1990). These are the only species to be recorded below 4000 m. However, the Portuguese dogfish *Centroscymnus coelolepis* occurs to 3675 m, leafscale gulper shark *Centrophorus squamosus* to 3280 m (Priede et al. 2006), and among the skates, pallid skate *Bathyraja pallida* reaches 3280 m (Priede et al. 2006), several other *Bathyraja* reach ~2900 m, while thickbody skate *Amblyraja frerichsi* and gray skate *Dipturus batis* have been documented to ~2600 m (Priede et al. 2006). The deepest records for holocephalans are for a *Harriotta* species at 3010 m and Atlantic chimaera *Hydrolagus affinis* at 2909 m (Priede et al. 2006).

TABLE 2.2

Diversity of Deepwater Chondrichthyan Fishes by Major Ocean Region

Ocean Region	Number of Species			Total
	Sharks	Batoids	Holocephalans	
Arctic Sea	1	0	0	1
Indo–West Pacific	181	116	25	322
Eastern Pacific	45	44	6	95
Western Atlantic	71	68	8	147
Eastern Atlantic	67	48	10	125
Antarctic seas	1	7	1	9

Note: The sum of totals exceeds the known number of deepwater species (530) as wider-ranging species occur in more than one region.

Priede et al. (2006) note that the chondrichthyans “have generally failed to colonize the oceans deeper than 3,000 m and it is unlikely that major new populations will be discovered in abyssal regions.” For many of the deepest recorded chondrichthyans, their core bathymetric range is at much shallower depths, including *E. princeps*, *C. coelolepis*, and *R. bigelowi* (Priede et al. 2006). Some of the *Bathyraja* skates, however, have very deep minimum depths and are thus more specialized to the deeper habitats (i.e., fine-spined skate *B. microtrachys* with a minimum depth of ~2000 m, and *B. pallida* with a minimum depth of 2200 m). The general absence of chondrichthyans from the abyssal plains and their complete absence from the hadal and hadopelagic zones (demersal and pelagic habitats >6000 m, respectively) are not related to a lack of surveying at depth, but rather may be a result of an inability to meet their high energy demands, and support their metabolism and large, lipid-rich livers (Priede et al. 2006).

2.3 Life History

For the vast majority of deepwater chondrichthyans, details of their life history characteristics are lacking. There is a reasonable amount of information on the biology of some species of dogfish sharks (Squalidae), gulper sharks (Centrophoridae), lanternsharks (Etmopteridae), sleeper sharks (Somniosidae), catsharks (Scyliorhinidae), softnose skates (Arhynchobatidae), and hardnose skates (Rajidae), with much of the information on the biology of deepwater sharks coming from the Northeast Atlantic and southeastern Australia.

2.3.1 Reproductive Biology

Many coastal and shelf chondrichthyans display seasonal reproductive cycles, but the majority of deepwater species exhibit aseasonal reproductive cycles, with asynchronicity among the population. This aseasonality—which may be related to the relative stability of the deep sea environment (Wetherbee 1996)—makes it difficult to determine the gestation period and for most species, reproductive periodicity remains unknown. Follicle and embryonic development rates and sizes, however, indicate a long reproductive cycle. Additionally, many deepwater squaloid sharks exhibit a resting period between parturition and the next ovulation (e.g., ovarian follicles do not develop while gestation proceeds), extending the reproductive cycle (Irvine 2004; Irvine, Stevens, and Laurenson 2006b).

For oviparous species, estimates of fecundity are difficult because egg-laying periods and rates are mostly unknown. Ovarian fecundity (counts of the number of developing or developed follicles) may provide a proxy. However, the relationship between the number of follicles and actual reproductive output is not clear. For example, among the viviparous squaloid sharks, Irvine (2004) noted that mean litter size was three to four less than mean ovarian fecundity in New Zealand lanternshark *Etmopterus baxteri*, with atretic follicles observed in some early pregnancies. Yano (1995) found a similar disparity between ovarian and uterine fecundity in black dogfish *Centroscyllium fabricii*. Very large numbers of follicles have been reported for *Somniosus* species, 372+ for Pacific sleeper shark *S. pacificus* (Ebert, Compagno, and Natanson 1987) and up to 2931 in Greenland shark *S. microcephalus* (Yano et al. 2007), although the few observed *Somniosus* litter sizes are in the range of only 8 to 10 young (Barrull and Mate 2001; Compagno, Dando, and Fowler 2005).

2.3.1.1 Sharks

Of the major deepwater shark groups, the squaloid dogfishes are viviparous, while the catsharks are either oviparous (the dominant reproductive mode) or viviparous. Deepwater squaloid dogfishes generally do not have well-defined reproductive seasons (Chen, Taniuchi, and Nose 1981; Yano 1995; Daley, Stevens, and Graham 2002; Irvine 2004; Graham 2005; Hazin et al. 2006) and it is difficult to elucidate their reproductive cycle. Gestation periods are generally unknown and many species have a resting period after parturition (e.g., kitefin shark *Dalatias licha* [Daley, Stevens, and Graham 2002]; etmopterids [Yano 1995; Daley, Stevens, and Graham 2002; Irvine 2004]; somniosids [Daley, Stevens, and Graham 2002; Irvine 2004]). The large size of preovulatory follicles suggests lengthy vitellogenesis because the energy demands to develop such large oocytes are high. It seems plausible then, that many reproductive cycles are biennial or triennial. For example, Tanaka et al. (1990) suggested a 3.5 year gestation period for frilled shark *Chlamydoselachus anguineus* based on growth rates of embryos held in artificial conditions, and Braccini, Gillanders, and Walker (2006) demonstrated that *S. megalops* off Australia has an ovarian cycle and gestation period of two years. The results of Braccini, Gillanders, and Walker (2006), as well as data from the shelf-occurring *S. acanthias* (Holden 1977; Jones and Geen 1977), suggest that many other squalids exhibit biennial reproductive cycles.

Reproductive output in deepwater hexanchoid and squaloid sharks is generally limited, with small litter sizes the normal condition for many species. Among the hexanchoids, reported litter sizes include 2 to 10 (average 6) for *C. anguineus* (Tanaka et al. 1990) and 9 to 20 in sharpnose sevengill shark *Heptranchias perlo* (Bigelow and Schroeder 1948), but up to 108 in bluntnose sixgill shark *Hexanchus griseus* (Vaillant 1901). Table 2.3 provides a summary of reported litter sizes for deepwater squaloid sharks. In *Squalus* (litter size range 1 to 15; see Table 2.3), smaller litter sizes are more common, for example, in *S. megalops*, Braccini, Gillanders, and Walker (2006) found that 69.3% of gravid females examined had a litter size of two, 30.0% a litter size of three, and only 0.7% a litter size of four. For some *Squalus* species larger females are able to carry more embryos (Watson and Smale 1998; Braccini, Gillanders, and Walker 2006). Similarly, Irvine (2004) found strong correlations between maternal size and the number of follicles and the number of embryos within *E. baxteri* from southern Australia, Yano and Tanaka (1988) found that fecundity increased with maternal size in *C. coelolepis*, and Yano (1995) found similar results for *C. fabricii*.

