J. Zool., Lond. (2001) **253**, 53–68 © 2001 The Zoological Society of London Printed in the United Kingdom

Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review

Michael R. Heithaus

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, V5A 1S6 Canada. mheithau@sfu.ca

(Accepted 13 December 1999)

Abstract

The importance of interactions between sharks and cetaceans has been a subject of much conjecture, but few studies have addressed these interactions. Sharks (order Selachii) have been hypothesized to be important predators on dolphins and porpoises (suborder Odontoceti). Unfortunately, there are often few data to back up claims that certain shark species are major threats to cetaceans. To help identify potential shark predators in specific locations, available data on interactions with odontocetes for all shark species that may include cetaceans in their diet are reviewed. Shark species are categorized into groups based on predatory interactions with dolphins and porpoises (regular predators, occasional predators, potential predators, ectoparasites and insufficient data). Several shark species that have been overlooked in the cetacean literature are identified as potentially important predators while others that have been suspected to be important predators are probably at most occasional predators. How shark predation can influence dolphin populations, habitat use, group size and behaviour is discussed. How risk of shark predation can vary with habitat attributes in both nearshore and pelagic waters is also discussed. Predator–prey interactions have been the focus of most studies of shark–dolphin interaction, but competitive interactions may also occur. The first analysis of shark–dolphin dietary overlap is presented, which shows it to be significant between common dolphins and several species of sharks, including species that prey upon these dolphins.

Key words: predation, competition, sharks, dolphins, behaviour

INTRODUCTION

Predation risk is a primary factor that can influence group composition, group size and habitat use (e.g. Bertram, 1978; van Schaik & van Noordwijk, 1985; Lima & Dill, 1990). Risk of predation has been suggested as the selective pressure leading to the evolution of sociality in many taxa (e.g. Terborgh, 1983; van Schaik & van Hoff, 1983; van Schaik & van Noordwijk, 1985), including odontocete cetaceans (toothed whales) (Norris, 1994). Most studies of predation on odontocetes are based largely on wounds and scars on living individuals and chance observations of predation events (e.g. Corkeron, Morris & Bryden, 1987; Paterson, Quayle & Van Dyk, 1993; Mann & Barnett, 1999). Other studies merely invoke predation to explain the patterns of grouping and habitat use that are observed without quantifying these relationships. Killer whales *Orcinus orca*, false killer whales *Pseudorca crassidens*, pygmy killer whales *Feresa attenuata*, polar bears *Ursus maritimus*, and a variety of sharks have been identified as natural predators of odontocetes. In a brief review of shark predation on cetaceans, Long & Jones (1996) listed only a handful of shark species as cetacean predators including the white *Carcharodon carcharius*, tiger *Galeocerdo cuvier*, dusky *Carcharinus obscurus*, bull *Carcharinus leucas*, oceanic whitetip *Carcharinus longimanus* and shortfin mako *Isurus oxyrinchus*. Unfortunately, the criteria for these listings were unclear.

Interactions among sharks and odontocetes are not limited to predator–prey interactions. Many sharks and odontocetes feed largely on teleost fishes and cephalopods and there is a possibility for competitive interactions. For example, tiger sharks in Hawaii and north-eastern Australia, small (< 2.2 m) white sharks in the Atlantic and Pacific and sandbar sharks *Carcharinus plumbeus* off South Africa feed on a variety of teleost fish, as do many dolphins and porpoises in these areas (Carey *et al*., 1982; Tricas & McCosker, 1984; Cliff, Dudley & Davis, 1988; Simpfendorfer, 1992; Lowe *et al*., 1996). Also, there are observations of sharks and dolphins feeding from the same school of fish (e.g. Leatherwood, 1977), and whaler sharks *Carcharinus* sp.

have been seen feeding with dolphins behind trawlers in Australia (Corkeron *et al.*, 1987). Off the Farallon Islands, competition with killer whales over pinniped prey, may have been responsible for the displacement of white sharks from a traditional foraging area (Pyle *et al.*, 1999). Competitive interactions help determine group size, habitat use and ranging patterns. Therefore, it is important to determine whether shark and odontocete diets may overlap significantly. Quantitative analysis of the potential for shark–odontocete competition is difficult, and competition has never been measured.

The primary goal of this paper is to compile the largely scattered literature on shark–odontocete interactions and shark feeding to provide a background for formulating testable hypotheses about shark–odontocete predator–prey and competitive interactions. This review investigates: (1) the species of sharks that are odontocete predators world wide; (2) odontocete predation on sharks; (3) competition between dolphins and sharks in South Africa; (4) the likely influences of sharks on dolphin and porpoise populations and behaviour.

MATERIALS AND METHODS

Classifying shark predator–prey interactions with odontocetes

It is not always apparent which species of sharks are predators on dolphins and porpoises and which are likely only to scavenge cetacean carcasses. Various methods have been used to determine whether a particular shark species is a predator on dolphins and porpoises when there are no direct observations. In this review, I only consider a shark to be a predator on cetaceans if it takes free-swimming animals; the killing of terminally ill, severely wounded, or stranded animals is not considered to be a predation event. Although scavenging of cetacean carcasses may be an important source of food for many shark species (e.g. Carey *et al.*, 1982; Long & Jones, 1996), scavenging is not treated in this review since it will not influence the behaviour or population dynamics of odontocetes.

There are several ways to determine if shark bites from unwitnessed attacks were predatory or the result of scavenging. Live-strandings of cetaceans with fresh shark-inflicted wounds are usually the result of a predation attempt, but this may not always be so (e.g. Ridgway & Dailey, 1972; see later). It is sometimes possible to determine predation events from dead strandings by analysis of the wounds (e.g. Long & Jones, 1996) and to determine the species and approximate size of the shark responsible for the bites from the characteristics of the wounds and any teeth that are recovered.

The stomach contents of many sharks need to be examined to assess whether a shark species is a potential predator or a scavenger. In general, if odontocetes are found in a large proportion of the sharks' stomachs or they constitute most of the diet (e.g. per cent of prey mass or number or frequency of occurrence), the species is probably a predator as it is unlikely to be able to scavenge such a large number of odontocete carcasses. Looking at the other prey of the sharks can strengthen this argument. If a shark species is known to prey upon large, fast-swimming prey, it is possible that it is also capable of capturing an odontocete.

The above approach is only useful for identifying regular predators on odontocetes. Low frequencies of occurrence of odontocetes in the stomachs of sharks might indicate that a species is only a scavenger, or an occasional predator. One important consideration is the size distribution of sharks being examined. Many shark species show shifts in diet with age (see later) and odontocetes may only be taken by the largest size classes. Therefore, if the diet analysis includes many small individuals, the importance of odontocetes in the diet of large sharks may be overlooked.

Determining whether individual stomach contents are from predation or scavenging is difficult. Shark predation might be inferred by the presence of flukes or vertebrae in the shark's stomach (Cockcroft *et al.*, 1989), because scavenging sharks would be expected to consume only the fat-rich portions of a carcass, not bony material (e.g. Carey *et al.*, 1982; Klimley, 1994). Also, many shark attacks on odontocetes are directed at the tail flukes (Arnold, 1972; Cockcroft, 1991; Long & Jones, 1996). Studies on white sharks in South Africa provide evidence that this method is probably an underestimate of the actual predation rate. From 1978 to 1982, 24.2% of white sharks contained cetacean remains, and between 1983 and 1988, 20.7% had cetacean remains in their stomachs (Cliff, Dudley & Davis, 1989). This is significantly higher than the 1% incidence of dolphin flukes and vertebrae that were found in white sharks from 1983 to 1987 by Cockcroft, Cliff & Ross (1989). The discrepancy between these results may be because of a high frequency of scavenging or sharks not necessarily consuming flukes and vertebrae in the process of a predatory attack. Although the fluke-and-vertebrae method underestimates the actual predation rate, it is still a useful technique for identifying odontocete predators.

Most studies on the diet of sharks do not provide enough detail to analyse the data using the fluke-and-vertebrae method. In the following section, I place shark species into several categories (regular predator, occasional predator, suspected predator, ectoparasite and insufficient data) using a combination of the above techniques. This analysis is meant to help guide future research as there is still a critical lack of data for many species, and it is not possible to be certain of some classifications. The rationale for the listing, and brief descriptions of the diet and behaviour of each shark should aid research into the influences of these species on many odontocetes. When considering the data, note that many shark species are opportunistic foragers. Thus, it is possible that interactions between particular shark species and cetaceans may vary geographically depending on the resources available to both sharks and dolphins.

Competition

Dietary data were available for 3 dolphin species and 8 shark species caught off the coast of South Africa (Table 1). Niche breadth was calculated using Levins' index (Ellis, Pawson & Shackley, 1996):

$$B = \frac{1}{\sum p_i^2} \tag{1}$$

where p_i is the proportion of each prey group in the diet (based on % mass of the prey in stomachs containing a type of prey or % number for humpback dolphins). Levins' niche breadth index ranges from 1 (specific diet) to the total number of prey groups (broadest diet).

Dietary overlap was calculated with the MacArthur–Levins' index (Ellis *et al.*, 1996). Two calculations are made for each pair of species to determine asymmetrical overlap.

$$M_{ij} = \frac{\sum p_{ij} p_{ik}}{\sum p_{ij}^2} \tag{2}$$

$$M_{kj} = \frac{\sum p_{ik} p_{ij}}{\sum p_{ik}^2} \tag{3}$$

where M_{jk} and M_{kj} are the degree to which species k overlaps species j's diet and vice versa. P_{ij} and P_{ik} are the proportions that each prey type i contributes to the diet of species j and k respectively. Comparisons are all based on percentage mass of prey except those with humpback dolphins which are all based on percentage number. A value >0.7 is considered significant (Macpherson, 1981; Ellis *et al.*, 1996).

Both niche breadth and dietary overlap were calculated for the South African data with family-level prey groups. Some ray families were lumped, but these always had similar ecologies (e.g. bottom-dwelling *vs* free swimming), and this is unlikely to influence comparisons significantly, especially shark–dolphin comparisons. Indices for genus level and more highly lumped prey groups were calculated when possible. Basic results are the same except where discussed below, so these data are not presented.

RESULTS

Shark predators of dolphins and porpoises

Regular predators

White *Carcharodon carcharius*, bull *Carcharhinus leucas*, tiger *Galeocerdo cuvier*, sixgill *Hexanchus griseus* and sevengill sharks *Notorynchus cepidianus* are all relatively frequent predators on dolphins and porpoises in at least some parts of their range (Tables 1 & 2). White sharks show a marked shift in diet with size: young sharks feed primarily on fishes, but larger sharks switch to a diet of marine mammals (Tricas & McCosker, 1984; Klimley 1985). White sharks have been recorded as predators of many cetaceans, including species as large as beaked whales (Long & Jones, 1996). White sharks are a major predator on harbour porpoises *Phocena phocena* along the east and west coasts of North America (Arnold, 1972; Long & Jones, 1996), and odontocetes may be the most important part of the white sharks' diet in some areas of the world. In South Africa, Cliff, Dudley & Davis (1989) found that marine mammals were the most important prey of large juvenile white sharks (no mature individuals were captured) from 1983 to 1988, with dolphins making up the majority of the marine mammal prey (Table 1). Dolphins are the primary prey of large white sharks off South Australia, with 44% of stomachs containing dolphin remains (Bruce, 1992). Habitat use by white sharks in this location may be determined by dolphin abundance as white sharks were sighted in locations where pinnipeds are rare but dolphins are common. Scavenging of cetacean carcasses may also be an important component of white shark diets in both the Atlantic and Pacific Oceans as a shark can survive for > 1 month on a single meal scavenged from a carcass (Carey *et al.*, 1982; Long & Jones, 1996).