Gulper sharks of the genus *Centrophorus* are among, if not the most, unproductive of chondrichthyan fishes. Fecundity is low, with litter sizes of one or two for most species examined, with the exception of recorded litter sizes of six and seven in *C. squamosus* (Bañón, Piñeiro, and Casas 2006; Figueiredo et al. 2008). Figueiredo et al. (2008) hypothesized that old *C. squamosus* may undergo senescence, which would further restrict the reproductive output of the species. Daley, Stevens, and Graham (2002) found that litter size in southern dogfish *C. zeehaani* was invariably one in 37 gravid females examined, and only a single embryo or ovum has been noted in gulper shark *C. granulosus* (Golani and Pisanty 2000; Guallart and Vicent 2001; Megalofonou and Chatzistryrou 2006). *Centrophorus* have a continuous reproductive cycle with follicles continuing to develop as gestation ensues and at the time of ovulation the follicles are very large (Guallart and Vicent 2001; Daley, Stevens, and Graham 2002; McLaughlin and Morrissey 2005). Irvine (2004) suggested that to allow for maturation of oocytes to these large ovulatory sizes in species with continuous reproductive cycles, a long gestation period is required. Gestation is two years in *C. granulosus* (Guallart and Vincent 2001) and *C. cf. uyato* may have a three-year gestation period (McLaughlin and Morrissey 2005). *Deania* also probably has a two- or three-year

TABLE 2.3

Summary of Litter Sizes for Deepwater Squaloid Sharks

Family	Species	Location	Litter Size (Average)	Reference
Echinorhinidae	<i>Echinorhinus brucus</i>	NE Brazil, SW Atlantic	15–26	Cadenat and Blanche (1981)
	<i>Echinorhinus cookei</i>	Hawaii, Eastern Central Pacific	114	Crow et al. (1996)
Squalidae	<i>Cirrhigaleus asper</i>	NE Brazil, SW Atlantic	12–19	Fischer et al. (2006)
	<i>Cirrhigaleus barbifer</i>	New Zealand, SW Pacific	6–10	Duffy et al. (2003)
	<i>Squalus blainville</i>	Mediterranean	2–6	Sion et al. (2003)
	<i>Squalus grahami</i>	SE Australia	2–7	Graham (2005)
	<i>Squalus japonicus</i>	Choshi, Japan, NW Pacific	2–8	Chen et al. (1981)
		Nagasaki, Japan, NW Pacific	2–8 (5.3)	Chen et al. (1981)
	<i>Squalus megalops</i>	Agulhas Bank, South Africa, SE Atlantic	2–4	Watson and Smale (1998)
		Andaman Is., Eastern Indian	5–7	Soundararajan and Dam Roy (2004)
	<i>Squalus mitsukurii</i>	SE Australia	1–3 (2.1)	Graham (2005)
		SE Australia	2–4	Braccini et al. (2006)
		NE Brazil, SW Atlantic	1–8	Hazin et al. (2006)
		Choshi, Japan, NW Pacific	4–15 (8.8)	Taniuchi et al. (1993)
		Masseiba, Japan, NW Pacific	6–9 (7.1)	Taniuchi et al. (1993)
		Ogasawara Is., Japan, NW Pacific	2–9 (4.5)	Taniuchi et al. (1993)
		Hancock Seamount, NW Pacific	1–6	Wilson and Seki (1994)
<i>Squalus montalbani</i>	NE Brazil, SW Atlantic	3–11	Fischer et al. (2006)	
	SE Australia	4–10	Daley et al. (2002); Graham (2005)	
Centrophoridae	<i>Centrophorus acus</i>	Andaman Is., Eastern Indian	1–2	Soundararajan and Dam Roy (2004)
	<i>Centrophorus granulosus</i>	Mediterranean	1	Golani and Pisanty (2000); Guallart and Vicent (2001); Megalofonou and Chatzisprou (2006)
	<i>Centrophorus harrissoni</i>	SE Australia	1–2	Daley et al. (2002)
	<i>Centrophorus moluccensis</i>	SE Australia	1–2	Daley et al. (2002)
	<i>Centrophorus squamosus</i>	Galicia, Spain, NE Atlantic	7	Bañón et al. (2006)
		Portugal, NE Atlantic	1–6	Figueiredo et al. (2008)
	<i>Centrophorus cf. uyato</i>	Cayman Trench, Western Central Atlantic	1–2	McLaughlin and Morrissey (2005)

TABLE 2.3 (Continued)

Summary of Litter Sizes for Deepwater Squaloid Sharks

Family	Species	Location	Litter Size (Average)	Reference
	<i>Centrophorus zeehaani</i>	SE Australia	1	Daley et al. (2002)
	<i>Deania calcea</i>	Rockall Trough and Porcupine Bank, NE Atlantic	8–14	Clarke et al. (2002b)
		SE Australia	1–17 (7)	Daley et al. (2002)
		SE Australia	5–10	Irvine (2004)
	<i>Deania quadrispinosum</i>	SE Australia	8–17	Daley et al. (2002)
Etmopteridae	<i>Aculeola nigra</i>	Chile, SE Pacific	(10)	Acuña et al. (2003)
	<i>Centroscyllium fabricii</i>	Greenland, NE Atlantic	4–40 (16.4)	Yano (1995)
	<i>Centroscyllium kamoharai</i>	SE Australia	3–22 (12)	Daley et al. (2002)
	<i>Etmopterus baxteri</i>	New Zealand, SW Pacific	9–15 (12.7)	Wetherbee (1996) ^a
		SE Australia	6–16 (10)	Daley et al. (2002) ^a
		SE Australia	1–16 (8.8)	Irvine (2004)
	<i>Etmopterus spinax</i>	Portugal, NE Atlantic	1–16 (7.6)	Coelho and Erzini (2008)
		Mediterranean	6–18	Serena et al. (2006)
Somniosidae	<i>Centroscymnus coelolepis</i>	Suruga Bay, Japan, NW Pacific	15–29	Yano and Tanaka (1988)
		West of British Isles, NE Atlantic	8–19 (14)	Girard and Du Buit (1999)
		West of British Isles, NE Atlantic	8–21 (13.8)	Clarke et al. (2001)
		SE Australia	8–19 (12)	Daley et al. (2002)
		Portugal, NE Atlantic	1–25 (9.9)	Veríssimo et al. (2003)
		Galicia, Spain, NE Atlantic	5–22 (14)	Bañón et al. (2006)
		Portugal, NE Atlantic	(11.3)	Figueiredo et al. (2008)
	<i>Centroscymnus owstoni</i>	Suruga Bay, Japan, NW Pacific	16–31	Yano and Tanaka (1988)
		SE Australia	5–13	Daley et al. (2002)
	<i>Centroselachus crepidater</i>	SE Australia	3–9 (6)	Daley et al. (2002)
		NE Atlantic	1–9	Nolan and Hogan (2003)
		SE Australia	4–8 (6)	Irvine (2004)

Continued

TABLE 2.3 (Continued)

Summary of Litter Sizes for Deepwater Squaloid Sharks

Family	Species	Location	Litter Size (Average)	Reference
	<i>Scymnodalatias albicauda</i>	SE Atlantic	59	Nakaya and Nakano (1995)
	<i>Somniosus rostratus</i>	Mediterranean	8	Barrull and Mate (2001)
Oxynotidae	<i>Oxynotus bruniensis</i>	SE Australia	7	Last and Stevens (2009)
	<i>Oxynotus centrina</i>	Mediterranean	10–15	Capapè et al. (1999); Megalofonou and Damalas (2004)
Dalatiidae	<i>Dalatias licha</i>	SE Australia; ?	7–16	Daley et al. (2002); Compagno et al. (2005)
	<i>Isistius brasiliensis</i>	Brazil, SW Atlantic	9	Gadig and Gomes (2002)
	<i>Squaliolus laticaudus</i>	Brazil, SW Atlantic	4	Cunha and Gonzalez (2006)

^a Referred to in Wetherbee (1996) and Daley et al. (2002) as *E. granulosus*, this is correctly *E. baxteri*.

reproductive cycle that is noncontinuous (i.e., with a resting period between parturition and the development of new oocytes) (Daley, Stevens, and Graham 2002).