White sharks have generally been studied in temperate waters, but they may be a threat to odontocetes in subtropical waters as well. In Moreton Bay, Australia, Corkeron *et al.* (1987) attributed bites on free-swimming bottlenose dolphins *Tursiops truncatus* to white shark attack. Although predation has not been documented on all small odontocetes sharing the white shark's range, this shark is almost certainly a predation threat to any small odontocete that it encounters.

The bull shark starts taking large prey at a relatively small size, and it is one of the only sharks that will attack prey larger than itself (Caldwell, Caldwell & Siebenaler, 1965; Cockcroft *et al.*, 1989; Long & Jones, 1996). Scars and wounds on bottlenose dolphins indicate that bull sharks begin attacking dolphins at a smaller shark size than do white, tiger, or dusky sharks (Cockcroft *et al.*, 1989). Wells (1991) and Irvine, Wells & Gilbert (1973) have identified the bull shark as a predator of dolphins in the north-east Gulf of Mexico, and bull sharks off South Africa preyed upon bottlenose dolphins more often than did white, tiger or dusky sharks (Cockcroft *et al.*, 1989); dolphin flukes and vertebrae were found in 2.2% of sharks > 1.8 m long. In an earlier study in South Africa, cetacean remains were found in 12 of 99 (12.1%) bull sharks examined (Bass, D'Aubrey & Kistnasamy, 1973), but a large portion of this may have been scavenged from whale carcasses being towed to a whaling station. In a post-whaling study, cetacean remains were found in 5.7% of stomachs, but the predation rate may have been as low as 1.6% based on the fluke-and-vertebrae method (Cliff & Dudley, 1991*a*). The bull shark may be one of the few predators on some river dolphins as it has been found almost 4000 km from the sea in the Amazon River

Table 1. Diet of three species of dolphins and eight species of sharks off South Africa. Numbers are % mass of each prey family. Data for all species are based on animals captured in protective shark nets off the Natal coast, except sixgill sharks which were caught on longlines, rod and reel, or trawls, and dusky sharks which were captured by longlines and shore- and boat-based fishermen. Only families that constituted at least 0.5% of at least one species' diet were included. An x denotes that a prey species was found in trace amounts (< 0.1% mass) and was not included in the analysis. Data for humpback dolphins are based on % number of prey items. However, these data allow for general comparisons of feeding habits. BOT, bottlenose dolphin; HUM, humpback dolphin; COM, common dolphin; BUL, bull shark; DUS, small dusky shark (< 2 m); DUL, large dusky shark (> 2 m); MAK, mako shark; BLA, blacktip shark; W83, white sharks (1983–1988); W89, white sharks (1989–93); COP, copper shark; JAV, java shark; SIS, small sixgill shark (< 1.2 m); SIM, medium sixgill shark (1.2– 2 m); SIL, large sixgill shark (> 2.0 m)

	BOT[1]	HUM[2]	COM[3]	BUL[4]	DUS[5]	DUL[5]	MAK[6]	BLA[7]	W83[8b]	W89[9b]	COP[10]	JAV[11]	SIS[12]	SIM[12]	SIL[12]
No. of stomachs examined	127	84	297	247	67	7	59	442	58	33	262	72	39	48	12
Levins, niche breadth	5.8	4.0[a]	3.5	7.8	3.9	2.9	3.3	9.3	4.2	4.1	1.1	6.8	2.6	7.2	3.6
No. of prey groups	18	7.0[a]	8	25	13	4	7	24	13	8	6	16	5	11	6
Prey species															
Teleosts															
Congridae (conger eels)	7.6								0.1						
Clupiedae (herring)	1.1	27.1	48.9	6.0	48.1	16.7		7.6		33.4	92.5		2.4		
Engraulidae (anchovies)			x	x		4.2		0.2						1.7	
Ariidae (seacatfish)	0.8			1.0	x			1.4	0.1	x		3.4			
Plotosidae (eel catfish)				0.2				1.1							
Exocoetidae (flyingfish)	1.2		3.1												
Serranidae (rockcods)	0.8			0.7				0.9				2.5			
Priacanthidae (bigeyes)	2.7														
Pomatomidae (elf)	2.0		8.7	0.5				2.0			x	0.8			
Haemulidae (grunters)	13.7	19.7	x	1.7	2.2		0.1	10.6		5.5	x	2.3			
Sparidae (seabream)	8.8	2.5	9.4	2.3	5.5			10.6	0.5	0.1		x			
Scorpididae (stonebreams)								0.6							
Sciaenidae (kobs)	1.3	15.9	x	4.0	1.7		5.9	1.3	11.2			9.5			
Mugilidae (mullets)	3.6	x	x	0.6	2.8			0.2			x	x			
Trichiuridae (frostfish)	0.7	4.2	x		0.9			0.2				0.8			
Scombridae (mackerel/tuna)	5.2		13.5	0.9	1.2		3.2	7.1	0.9		x	11.1		2.2	
Bothidae (flounders)	0.8														
Carangidae (kingfish)	4.9		3.5	x			2.4	17.7			0.1	0.1			
Oplegnathidae (knifejaws)								0.9				1.5			
Cichlidae (cichlids)				1.7				4.4							
Drepanidae (sicklefishes)				0.9											
Merlucciidae (hake)			x										22.0	17.0	9.9
Myctophidae (lanternfish)		0.3											3.3		
Scorpaenidae (rockfishes)															32.3
Macrouridae (rattails)														1.2	
Crustacea					0.4										
Cephalopods															
Sepia spp (cuttlefish)	32.7		1.1	0.1	2.1			1.0	0.2	0.1		0.3			
Teuthoidea (squid)	3.5	6.5	10.1	x	24.3	35.9		x	x	x			47.7	10.4	2.9
Octopus	1.3			0.6	2.3			1.7				0.2			
Elasmobranchs															
Rhinobatidae (guitarfish)	x			17.8	3.9			1.0	1.4			5.7			
Orectolobidae (carpet sharks)				1.0											
Callorhynchidae (chimaeras)														1.8	6.7
Scyliorhinidae (catsharks)				0.1			x	0.1			x	0.6	12.4		
Squalidae (dogfish)							x		2.4		0.9			16.4	
Caracharhinidae (requiem sharks)				13.3			35.6	10.7	22.9	16.0		19.2		3.2	
Lamnidae (mackerel sharks)				3.9											
Sphyrnidae (hammerhead sharks)				3.3			10.5	1.0	2.8	9.1		7.2			
Squantidae (angel sharks)				0.2							0.8	x			
Odontaspididae (ragged-tooth sharks)				0.3					1.7						
Skates and bottom rays				1.7	3.9	42.5		2.5	x					17.9	
Manta and eagle rays				1.7			20.3		x		0.2	17.8			
Marine mammals															
Cetacea (whales and dolphins)				5.1			x	1.7	31.2	4.2	1.9	x		4.6	9.4
Pinnipeds (seals and sea lions)									9.6	19.2				9.7	38.8

[a] Niche breadth and prey groups for *Sousa* are underestimates as only prey groups constituting more than 1.3% were included in Ross *et al.* (1994).

[b] Only juvenile white sharks were examined from 1983–1988, and the 1989–93 sample was mostly juveniles.

[1]Cockcroft & Ross (1990); [2]Ross, Heinsohn & Cockcroft (1994); Barros & Cockcroft (1999); [3]Young & Cockcroft (1994); [5]Smale (1991); [4]Cliff & Dudley (1991a); [6]Cliff, Dudley & Davis (1990); [7]Dudley & Cliff (1993); [8]Cliff, Dudley & Davis (1989); [9]Cliff, Dudley & Davis (1996); [10]Cliff & Dudley (1992); [11]Cliff & Dudley (1991*b*); [12]Ebert (1994).

system and in many river systems in northern Australia, North America, Asia and Africa (Last & Stevens, 1994). The bull shark seems to be a highly adaptable forager, and its diet and interactions with cetaceans may vary considerably among locations.

Tiger sharks are another predator on small odontocetes, but they migrate into higher latitudes as water temperature rises, so they may only pose a seasonal threat to small odontocetes in some areas. Like white sharks, tiger sharks change their diet as they grow. Small sharks seem to feed near the bottom at night, while large individuals (> 3 m) diversify their diet to feed on large-bodied prey and feed throughout the water column diurnally as well as at night (Simpfendorfer, 1992; Lowe *et al.*, 1996). The broad, heavily calcified jaws and nearly terminal mouth, combined with robust, serrated teeth enable the tiger shark to take and handle large prey like turtles and marine mammals (Randall, 1992). Tiger sharks show considerable geographic variation in their diet and their propensity to attack cetaceans will probably be dependent on the abundance of other prey in a given location.

Tiger sharks generally swim slowly, which, combined with cryptic coloration, may make them difficult for prey to detect in some habitats. Despite their sluggish appearance, tiger sharks are one of the strongest swimmers of the carcharhinid sharks (Baughman & Springer, 1950; Compagno, 1984*b*). Once the shark has come close, a speed burst allows it to reach the intended prey before it can escape.

Bottlenose dolphin calves have been killed by tiger sharks in Sarasota, Florida and Shark Bay, Western Australia (Wells, 1991; Mann & Barnett, 1999), and dolphins have been found in the stomachs of tiger sharks in both locations (Irvine *et al.*, 1973; Simpfendorfer, Goodreid & McAuley, in press). Seven of 36 (19.4%) tiger sharks caught in gill nets off North Carolina contained dolphin remains, but there is a chance that up to six of these had scavenged dolphins caught in the same net (Bell & Nichols, 1921). In Hawaii, dolphins were found in 7% of 135 stomachs from large sharks (> 3 m) and 2% of 118 stomachs from medium-sized sharks (2–3 m) (Lowe *et al.*, 1996). Only 1.3% of 558 tiger sharks caught in north-eastern Australia had consumed dolphins (Simpfendorfer, 1992), but if all dolphin remains came from large sharks (> 3 m), the frequency of occurrence for this size class would be 9%. Finally, 1.9% of tiger sharks off South Africa had dolphin flukes or vertebrae in their stomach contents (Cockcroft *et al.*, 1989).

The sixgill shark has not previously been identified as a major odontocete predator in the cetacean literature, and is perhaps one of the most overlooked predators on odontocetes. They are large deep-water sharks and are the dominant predators along the outer continental shelves and upper continental slopes (Clark & Kristof, 1990; Ebert, 1990). Sixgill sharks are active hunters and the 'sixgill shark's large size, relatively broad mouth and huge cutting teeth . . . is indicative of a predator with a voracious appetite and one that must have a substantial impact on the prey organisms within its area of distribution' (Ebert, 1994).

Large (> 2 m) sixgill sharks off South Africa take many dolphins (Ebert, 1994; Table 1). Dolphins occurred in 18.2% of stomachs, and were one of the most important components of the diet based on an index of relative importance. These sharks were caught by longline and trawler, so they would not have scavenged dolphin carcasses in nets. Despite this, the frequency of occurrence of odontocete remains in sharks > 2 m long is similar to that of known dolphin predators in South Africa, including white and bull sharks. The frequency of dolphin occurrence in the stomachs of sharks suggests that the sixgill shark is an active odontocete predator (Ebert, 1994). Other evidence for the sixgill shark being capable of attacking free-swimming odontocetes comes from observations of sixgill sharks attacking large, fast-swimming prey such as swordfish and other billfish (Ebert, 1990), and a high occurrence of South African fur seals *Arctocephalus pusillus* in the diet of large sixgill sharks (Ebert, 1994).