Specific information on the reproductive biology of the deepwater mackerel sharks (Lamniformes) is limited. While oophagy has been confirmed in several lamnoids (see Compagno 2001), gravid females have never been observed in some deepwater species, such as the rare goblin shark *Mitsukurina owstoni*, and the smalltooth sand tiger *Odontaspis ferox* (Compagno 2001; Yano et al. 2007; Fergusson, Graham, and Compagno 2008). Sund (1943) reported a litter size of six from a single basking shark *Cetorhinus maximus*, and the litter size of the deepwater odontaspids is likely two (with biennial reproduction) based on the mode of reproduction of the inshore sand tiger shark *Carcharias taurus* (Compagno 2001; Lucifora, Menni, and Escalante 2002). In the crocodile shark *Pseudocarcharias kamoharui*, two embryos develop in each uterus by feeding on ova in uterine egg capsules (Fujita 1981; Compagno 2001).

The false catsharks (Pseudotriakidae) are the only carcharhinoid sharks, and indeed the only nonlamnoid sharks, to display oophagy (Yano 1992, 1993; Musick and Ellis 2005). Consequently, fecundity is low. Yano (1993) found the slender smoothhound *Gollum attenuatus* to generally possess two embryos, one in each uterus, although a small number of specimens contained only a single embryo (1.8% of gravid females examined) and two females contained three embryos (in both cases, one of these had failed to develop). In the false catshark *Pseudotriakis microdon*, only litter sizes of two have been observed (Saemundsson 1922; Taniuchi, Kobayashi, and Otake 1984; Yano 1992; Stewart 2000). The gestation period of both species is unknown, but for *P. microdon* at least, it is likely extended, presumably more than year and possibly two or three years (K. Yano, unpublished data, cited in Kyne, Yano, and White 2004).

Of the species of catsharks (Scyliorhinidae) for which reproductive mode has been confirmed, the majority are oviparous (Ebert, Compagno, and Cowley 2006). Viviparity is known only from a small number of species, and has been confirmed from broadhead catshark *Bythaelurus clevoi*, mud catshark *B. lutarius*, lollipop catshark *Cephalurus cephalus*, and African sawtail catshark *Galeus polli* (Springer 1979; Séret 1987; Balart, Gonzalez-Garcia, and Villavicencio-Garayzar 2000; Compagno, Dando, and Fowler 2005; Ebert, Compagno, and Cowley 2006; Francis 2006). Despite earlier reports of viviparity in Dawson's catshark

B. dawsoni and roughtail catshark *G. arae*, these species have since been shown to be oviparous (Konstantinou, McEachran, and Woolley 2000; Francis 2006). Furthermore, a report of viviparity in the Saldanha catshark *Apristurus saldanha* by Myagkov and Kondyurin (1978) is in error, and that manuscript is in fact referring to *G. polli* (Ebert, Compagno, and Cowley 2006).

Litter size is small in the viviparous catsharks: two (one embryo per uterus) in both *B. clevai* and *B. lutarius* (Compagno, Dando, and Fowler 2005), one or two in *C. cephalus* (Balart, Gonzalez-Garcia, and Villavicencio-Garayzar 2000) and 5 to 13 in *G. polli* (Ebert, Compagno, and Cowley 2006). Both single and multiple oviparity can occur among the *Galeus* species, but only single oviparity is known in *Apristurus*, *Parmaturus*, and *Scyliorhinus* (Cross 1988; Ebert, Compagno, and Cowley 2006). Of the multiple oviparous sawtail sharks, blackmouth catshark *G. melastomus* can possess up to 13 egg cases in the uteri at one time, while Atlantic sawtail catshark *G. atlanticus* has been observed to carry up to nine egg cases in the uteri at one time (Muñoz-Chápuli and Perez Ortega 1985; Iglésias, Du Buit, and Nakaya 2002). For the oviparous *Bythaelurus*, only single oviparity has been observed, while *Halaaelurus* are multiple oviparous (Compagno, Dando, and Fowler 2005; Francis 2006).

Catsharks generally reproduce throughout the year, and while most species lack significant patterns of reproductive seasonality, there are often seasonal peaks in egg production (Ebert, Compagno, and Cowley 2006). Richardson et al. (2000) suggested year-round reproduction in Izak catshark *Holohalaelurus regani* with no significant difference observed in the proportion of mature females carrying egg cases between seasons, similar to *B. dawsoni* (Francis 2006). Cross (1988) suggested that brown catshark *A. brunneus* and filetail catshark *P. xaniurus* may be reproductively active throughout the year, although in *A. brunneus* more females carried egg cases in December to May than June to November. Both gecko catshark *G. eastmani* and broadfin sawtail catshark *G. nipponensis* from Suruga Bay, Japan, reproduce throughout the year, but *G. nipponensis* has a higher incidence of carrying egg cases in December and January (Horie and Tanaka 2000). Off southern Portugal, *G. melastomus* is reproductively active year-round but with bimodal peaks in summer and winter (Costa, Erzini, and Borges 2005).

Chain catshark *Scyliorhinus retifer* held in captivity laid pairs of eggs at intervals of 14.1 to 16.7 days (average ~15.3 days; Castro, Bubucis, and Overstrom 1998). If egg-laying continued at this level all year, an individual could produce 46 egg cases annually. Capapé et al. (2008) estimated a maximum annual egg case production of 97 in *G. melastomus* off Mediterranean France, and Richardson et al. (2000) suggested that fecundity is high in *H. regani*, based on the proportion of mature females carrying egg cases and a continuous reproductive cycle. Like many other oviparous chondrichthyans (see Hoff 2008), development time of embryos is long in *S. retifer* (mean = 256 days; Castro, Bubucis, and Overstrom 1988). Little is known about egg-laying sites in the deep sea, although underwater video footage analyzed by Flammang, Ebert, and Cailliet et al. (2007) revealed that *A. brunneus* and *P. xaniurus* entangle egg case tendrils on sessile invertebrates on rocky outcrops at depths of 300 to 400 m.

2.3.1.2 Skates

Despite the high diversity of the softnose skates (Arhynchobatidae), there is little detailed information on their biology. There is considerably more information available on the hardnose skates (Rajidae) than most other batoid families, particularly for shelf species. The biology of the entirely deepwater family Anacanthobatidae is very poorly known.

Skates are oviparous and many species exhibit year-round or protracted egg-laying seasons, although inshore species may have more defined laying seasons (Sulikowski et al.