As with the sixgill shark, there are no direct observations of sevengill shark predation on odontocetes, but there is indirect evidence that suggests that this shark may be an important predator on coastal odontocetes in some areas. This shark feeds on a variety of prey including teleosts, cephalopods, sharks, rays, pinnipeds and cetaceans (Brownell, 1975; Ebert, 1991*a*; Cawthorn, 1988), but there is a high degree of geographic variation in the diet (Ebert, 1991*a*). Two predatory tactics have been suggested which would facilitate the capture of large, actively swimming prey by this relatively small (3 m) shark. Some sharks have been observed 'gliding' up to the surface to attack South African fur seals lying there (Ebert, 1991*b*), and it has been suggested that minimizing swimming movement might be a form of stealth so the intended prey would not see the predator before escape became unlikely. A preference for turbid water would further reduce the probability of detection, and aid in the capture of large, fast-swimming prey like small cetaceans (Ebert, 1991*b*).

Sevengill sharks also hunt in groups. Ebert (1991*b*) found that sevengill sharks hunt socially when they attack South African fur seals, which grow up to 350 kg. During this behaviour, a group circles around the intended prey until one or several sharks rush in to bite it; the rest of the group then quickly follows. These groups may travel together through a shared home range which would facilitate taking other large prey like dolphins (Ebert, 1991*b*).

Ebert (1991*a*,*b*) noted that the frequency of occurrence of marine mammals in the diet of sevengill sharks seemed to be too high to be attributed exclusively to scavenging. The sharks were angler-caught, so were unlikely to have scavenged dolphins drowned in nets. The best evidence for predation on odontocetes comes from the Eastern Cape of South Africa where 12.5% of sevengill sharks contained dolphin remains (Ebert, 1991*a*). In these sharks, dolphins constituted 29.3% of prey mass, which is much higher than most dolphin predators in Natal, where scavenging opportunities from shark nets are higher. Other sevengill populations in southern Africa also consume dolphins, but at a lower frequency (Ebert, 1991*a*).

Occasional predators

The dusky *Carcharhinus obscurus* and oceanic whitetip *Carcharhinus longimanus* sharks are best classified as occasional predators (Table1). These species are known to attack living odontocetes, but probably only rarely. In South Africa, only 0.2% of dusky sharks (probably an individual) were implicated as predators on bottlenose dolphins using the fluke-and-vertebrae method (Cockcroft *et al.*, 1989), and another study off the eastern Cape of South Africa found no cetacean remains in seven dusky sharks > 2 m long (Smale, 1991). This is not surprising since dusky sharks primarily prey on bony fish and other elasmobranchs (Smale, 1991; C. Simpfendorfer, pers. comm.) and only the largest dusky sharks are likely to pose a threat to small odontocetes. Compagno (1984*b*) commented on the relative rarity of mammalian remains (including carrion) in this species compared to tiger and bull sharks, but whale meat (probably scavenged) was found in three of 118 sharks off the east coast of southern Africa (Bass *et al.*, 1973).

Oceanic whitetip sharks are common scavengers, and during whaling years, they were responsible for most of the damage to whale carcasses off Durban, South Africa (Compagno, 1984*b*). In the eastern tropical Pacific, oceanic whitetip sharks are the most common shark found in association with dolphin and tuna schools (Au, 1991), and an oceanic whitetip shark was implicated in killing a dolphin encircled by a purse seine (Leatherwood *et al.*, 1973). Although these sharks probably feed on the same prey as the dolphins (teleosts and cephalopods; Last & Stevens, 1994), they may also be a threat to dolphins, especially calves, that stray too far from pelagic dolphin schools.

Suspected predators

Suspected predators on cetaceans include the shortfin mako shark *Isurus oxyrinchus*, Pacific sleeper shark *Somniosus pacificus* and Greenland (sleeper) shark *Somniosus microcephalus* (Table 2). An adult common dolphin *Delphinus delphis* was found stranded alive with fresh mako shark bite wounds, but the dolphin was highly parasitized by liver flukes and had trematodes in its brain (Ridgway & Dailey, 1972). As this dolphin may have been incapacitated at the time of the attack this cannot be treated as a definitive predation event. Stomach content analyses of mako sharks in the north-west Atlantic Ocean, off South Africa and south-east Australia do not implicate this shark as a regular predator of cetaceans: dolphin remains were found in three of 273, one of 88 and one of 63 mako sharks, respectively (Stillwell & Kohler, 1982; Stevens, 1984; Cliff, Dudley & Davis, 1990). All these odontocete remains were thought to have been scavenged. In South Africa, mako sharks primarily feed on other elasmobranchs and teleosts (Cliff, Dudley & Davis, 1990), and prey size was 23–35% of the body length of the attacking shark. The above studies did not contain many large sharks, and this may bias the view of mako shark predation on odontocetes. Last & Stevens (1994) commented that large mako sharks (> 3 m) might take small cetaceans, but only female makos reach this size and very few of these were examined in the above studies.

The Pacific sleeper shark is a dogfish that is large enough to prey on cetaceans. This shark does not possess dentition that is designed for taking large prey and it is generally considered to be a sluggish bottom dweller (Compagno, 1984*a*; Ebert, Compagno & Natanson, 1987; Last & Stevens, 1994), so it would not seem to pose a threat to cetaceans. However, sleeper sharks may be very cryptic and able to closely approach unwary fast-swimming prey; albacore, tuna, billfish and harbour seals *Phoca vitulina* have all been found in their stomachs (Bright, 1959; Compagno, 1984*a*; Ebert *et al.*, 1987). A 3.6 m shark caught on a longline off Valdivia, Chile, contained the genital area of an adult female southern right whale dolphin *Lissodelphis peronii* and a complete 87 cm foetus (Crovetto, Lamilla & Pequeno, 1992). Due to the lack of decomposition of the foetus and genital region recovered from the stomach, the authors suggested that the shark had attacked a living pregnant female. Southern right whale dolphins feed at considerable depth (Baker, 1981), and it is possible that the shark attacked the dolphin while it was feeding (Crovetto *et al.*, 1992).