2005b, 2007; Ruocco et al. 2006). Henderson, Arkhipkin, and Chtcherbich (2004) observed year-round egg-laying in white-dotted skate *Bathyraja albomaculata* from the Falkland/Malvinas Islands, with peaks in deposition in autumn and winter. *Bathyraja albomaculata* from off continental South America (Uruguay, Argentina, and southwest Chile) were carrying egg cases in April, September, and October, also suggesting year-round laying (Ruocco et al. 2006). An examination of a small (~2 km²) Alaska skate *B. parmifera* nursery area on the shelf-slope edge in the eastern Bering Sea showed a peak in reproductive activity in June and July, although egg-laying occurred year-round (Hoff 2008). Egg case densities were as high as 549,843 eggs/km² in this nursery ground (with 53% to 84% viability) (Hoff 2008).

Ebert (2005) provided a detailed account of the reproductive biology of seven *Bathyraja* and one *Rhinoraja* skate from the eastern Bering Sea in the North Pacific, noting that for these skates there is an extended juvenile stage, a brief adolescent stage, and little growth after maturity. In Aleutian skate *B. aleutica*, Ebert (2005) recognized that ovarian fecundity increased in females up to 1450 mm TL, only to decline in the larger animals. In addition, he observed that some of the largest *B. aleutica*, commander skate *B. lindbergi*, and small-thorn skate *B. minispinosa* were reproductively inactive with atrophied ovaries, suggesting either a period of reproductive inactivity or senescence.

Estimates of annual fecundity of rajid skates are highly variable between species. Two species of rajids are known to carry multiple embryos per egg case: mottled skate *Raja pulchra*, an inshore coastal species from the Northwest Pacific, and *R. binoculata* from the eastern North Pacific (Ishiyama 1958; Hitz 1964; Ebert and Davis 2007). *Raja binoculata* can carry two to seven embryos per egg case, with an average of three to four (Hitz 1964). Annual fecundity has been estimated as 90 for cuckoo skate *Leucoraja naevus* (Du Buit 1976) and 10 to 20 for thorny skate *Amblyraja radiata* (Berestovskii 1994) (40.5 in captivity; Parent et al. 2008). Parent et al. (2008) provided annual fecundities of 69 to 115 for an individual *D. laevis* held in captivity, with very long incubation periods of 342 to 494 days (mean = 421 days). Ebert and Davis (2007) calculated that annual fecundity in *R. binoculata* may reach 1260 based on an assumed average of 3.5 embryos per egg case, and egg-laying rates of 360 egg cases per year in captivity (K. Lewand, personal communication in Ebert and Davis 2007). Temperature, however, affects egg-laying rates (Holden, Rout, and Humphreys 1971) and will alter estimates of fecundity. Hoff (2008) showed that the protracted incubation period of oviparous chondrichthyans was correlated with the rearing temperature; development is longest in *B. parmifera* in the Bering Sea (~3.5 years). It is reasonable then to suggest that incubation times could be very protracted for deepwater oviparous skates, catsharks, and holocephalans in the cold waters of the continental slope and beyond.

2.3.1.3 Holocephalans

Holocephalans are oviparous but, as with many other deepwater groups, their biology is poorly known. Chimaeras may be reproductively active throughout the year, without an apparent well-defined egg-laying season (ninespot chimaera *Hydrolagus barbouri*; Kokuho, Nakaya, and Kitagawa 2003) or with a seasonal peak in activity (*H. colliei*; see Sathyanesan 1966). Barnett et al. (2009) hypothesized that *H. colliei* has a six- to eight-month parturition season and Malagrino, Takemura, and Mizue (1981) suggested that rabbitfish *Chimaera monstrosa* has a reproductive season lasting six to seven months, with a peak in activity in the northern winter. In captivity, *H. colliei* egg cases are laid in pairs every 10 to 14 days over a period of several months (Didier and Rosenberger 2002). Barnett et al. (2009)

combined captive egg-laying rates with the duration of the parturition season in *H. colliei* to arrive at an estimated annual fecundity of 19.5 to 28.9 for that species, the only estimate of annual fecundity for a deepwater holocephalan.

2.3.2 Age and Growth

Determining age at maturity, longevity, and growth rates is crucial to provide management advice through stock assessment and population models, and to accurately assess productivity and vulnerability of a species to fisheries (Cailliet and Goldman 2004). Sharks and rays have traditionally been aged by examining seasonal changes in the deposition of growth bands in their vertebrae (Cailliet and Goldman 2004). Band counts can be correlated to age where the pattern of deposition has been shown to be annual (processes termed verification and validation; see Cailliet and Goldman 2004). For most sharks and rays examined, growth bands are laid down annually, although there are exceptions (i.e., angel sharks *Squatina* spp; Natanson and Cailliet 1990). Vertebral ageing of deepwater chondrichthyans has generally been unsuccessful and alternative methods have had to be developed, many still in their infancy.

The internal and external examination of the dorsal spines of dogfishes (Squaliformes) and holocephalans has proved useful for estimating age (Sullivan 1977; Tanaka 1990; Irvine 2004; Irvine, Stevens, and Laurenson 2006b), while skates can be aged using caudal thorns (Gallagher and Nolan 1999). Neural arches have shown potential for estimating age in sixgill sharks (Hexanchiformes) (McFarlane, King, and Saunders 2002) and radiometric ageing has been tested on some dogfishes (Fenton 2001). Gennari and Scacco (2007) successfully enhanced growth bands on the small, poorly calcified, fragile, deep-coned vertebrae of *E. spinax*, and the use of their technique may prove useful for other deepwater species with similar vertebral structure. In other deepwater groups, attempts at ageing have proved unsuccessful; for sleeper sharks *Somniosus* spp., which lack dorsal spines, an examination of vertebrae and neural arches could not identify any bands that may represent growth (S. Irvine, personal communication). There is a complete lack of age and growth estimates for the deepwater catsharks (Scyliorhinidae); the vertebrae of many species may be too poorly calcified to yield age estimates and attempts to age various scyliorhinids, including *Apristurus* spp. and *Parmaturus* spp., have proved unsuccessful (B. Flammang, personal communication). The continued development of ageing methods for deepwater chondrichthyans (particularly those lacking dorsal spines) is required.

Table 2.4 provides a summary of all available age and growth studies for deepwater chondrichthyan species. Published estimates of age and growth for deepwater chondrichthyans are available for only 34 of the 530 species (13 dogfishes, one thresher shark, 19 skates, and one chimaera) (Table 2.4). Many of these aging estimates are unvalidated and there is a clear need for research into suitable validation techniques for age determination in the deepwater sharks. A correlation between external dorsal spine band counts and the results of radiometric age estimates (Fenton 2001) in *C. crepidater* allowed Irvine, King, and Saunders (2006b) to suggest that external bands were laid down annually.