The Greenland shark is the Atlantic equivalent of the Pacific sleeper shark. This shark is primarily a fish eater, but is capable of taking large, active prey (Compagno, 1984*a*). Seals are common in the diet and small cetaceans are also found (Compagno, 1984*a*). Williamson (1963) reported a 79 cm long calf of a harbour porpoise in the stomach of a 4.15 m long Greenland shark off Newfoundland, but suggested that the calf was either stillborn or only a few hours old when it was taken. Greenland sharks have been recorded feeding on narwhals *Monodon monoceros* and a beluga whale *Delphinapterus leucas* caught in nets (Beck & Mansfield, 1969). Sharks in this study were only reported as scavengers, but like the Pacific sleeper shark, they may be capable of attacking free-swimming cetaceans.

Ectoparasites

The cookie cutter shark *Isistius brasiliensis* and Portuguese dogfish *Centroscymmus coelolphis* are cetacean ectoparasites. Cookie-cutter sharks are found in deep water (> 1000 m), during the day and migrate toward the surface with the deep scattering layer at night (Jones, 1971; Norris & Dohl, 1980*a*; Last & Stevens,

Table 2. Shark species with cetacean remains found in stomach contents, grouped into categories of possibility for predation on living cetaceans. Sharks were placed into categories based on frequency of odontocetes in stomachs, observations of attacks, and wounds on living cetaceans. Tt, *Tursiops truncatus*; Dd, *Delphinus delphis*; Pp, *Phocena phocena*; Sp, *Sousa plumbea*; Gg, *Grampus griseus*; Pd, *Phocenoides dalli*; Kb, *Kogia breveceps*; Ks, *Kogia simus*; Lo, *Lagenorhynchus obliquidens*; Lb, *Lagenorhynchus obscurus*; Ms, *Mesoplodon stejnegeri*; Zc, *Ziphia cavirostris*; Sa, *Stenella attenuata*; Pb, *Pontoporia blanvilli*; Ch, *Cephalorhynchus hectori*; Lp, *Lissodelphis peronii*; Mm, *Monodon monoceros*; Dl, *Delphinapterus leucas*; Sl, *Stenella longirostrus*; Sb, *Steno bredanensis*; Pc, *Pseudorca crassidens*; Fa, *Feresa attenuata*; Md, *Mesoplodon densirostris*; Pm, *Physter macrocephalus*; Us, *Stenella* sp.; Ud, unidentified Delphinidae; Uc, unidentified cetacean

Species	Scientific name	TL[a]	Cetaceans in diet	References
Regular predators				
White shark	*Carcharodon carcharias*	6.4[b]	Tt, Dd, Pp, Sp, Gg, Pd, Kb, Ks, Lo, Lb, Ms, Zc	Arnold (1972), Randall (1973), Carey *et al.* (1982), Cliff, Dudley & Davis (1989), Cockcroft *et al.* (1989), Bruce (1992), Last & Stevens (1994), Cliff, Dudley, & Jury (1996), Fergusson (1996), Long & Jones (1996)
Tiger shark	*Galeocerdo cuvier*	6.0	Tt, Sa	Bell & Nichols (1921), McBride & Hebb (1948), Irvine *et al.* (1973), Compagno (1984*b*), Stevens (1984), Cockcroft *et al.* (1989), Stevens & McLoughlin (1991), Wells (1991), Randall (1992), Last & Stevens (1994)
Bull Shark	*Carcharhinus leucas*	3.4	Tt, Dd	Bell & Nichols (1921), Bass *et al.* (1973), Irvine *et al.* (1973), Compagno (1984*b*), Cockcroft *et al.* (1989), Cliff & Dudley (1991*a*), Last & Stevens (1994)
Sixgill shark	*Hexanchus griseus*	5.5[c]	Tt, Ud	Ebert (1986, 1994), Clark & Kristof (1990)
Sevengill shark	*Notorynchus cepedianus*	3.0	Pb, Ch, Lb	Brownell (1975), Compagno (1984*a*), Cawthorn (1988), Ebert (1991*a*, *b*)
Occasional predators				
Dusky shark	*Carcharhinus obscurus*	4.0[d]	Tt	Irvine *et al.* (1973), Compagno (1984*b*), Cockcroft *et al.* (1989), Last & Stevens (1994)
Oceanic whitetip shark	*Carcharhinus longimanus*	3.9[e]	Us	Leatherwood *et al.* (1973), Bass *et al.* (1973), Compagno (1984*b*), Stevens (1984), Long & Jones (1996)
Suspected predators				
Shortfin mako shark	*Isurus oxyrinchus*	3.9	Us, Dd	Ridgway & Dailey (1972), Leatherwood *et al.* (1973), Stillwell & Kohler (1982), Stevens (1984), Cliff, Dudley & Davis (1990), Last & Stevens (1994)
Pacific sleeper shark	*Somniosus pacificus*	6.0	Lp	Crovetto *et al.* (1992), Last & Stevens (1994)
Sleeper (Greenland) shark	*Somniosus microcephalus*	6.4[d]	Mm, Dl	Williamson (1963), Beck & Mansfield (1969)
Ectoparasites				
Cookie-cutter shark	*Isistius brasiliensis*	0.5	Sl, Sb, Pc, Fa, Md	Jones (1971), Paterson *et al.* (1993), Last & Stevens (1994), Norris (1994)
Portugueese dogfish	*Centroscymnus coelolphis*	1.2	Pm, Uc	Clarke & Merrett (1972), Mauchline & Gordon (1983), Ebert, Compagno & Cowley (1992), Last & Stevens (1994)
Insufficient data				
Java (pigeye) shark	*Carcharhinus amboinensis*	2.8	Uc	Bass *et al.* (1973), Compagno (1984*b*), Cliff & Dudley (1991*b*)
Copper shark (Bronze whaler)	*Carcharhinus brachyurus*	3.0	Dd	Cliff & Dudley (1992), Compagno (1984*b*)
Sandbar shark	*Carcharhinus plumbeus*	2.4	Uc	Stillwell & Kohler (1992), Compagno (1984*b*), Cliff, Dudley & Davis (1988)
Blacktip shark	*Carcharhinus limbatus*	2.5	Uc	Compagno (1984*b*), Dudley & Cliff (1993)
Galapagos shark	*Carcharhinus galapagensis*	3.0	Uc	Wetherbee *et al.* (1994)
Blue shark	*Prionace glauca*	3.8	Uc	Stevens (1973), Compagno (1984b), Stevens (1984)
Hammerhead shark	*Sphyra* sp.	6.0	Dd	Leatherwood *et al.* (1973)

[a] Maximum reported total length (m). All measurements from Last & Stevens (1994) except where noted.

[b] This figure is the largest reliably measured white shark, but bite scars on whale carcasses suggest that individuals of 7.5–8.0 m may exist (Randall, 1973).

[c] This is the size of a single female described by Clark & Kristof (1990), and may not represent a maximum length.

[d] Compagno (1984*b*).

[e] Compagno (1984*b*), but most individuals < 3.0 m.

1994). The shark is neutrally buoyant, with a bioluminescent body, and it may mimic squid (Jones, 1971; Last & Stevens, 1994). It probably remains motionless and the luminescence could lure cetaceans toward it (Jones, 1971; Norris & Dohl, 1980*a*; Last & Stevens, 1994). The shark attaches itself to the cetacean with suctorial lips and modified pharynx, then spins and cuts out a crater of flesh with its lower teeth. The plug is then pulled out using the tongue and lips to create a vacuum (Clark & Kristof, 1990). Almost every adult spinner dolphin *Stenella longirostrus* off Hawaii shows scars caused by this shark with bites found all over the dolphins' bodies except the appendages (Norris & Dohl, 1980*a*). Cookiecutter sharks are likely to attack any cetaceans that feed on the deep scattering layer organisms, especially squid feeders.

It is unclear whether the Portuguese dogfish represents an ectoparasitic threat to odontocetes. Three studies on this shark have found whale remains in their stomachs. Clarke & Merrett (1972) found sperm whale *Physeter macrocephalus* remains in the stomachs of three of 12 sharks they collected from the north-east Atlantic. The skin and blubber in the sharks may have been scavenged but the authors suggest that living whales may have been attacked when diving. Mauchline & Gordon (1983) also reported that six of 24 (35%) sharks in the same area had eaten whale meat, and Ebert, Compagno & Cowley (1992) found that unidentified cetaceans constituted 12.6% of the food mass in 71 stomachs examined.

Insufficient data

There are several species of sharks that either scavenge cetaceans or rarely take living individuals. With current data, these species cannot be considered cetacean predators, but future studies may change this conclusion.

The sandbar shark *Carcharhinus plumbeus* has been studied in South African waters and off the north-east coast of the U.S.A. This shark is almost certainly only a scavenger as it does not attack large prey (Stillwell & Kohler, 1992), and even young dolphins and porpoises probably have a refuge in size. In Atlantic Ocean sharks, cetacean remains were present in only one out of a sample of 415 stomachs (Stillwell & Kohler, 1992), and in South Africa, cetacean remains were found in one of 178 stomachs (Cliff, Dudley & Davis, 1988).

Although Java (pigeye) sharks *Carcharhinus amboinensis* may attain sizes of 2.8 m, Cliff & Dudley (1991*b*) only examined sharks > 1.8 m long and most were > 1.5m. Cetacean remains were found in only one of 72 sharks. It is unclear whether large individuals pose a predation threat to cetaceans.

Despite their relatively large size, copper sharks (bronze whalers, *Carcharhinus brachyurus*) have a narrow diet and feed on small fish prey (Cliff & Dudley, 1992). Only 1.4% of the sharks caught in South African shark nets contained cetacean remains, including common dolphins, but Cliff & Dudley (1992) concluded that they were scavenged from carcasses of dolphins caught in the nets or elsewhere.

Less than 1% of 442 blacktip sharks *Carcharhinus limbatus* caught off South Africa contained dolphin remains (Dudley & Cliff, 1993), and none of 85 sharks with food in their stomachs off the south-eastern U.S.A. had consumed cetacean flesh (Castro, 1996). Most of this shark's prey is small (Dudley & Cliff, 1993; Castro, 1996), so it is unlikely that even large blacktip sharks attack living cetaceans.

A single Galapagos shark *Carcharhinus galapogensis*, of 65 examined in Hawaii, contained cetacean remains (Wetherbee, Lowe & Crow, 1994), and this species is probably a scavenger of cetaceans.

Blue sharks *Prionace glauca* from the north-east Atlantic ate mainly teleosts, with cetacean remains (probably scavenged) found in two of 98 stomachs (Stevens, 1973). Only one of 31 sharks caught off the coast of New South Wales had small odontocete remains in its stomach (Stevens, 1984).

Hammerhead sharks *Sphyrna* spp. attain sizes that may be capable of taking small odontocetes, but feed primarily on bottom fishes, including teleosts, small sharks and rays, as well as cephalopods and crustaceans (Last & Stevens, 1994; Cliff, 1995). Two studies on hammerhead sharks feeding in South Africa found no cetacean remains (Smale, 1991; Cliff, 1995). Furthermore, no prey > 1 m long were reported, suggesting that hammerhead sharks are unlikely to be a major threat to most cetaceans. However, a hammerhead shark may have been responsible for a lethal attack on a bottlenose dolphin in Florida (Wood, Caldwell & Caldwell, 1970), and these sharks have been seen scavenging odontocete carcasses (Leatherwood *et al.*, 1973).