The oldest age estimates of a deepwater shark are 70 years for female and 71 years for male *C. squamosus* from the Northeast Atlantic (Clarke, Connolly, and Bracken 2002a). Maturity was suggested to be reached at 35 years (Clarke, Connolly, and Bracken 2002a). Fenton (2001) provided a preliminary age estimate of 46 years for *C. zeehaani* from Australia (although this included only immature individuals). Maximum age estimates for needle dogfish *C. acus* from Japan were considerably lower at 18 years for females and 17 years for males (Tanaka 1990), while *C. granulatus* in the western Mediterranean has been estimated

TABLE 2.4
Summary of Age and Growth Studies for Deepwater Chondrichthyan Species

Family	Species	Species Depth Range (m)	Location	Method	von Bertalanffy Growth Parameters				Max Age (t_{max})	Age at Maturity (t_{mat})	Reference
					L_{∞}	k	t_0				
Squalidae	<i>Squalus blainville</i>	16→440	Western Mediterranean	Vertebrae	♀ 1179 mm TL	0.102	-1.380	8	5.1	Cannizzaro et al. (1995)	
					♂ 960 mm TL	0.135	-1.397	8	3.3		
	<i>Squalus megalops</i>	0-732	Agulhas Bank, South Africa, SE Atlantic	External DS	♀ 932 mm TL	0.03	-8.1	32	15	Watson and Smale (1999)	
					♂ 526 mm TL	0.09	-6.9	29	9		
	<i>Squalus mitsukurii</i>	4-954	SE Australia	External DS	♀ 756 mm TL	0.042	-9.77	28	—	Braccini et al. (2007)	
					♂ 455 mm TL	0.158	-4.86	15	—		
Sala y Gomez Seamout, SE Pacific			External DS	♀ -	—	—	16	—	Litvinov (1990)		
				♂ -	—	—	14	—			
	Hancock Seamout, NW Pacific		External DS	♀ 1070 mm TL	0.041	-10.09	27	15	Wilson and Seki (1994)		
				♂ 660 mm TL	0.155	-4.64	18	4			
	Hancock Seamout, NW Pacific		External DS	♀ 831 mm TL	0.103	-2.94	17	14-16	Taniuchi and Tachikawa (1999)		
				♂ 645 mm TL	0.252	-0.430	12	6-7			
	Choshi, Japan, NW Pacific		External DS	♀ 1628 mm TL	0.039	-5.21	21	9	Taniuchi and Tachikawa (1999)		
				♂ 1093 mm TL	0.066	-5.03	20	10-11			
Centrophoridae	<i>Centrophorus acus</i>	150-950	Ogasawara Is., Japan, NW Pacific	External DS	♀ 1112 mm TL	0.051	-5.12	27	9	Taniuchi and Tachikawa (1999)	
					♂ 880 mm TL	0.060	-5.51	21	5		
	<i>Centrophorus granulatus</i>	50-1440	Suruga Bay, Japan, NW Pacific	Internal DS	♀ 1262 mm TL	0.155	-0.485	18	—	Tanaka (1990)	
					♂ 1172 mm TL	0.173	-1.403	17	10		
	<i>Centrophorus squamosus</i>	230-2400	Western Mediterranean	Internal DS	♀ 1094 mm TL	0.096	-5.48	39	16.5	Gualart (1998)	
			Rockall Trough and Porcupine Bank, NE Atlantic	Internal DS	♂ 917 mm TL	0.107	-9.78	25	8.5	Clarke et al. (2002a)	
				♀ -	—	—	70	35			
				♂ -	—	—	71	30			

<i>Centrophorus zeehaani</i>	208–701	Australia	Radiometric	♀ + ♂	—	—	—	46 ^a	—	Fenton (2001)
<i>Deania calcea</i>	70–1470	Rockall Trough and Porcupine Bank, NE Atlantic SE Australia	Internal DS	♀	0.077	-0.933	35	25	25	Clarke et al. (2002b)
				♂	0.135	-0.165	32	—	—	
Etmopteridae	250–1500	SE Australia	External DS	♀	0.051	-5.11	37	21.5	21.5	Irvine (2004)
				♂	—	—	33	13.5	—	
	250–1500	SE Australia	External DS	♀	0.040	-4.51	57	30	30	Irvine et al. (2006a)
				♂	0.082	-1.43	48	20	20	
	274–1000	Portugal, NE Atlantic	Internal DS	♀	0.163	-2.00	22	10.5	10.5	Irvine et al. (2006a)
				♂	0.13	—	17	10	10	
70–2000	Western Mediterranean	Vertebrae	♀	0.13	—	17	10	10	Coelho and Erzini (2007)	
			♂	0.17	—	13	7	7		
70–2000	Western Mediterranean	Vertebrae	♀	0.16	-1.09	9	—	—	Gennari and Scacco (2007)	
			♂	0.19	-1.41	7	—	—		
Somniosidae	270–2080	SE Australia	Internal DS	♀	0.12	—	11	4.67	4.67	Coelho and Erzini (2008)
				♂	0.09	—	8	3.97	3.97	
	270–2080	SE Australia	External DS	♀	0.072	-6.13	54	20	20	Irvine et al. (2006b)
				♂	0.141	-2.99	34	~9	~9	
	270–2080	SE Australia	Internal DS	♀	0.163	-1.92	27	—	—	Irvine (2004)
				♂	0.362	-1.51	22	—	—	
219–1427	SE Australia	Radiometric	♀ + ♂	—	—	43	—	—	Fenton (2001)	
			♀	—	—	39	29	29	Irvine (2004)	
219–1427	SE Australia	External DS	♂	—	—	32	18	18	—	
			♀	—	—	32	18	18		
Alopiidae	0–732	Taiwan, NW Pacific	Vertebrae	♀	0.092	-4.21	20	12.3–13.4	12.3–13.4	Liu et al. (1998)
				♂	0.088	-4.24	19	9–10	9–10	
Arhynchobatidae	55–861	Falkland/Malvinas Is., SW Atlantic	Caudal thorn	♀	0.09	-1.94	17	10	10	Henderson et al. (2004)
				♂	0.07	-2.39	17	11	11	
	28–604	Falkland/Malvinas Is., SW Atlantic	Caudal thorn	♀	0.07	-1.95	20	8.2	8.2	Arkhipkin et al. (2008)
				♂	0.05	-2.55	20	10	10	

Continued

TABLE 2.4 (Continued)
Summary of Age and Growth Studies for Deepwater Chondrichthyan Species

Family	Species	Species Depth Range (m)	Location	Method	von Bertalanffy Growth Parameters			Max Age (t_{max})	Age at Maturity (t_{mat})	Reference
					L_{∞}	k	t_0			
Rajidae	<i>Bathyraja griseocauda</i>	82–941	Falkland/Malvinas Is., SW Atlantic	Caudal thorn	♀ 3652 mm TL ^b ♂ 3589 mm TL ^b	0.02	-3.46 -3.04	28 23	17.8 14	Arkhipkin et al. (2008)
	<i>Bathyraja parvifera</i>	20–1425	Eastern Bering Sea, North Pacific	Vertebrae	♀ 1446 mm TL ♂ 1263 mm TL	0.087	-1.75 -1.39	17 15	10 9	Matta and Gunderson (2007)
	<i>Bathyraja trachura</i>	213–2550	United States, NE Pacific	Vertebrae	♀+♂ 1013 mm TL	0.09	—	♀ 17 ♂ 20	—	Davis et al. (2007)
	<i>Amblyraja georgiana</i>	20–800	Ross Sea, Antarctica	Caudal thorn	♀ 692 mm PL ♂ 799 mm PL	0.402	-0.73 -2.41	14 12	8–11 6–7	Francis and Ó Maolagáin (2005) ^c
	<i>Amblyraja radiata</i>	18–1400	Gulf of Maine, NW Atlantic	Vertebrae	♀ 1270 mm TL ♂ 1200 mm TL	0.12	-0.4 -0.37	16 16	11 10.9	Sulikowski et al. (2005a, 2006)
	<i>Dipturus batis</i>	100–1000	Celtic Sea, NE Atlantic	Vertebrae	♀+♂ 2537 mm TL	0.057	-1.629	50	11	Du Buit (1972)
	<i>Dipturus innotinatus</i>	15–1310	New Zealand, SW Pacific	Vertebrae	♀+♂ 1505 mm PL	0.095	-1.06	♀ 24 ♂ 15	13.0 8.2	Francis et al. (2001)
	<i>Dipturus laevis</i>	0–430	Georges Bank, NW Atlantic	Vertebrae	♀+♂ 1663 mm TL	0.141	-1.291	—	♀ 6.5–7.2 ♂ 5.8–6.1	Gedamke et al. (2005)
	<i>Dipturus pullouunctata</i>	15–457	South Africa, SE Atlantic	Vertebrae	♀ 1327 mm DW ♂ 771 mm DW	0.05	-2.20 -2.37	14 18	9	Walmsley-Hart et al. (1999)
	<i>Dipturus trachydermus</i>	20–450	Chile, SE Pacific	Vertebrae	♀ 2650 mm TL ♂ 2465 mm TL	0.079	-1.438 -1.157	26 25	17 15	Licandeo et al. (2007)
<i>Leucoraja naucus</i>	20–500	Celtic Sea, NE Atlantic	Vertebrae	♀+♂ 916 mm TL	0.1085	-0.465	14	9	Du Buit (1972)	
			Irish Sea, NE Atlantic	Vertebrae	♀ 839 mm TL ♂ 746 mm TL	0.197	-0.151 -0.997	8 6	4.25 4.17	Gallagher et al. (2004)

<i>Leucoraja wallacei</i>	70–500	South Africa, SE Atlantic	Vertebrae	♀ 435 mm DW ♂ 405 mm DW	0.26 0.27	-0.21 -0.8	15 12	7	Walmsley-Hart et al. (1999)
	46–914	Gulf of Maine, NW Atlantic	Vertebrae	♀ 696 mm TL ♂ 754 mm TL	0.12 0.12	— —	14 15	—	Natanson et al. (2007)
<i>Raja binoculata</i>	3–800	Canada, NE Pacific	Vertebrae	♀ 2935 mm TL ♂ 2330 mm TL	0.04 0.05	-1.60 -2.10	26 25	8 6	McFarlane and King (2006)
	9–1069	California, Eastern Central Pacific Gulf of Alaska, NE Pacific Canada, NE Pacific	Vertebrae Vertebrae Vertebrae	♀ - ♂ 2475 mm TL ♀ 1533 mm TL ♂ 1372 mm TL ♂ 1315 mm TL	— 0.0796 0.1524 0.06 0.07	— -1.075 -0.632 -1.80 -2.17	12 11 14 15 26 23	10–12 7–8 — 10 7	Zeiner and Wolf (1993) Gburski et al. (2007) McFarlane and King (2006)
<i>Zearaja chilensis</i>	28–500	California, Eastern Central Pacific Gulf of Alaska, NE Pacific Valdivia, Chile, SE Pacific Southern fjords, Chile, SE Pacific	Vertebrae Vertebrae Vertebrae Vertebrae	♀ 1067 mm TL ♂ 967 mm TL ♀ 2341 mm TL ♂ 1688 mm TL ♀ 1283 mm TL ♂ 1078 mm TL ♀ 1364 mm TL ♂ 1179 mm TL	0.16 0.25 0.0368 0.0561 0.112 0.134 0.104 0.116	-0.3 0.73 -1.993 -1.671 -0.514 -0.862 -0.669 -1.056	13 13 24 25 21 18 21 17	10 7 — 14 11 13.5 10.7	Zeiner and Wolf (1993) Gburski et al. (2007) Licandeo et al. (2006) Licandeo and Cerna (2007)
	10–1500	Patagonia fjords, Chile, SE Pacific New Zealand, SW Pacific	Vertebrae Vertebrae	♀ 1496 mm TL ♂ 1220 mm TL ♀+♂ 913 mm PL	0.087 0.110 0.16	-1.266 -1.263 -1.20	22 19 ♀ 9 ♂ 7	12.8 10.3 5.7 4.3	Licandeo and Cerna (2007) Francis et al. (2001)
Chimaeridae	50–1000	Portugal, NE Atlantic	Internal DS	♀ 636 mm PSCFL ♂ 533 mm PSCFL	0.10 0.14	-1.08 -0.50	17 15	— —	Moura et al. (2004)

^a No mature specimens were aged.

^b The estimates of L_{∞} for *B. griseocauda* are inflated (maximum size of species ~2000 mm TL) (Arkhipkin et al. 2008).

^c Francis and Ó Maolagáin (2005) advise that their aging estimates are preliminary and should be utilized with caution. DS, dorsal spine; PL, pelvic length; PSCFL, pre-supracaudal fin length; DW, disc width.

to reach 39 years (Guallart 1998). Female birdbeak dogfish *Deania calcea* were estimated to reach similar maximum ages of 37 and 35 years off southern Australia (Irvine 2004) and in the Northeast Atlantic (Clarke, Connolly, and Bracken 2002b), respectively. This species also exhibited late maturity, at 21.5 years for Australia and 25 years for the Northeast Atlantic (Clarke, Connolly, and Bracken 2002b; Irvine 2004).

Estimating the age of squaloid sharks using dorsal spines has been undertaken using counts of either internal or external bands. Irvine, Stevens, and Laurenson (2006a, 2006b) showed that there were considerable differences in age estimations between these techniques for *E. baxteri* (maximum age 57 years using external band counts; 26 years using internal band counts) and *C. crepidater* (54 years external; 27 years internal). Irvine, Stevens, and Laurenson (2006b) suggested that internal bands were inaccurate and underestimate age, and Irvine, Stevens, and Laurenson (2006a) noted that internal bands become unreadable as internal dentine appears to stop forming in adult fish. As such, count estimates from external bands likely are more reliable (Irvine, Stevens, and Laurenson 2006a, 2006b). *Etmopterus spinax* reaches a far smaller size (rarely >450 mm TL, although it can reach 600 mm TL) than *E. baxteri* (880 mm TL) (Compagno, Dando, and Fowler 2005), but even this small species is relatively slow-growing (Coelho and Erzini 2008) and long-lived (extrapolated longevity 22 years; Gennari and Scacco 2007).

Until recently, age and growth data for the softnose skates (Arhynchobatidae) were very limited; there have been several aging studies of hardnose species (Rajidae). For many species here included as deepwater fauna, aging studies were conducted on the shelf end of their bathymetrical range, for example broadnose skate *Bathyraja brachyurops* from the Falkland/Malvinas Islands (Arkhipkin et al. 2008), and *R. binoculata* and *R. rhina* from the Northeast Pacific (McFarlane and King 2006; Gburski, Gaichas, and Kimura 2007; Ebert, Smith, and Cailliet 2008), among others. Maximum age estimates for arhynchobatid skates (*Bathyraja*) are 17 to 28 years (Henderson, Arkhipkin, and Chtcherbich 2004; Davis, Cailliet, and Ebert 2007; Matta and Gunderson 2007; Arkhipkin et al. 2008), and for rajid species 8 to 26 years (see Table 2.4), with the exception of *D. batis*, for which Du Buit (1972) estimated a maximum age of 50 years. Longevity of at least 20 years has been confirmed for *A. radiata* from skates tagged off Newfoundland (Templeman 1984). Age and growth estimates follow the general trend that larger skates are slower growing and longer lived than the smaller species, which are faster growing (Sulikowski et al. 2005b).

Age and growth estimates are available for a single deepwater holocephalan *C. monstrosa* from the Northeast Atlantic (Moura et al. 2004; Calis et al. 2005), with males aged to 30 years and females to 26 years off the west of Ireland. Age estimates off Portugal were considerably lower, up to 17 years for females and 15 years for males. Variation in these estimates is likely due to the size range of fish sampled, with Calis et al. (2005) sampling individuals to a far greater maximum size than Moura et al. (2004) (i.e., 740 mm vs. 571 mm PSCFL). Johnson and Horton (1972) attempted several methods to age *H. collicii*; however, none proved successful.

2.3.3 Demography and Population Dynamics

Combining some of the information on reproductive biology and age for deepwater chondrichthyan species can provide estimates of the number of reproductive years, and possible lifetime reproductive output (lifetime fecundity). The number of reproductive years for some deepwater chondrichthyans may be very small, particularly for the skates, which may also undergo senescence at large sizes (Ebert 2005). Table 2.5 gives the estimated number

TABLE 2.5

Estimates of the Number of Reproductive Years and Lifetime Fecundities for a Selection of Deepwater Squaloid Sharks, Assuming Different Reproductive Periodicities (i.e., Biennial or Triennial)

Species	Reproductive Periodicity	No. of Reproductive Years	Lifetime Fecundity	References
<i>Centrophorus granulosus</i>	Biennial	23.5	12	Guallart (1998); Irvine (2004)
<i>Deania calcea</i>	Biennial	15.5	62	Irvine (2004)
	Triennial		41	
<i>Etmopterus baxteri</i>	Biennial	28	128 ^a	Irvine (2004)
	Triennial		81 ^a	
<i>Centroselachus crepidater</i>	Biennial	34	102	Irvine (2004)
	Triennial		68	
<i>Proscymnodon plunketi</i>	Biennial	10	85	Irvine (2004)
	Triennial		56	

Source: Irvine SB (2004) Ph.D. Thesis, Deakin University, Australia.

^a These calculations consider the maternal–litter size relationship (Irvine 2004).

of reproductive years and lifetime fecundities of several deepwater squaloid sharks, based largely on Irvine (2004), and Table 2.6 gives those for a selection of deepwater rajid skates, based largely on Ebert (2005).

The lowest calculated lifetime fecundity is for *C. granulosus*; a single female will produce a maximum of 12 pups throughout its lifetime (assuming continuous breeding from maturity to maximum age with no senescence) (Table 2.5). Among the skates, lifetime fecundity in *A. radiata* may be low if one applies the upper annual egg case production of 20 from

TABLE 2.6

Estimates of the Number of Reproductive Years and Lifetime Fecundities for a Selection of Deepwater Rajid Skates

Species	No. of Reproductive Years	Lifetime Fecundity	References
<i>Amblyraja georgiana</i>	4–7	—	Francis and Ó Maolagáin (2005)
<i>Amblyraja radiata</i>	6–10	120–200	Berestovskii (1994); Templeman (1984); Sulikowski et al. (2005a; 2006)
<i>Dipturus innominatus</i>	13	—	Francis et al. (2001); Ebert (2005)
<i>Dipturus pullopunctata</i>	6	—	Walmsley-Hart et al. (1999); Ebert (2005)
<i>Leucoraja naevus</i>	6	540	Du Buit (1972, 1976); Ebert (2005)
	4	360	Du Buit (1976); Gallagher et al. (2004)
<i>Leucoraja wallacei</i>	9	—	Walmsley-Hart et al. (1999); Ebert (2005)
<i>Raja binoculata</i>	1–3	—	Zeiner and Wolf (1993); Ebert (2005)
	17	21,420	McFarlane and King (2006); Ebert and Davis (2007)
<i>Raja rhina</i>	4	—	Zeiner and Wolf (1993); Ebert (2005)
	19	—	McFarlane and King (2006)
<i>Zearaja chilensis</i>	8	—	Licandeo et al. (2006)
<i>Zearaja nasutus</i>	4	—	Francis et al. (2001); Ebert (2005)

Berestovskii (1994), together with maximum ages of 16 to 20 (Templeman 1984; Sulikowski et al. 2005a) and a female age at maturity of 11 years (Sulikowski et al. 2006). This results in an estimated lifetime fecundity of 120 to 200 egg cases. At the other end of the scale, if the annual fecundity estimate of *R. binoculata* from Ebert and Davis (2007) (1260 young per year) is combined with the aging results of McFarlane and King (2006; 17 reproductive years), the big skate in the eastern North Pacific may have a lifetime fecundity of 21,420 young. This calculation assumes no senescence and continuous breeding throughout the adult life of the species, which likely overestimate lifetime reproductive output.

García, Lucifora, and Myers (2008) showed that when compared to continental shelf and oceanic chondrichthyans, deepwater species had a later age at maturity, higher longevity, and a lower growth completion rate. They estimated that the average fishing mortality required to drive a deepwater species to extinction was 38% of that of an oceanic species, and 58% of that of a continental shelf species (García, Lucifora, and Myers 2008).

2.3.4 Diet and Feeding Habits

Many sharks are upper trophic level predators (Cortés 1999; Wetherbee and Cortés 2004), but an overall understanding of their diets, food consumption patterns, and feeding habits lags behind our knowledge of other marine groups, including the teleost fishes (Wetherbee and Cortés 2004). That lag is even more apparent in relation to the deepwater chondrichthyans. Stomach content analysis has been conducted for a number of species, allowing standardized estimates of trophic levels for deepwater sharks, which are tertiary consumers (trophic levels 4.2 to 4.3 for hexanchids, 3.8 to 4.4 for squaloids, 3.6 to 4.2 for scyliorhinids, and 4.1 to 4.3 for pseudotriakids; Cortés 1999), and for skates (mean trophic levels 3.8 for Rajidae, 3.9 for Arhynchobatidae, and 3.5 for Anacanthobatidae; Ebert and Bizzarro 2007). Among the skates, many of the larger deepwater species showed the highest trophic level estimates (Ebert and Bizzarro 2007).

Many deepwater sharks show fairly opportunistic feeding, although teleosts are often primary prey. In addition, deepwater sharks scavenge on cetacean falls at depth (Smith and Baco 2003) while the cookiecutter sharks (*Isistius* spp.) are parasitic on large marine fauna (see Chapter 1). Jakobsdóttir (2001) found that teleosts, cephalopods, and crustaceans occurred frequently in the diet of *C. fabricii*. Teleosts were the most frequent prey class in the stomachs of *E. princeps*, but cephalopods and crustaceans were also important (Jakobsdóttir 2001). Similarly, *E. spinax* exhibits a generalized benthopelagic diet (Neiva, Coelho, and Erzini 2006) as does the catshark *G. melastomus* (Carrassón, Stefanescu, and Cartes 1992). In contrast, the diet of *C. coelolepis* in the Mediterranean is highly specialized on cephalopods (Carrassón, Stefanescu, and Cartes 1992). Blaber and Bulman (1987) classified *D. calcea* as an epibenthic piscivore with a diet consisting almost entirely of teleosts (these authors observed little dietary overlap with a sympatric teleost epibenthic piscivore, suggesting resource partitioning between these upper slope species).

Ontogenetic dietary shifts are evident in some deepwater sharks. Larger *C. fabricii* specialized more on teleosts (Jakobsdóttir 2001), and *E. spinax* showed a shift from a diet dominated by crustaceans in smaller size classes to a more diverse diet in larger size classes, with a higher relative importance of teleosts and cephalopods (Neiva, Coelho, and Erzini 2006). Such shifts may be related to changes in habitat with size (Neiva, Coelho, and Erzini 2006). Carrassón, Stefanescu, and Cartes (1992) showed that *G. melastomus* diet varied between the upper and mid slope, probably due to a change in resource availability. Some geographic variation in the diet of *H. perlo* is apparent, as would be expected from such a wide-ranging species. This shark is a teleost specialist off southern Australia and off

Tunisia, while on the Great Meteor Seamount in the Eastern Atlantic, teleosts and cephalopods are of similar importance (see Braccini 2008).

Skates feed primarily on decapod crustaceans and secondarily teleosts, with polychaetes and amphipods also important prey groups (see Ebert and Bizzarro 2007 for a review). There is relatively little information on the diets of the benthic-feeding holocephalans. The diet of *C. monstrosa* is dominated by crustaceans, with a shift evident from smaller fish that fed mostly on amphipods, to larger individuals that ate mainly decapods (Moura et al. 2005). MacPherson (1980) recorded rather different prey preferences for *C. monstrosa* than Moura et al. (2005), with ophiuroid echinoderms a significant prey group in all but the largest size class of fish. Indeed, Moura et al. (2005) observed geographical and bathymetric differences in diet, suggesting opportunistic foraging.

2.3.5 Population Segregation, Movements, and Migration

Deepwater chondrichthyans are often segregated bathymetrically by size, sex, or maturity stage. Segregation has been demonstrated by changes in the catch composition with depth, including for such species as *E. baxteri*, *C. fabricii*, *E. princeps*, roughskin dogfish *Centroscymnus owstoni*, *C. coelolepis*, and *H. colliei* (Yano and Tanaka 1988; Wetherbee 1996; Jakobsdóttir 2001; Didier and Rosenberger 2002). Several studies have noted a lack of gravid females, and it has been suggested that these may make movements into, or occur in, deeper water (possibly occupying nursery areas; although this is uncertain and nursery areas have not been identified for any deepwater viviparous shark species) or that they may be bathypelagic (and thus less susceptible to capture in benthic sampling/fishing gear; Yano and Tanaka 1988; Wetherbee 1996; Jakobsdóttir 2001; Figueiredo et al. 2008).

A number of deepwater squaloid sharks, particularly small pelagic species in the family Dalatiidae but also sleeper sharks, undertake daily migrations from deep water toward the surface at night, returning to depth during the day. Daily vertical movements appear to be linked to the diel migrations of prey. Hulbert, Sigler, and Lunsford (2006) showed that diel vertical migrations in *S. pacificus* occurred only 25% of the time (i.e., 177 out of 726 days) and as such movement patterns are more complex than repeated daily vertical movements. Sharks were also seen to undertake "systematic vertical oscillations" ("methodical ascents and descents with little pause in transition") and "irregular vertical movements" ("small-amplitude movements with random frequency") with the most time spent at depths of 150 to 450 m (Hulbert, Sigler, and Lunsford 2006).

The basking shark, a highly migratory species occurring in coastal, pelagic, and deep-water habitats, was previously thought to migrate to deep water to undertake a winter hibernation (Compagno 2001; Francis and Duffy 2002). However, basking sharks tracked over extended periods (up to 6.5 months) have shown that they do not hibernate, but undertake horizontal and vertical (>750 m) movements to exploit prey concentrations (Sims et al. 2003). Around New Zealand, basking sharks overwinter, probably on or near the bottom, in deep slope waters (to 904 m; Francis and Duffy 2002).

The short- and long-term (including seasonal) movement and migration patterns of deep-water chondrichthyans are poorly known. The problems associated with tagging animals caught from depth and ensuring their survival once returned to the water, along with logistical constraints, has limited the tagging and tracking of deepwater species. Bagley, Smith, and Priede (1994) used acoustic transmitters imbedded in baits employed at 1517 to 1650 m to briefly track three *C. coelolepis*, the deepest tracked chondrichthyan. All sharks moved outside the range of the recording equipment (500 m) within six hours of bait deployment and, although Bagley, Smith, and Priede (1994) suggested that this indicated

no site fidelity, the spatial and temporal scales of the study were limited. A single *C. acus* tracked acoustically for nearly 21 hours in Japan generally swam parallel to the 500 m depth contour, mostly remaining close to the seafloor although making some vertical movements to between 10 and 50 m into the water column (Yano and Tanaka 1986). Short-term acoustic tracking of two *H. griseus* (2 to 4 days) revealed that the sharks generally remained between depths of 600 and 1100 m, swimming back and forth within limited areas, although one took a deep excursion to 1500 m (Carey and Clark 1995).

2.4 Exploitation, Management, and Conservation

2.4.1 Exploitation and Threats

As traditional marine resource stocks are depleted, global demand for fish products increases, and fishing technology advances, fisheries are moving into deeper water and new commercial deepwater fisheries are continuing to develop (Gordon 1999; Haedrich, Merrett, and O'Dea 2001; Morato et al. 2006). Deepwater chondrichthyans are taken as either targeted species or as bycatch in these deep-sea fishing operations, although there is a general lack of available trade and landings data for deepwater sharks, rays, and chimaeras (Cavanagh and Kyne 2005). An assessment of the global catch of deepwater chondrichthyans is made difficult because many species are taken as bycatch, are often discarded, or landed under generic species-codes such as "shark" or "other." Additionally, catches are under-reported globally, and poor taxonomic resolution and species identification limits the availability of species-specific data. As chondrichthyans are generally absent from the deepest oceans, they do not have a refuge at depth; all species are within the depths exploited by commercial fisheries (Priede et al. 2006).

There are few time-series data available for catches of deepwater chondrichthyans, but what data are available show considerable declines for a variety of species (Graham, Andrew, and Hodgson 2001; Devine, Baker, and Haedrich 2006). There are also several examples of the collapse of deepwater stocks due to direct or indirect fishing. Below are four case studies of the effects of commercial fishing activities on deepwater chondrichthyan stocks. These are among the few such instances where sufficient information is available to discuss the impacts of fishing. Also of concern for the deep sea are the impacts of trawling on habitat, including seamounts (Koslow et al. 2000). For example, Hoff (2008) noted that skate nursery areas are in highly productive areas, and thus vulnerable to the impacts of benthic trawling.

2.4.1.1 Case Study 1: Australian Southern and Eastern Scalefish and Shark Fishery

In the Australian Southern and Eastern Scalefish and Shark Fishery (SESSF), which extends across southern and southeastern Australia over an extensive area of the Australian Fishing Zone, intensive fishing has depleted upper slope chondrichthyan species. The SESSF is a complex multispecies, multigear fishery that comprises several sectors. Little information is available on the catch of deepwater sharks from the earlier years of slope fishing, which developed off the east coast (the state of New South Wales, NSW) in the 1970s and off the southern states of Victoria and Tasmania in the 1980s. Initial catch levels off NSW were reportedly high and as there was no market for deepwater shark carcasses, discarding