Odontocete predation on sharks

In general, sharks seem to be of little importance in the diet of most odontocetes but predation does occasionally occur (e.g. Wood *et al.*, 1970). Bottlenose dolphins are known to eat elasmobranchs, including sharks, in South Africa, the Atlantic Ocean and the Gulf of Mexico (Gunter, 1942; Cockcroft & Ross, 1990; Mead & Potter, 1990). In South Africa, 1.3% of bottlenose dolphin prey mass was unidentified elasmobranch, but it is unclear what proportion of this prey was from small sharks (Cockcroft & Ross, 1990). Most sharks found in bottlenose dolphin stomachs have been unidentified, and small hammerhead sharks are the only group positively identified. Bottlenose whales *Hyperoodon ampullatus* have been recorded consuming piked dogfish *Squalus acanthias* off the coast of Labrador, but squid and teleost fish are much more common prey (Benjaminsen & Christensen, 1979). Pilot whales *Globicephala* sp. and harbour porpoises have also been recorded consuming small sharks (Wood *et al.*, 1970).

While small odontocetes may occasionally consume small sharks, killer whales are the only cetacean species currently recorded attacking and killing large sharks,

Table 3. MacArthur–Levins' dietary overlaps based on proportion of prey groups in the diet of three species of dolphins and eight species of sharks found off the coast of South Africa. Dietary overlap is asymmetrical and is expressed as the overlap of the species along the top row on the diet of the species in the left hand column. Overlaps are based on % mass for all comparisons except those with humpback dolphins which are all based on % number. Data for all species except the sixgill and dusky sharks are from animals caught in the protective shark nets off Natal, South Africa. Values of > 0.7 are considered significant and are in bold. BOT, bottlenose dolphin; HUM, humpback dolphin; COM, common dolphin; BUL, bull shark; DUS, small dusky shark (< 2 m); DUL, large dusky shark (> 2 m); MAK, mako shark; BLA, blacktip shark; W83, white sharks (1983–1988); W89, white sharks (1989–93); COP, copper shark; JAV, java shark; SIS, small sixgill shark (< 1.2 m); SIM, medium sixgill shark (1.2–2 m); SIL, large sixgill shark (> 2 m)

	BOT	HUM	COM	BUL	DUS	DUL	MAK	BLA	W83	W89	COP	JAV	SIS	SIM	SIL
BOT	–	0.53	0.17	0.06	0.14	0.01	0.03	0.30	0.02	0.08	0.07	0.09	0.12	0.04	0.01
HUM	0.57	–	**0.72**	0.64	**0.77**	0.24	0.07	0.47	0.06	**1.35**	**1.39**	0.37	0.32	0.17	0.01
COM	0.10	0.64	–	0.17	**0.90**	0.29	0.02	0.24	0.01	0.67	**1.68**	0.07	0.05	0.01	0.00
BUL	0.08	**0.77**	0.38	–	0.46	0.20	**0.82**	0.37	**0.72**	0.61	0.66	0.63	0.02	0.13	0.05
DUS	0.09	**0.74**	**0.99**	0.23	–	0.48	0.01	0.22	0.01	**0.74**	**1.80**	0.03	0.05	0.03	0.00
DUL	0.01	0.28	0.40	0.18	0.39	–	0.00	0.13	0.00	0.30	**0.76**	0.00	0.02	0.42	0.00
MAK	0.02	0.05	0.02	0.35	0.01	0.00	–	0.23	0.46	0.32	0.00	0.62	0.00	0.05	0.00
BLA	0.48	**0.73**	0.64	0.44	0.53	0.25	0.64	–	0.35	0.60	**0.79**	0.45	0.02	0.12	0.00
W83	0.02	0.20	0.01	0.38	0.01	0.00	0.57	0.16	–	0.32	0.00	0.34	0.00	0.07	0.18
W89	0.06	0.38	**0.78**	0.32	**0.78**	0.26	0.40	0.27	0.32	–	**1.50**	0.05	0.00	0.05	0.00
COP	0.01	0.37	0.52	0.09	0.51	0.18	0.00	0.09	0.00	0.40	–	0.00	0.03	0.00	0.00
JAV	0.10	0.50	0.13	0.55	0.05	0.00	**1.28**	0.33	0.56	0.05	0.00	–	0.01	0.08	0.00
SIS	0.06	0.14	0.04	0.01	0.04	0.61	0.00	0.01	0.00	0.00	0.07	0.00	–	0.30	0.11
SIM	0.04	0.15	0.03	0.12	0.06	0.64	0.13	0.09	0.11	0.05	0.01	0.09	**0.83**	–	0.18
SIL	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.14	0.09	–

and sharks may be taken relatively often (Fertl, Acevedo-Guiterrez & Darby, 1996). Killer whales have been recorded feeding on various carcharhinid sharks as well as larger sharks, including basking *Cetorhinus maximus* and whale *Rhiniodon typus* sharks (Fertl *et al.*, 1996). Off the Farallon Islands, California, killer whales were observed attacking and killing a 3–4 m long white shark (Pyle *et al.*, 1999).

COMPETITION

There were 21 significant dietary overlaps at the family-level and 10 of these were between sharks and dolphins (Tables 3). Although there are several significant overlaps between humpback dolphins and sharks at the family level, these overlaps are the result of prey category lumping. The frequency of clupeid fishes is the primary factor in all of these interactions, and a detailed look at diets of these species shows that they feed on different prey genera within this family. The clupeid fish taken by humpback dolphins *Sousa plumbea* are primarily *Thryssa* while the sharks consume *Sardinops*.

The diets of common dolphins significantly overlapped with the diet of white (1989–93) and small dusky sharks while those of small dusky and copper sharks overlapped significantly with the common dolphin's diet (Table 3). The largest overlap recorded was that of copper sharks on common dolphins. Unlike overlaps between sharks and humpback dolphins, all overlaps between sharks and common dolphins were upheld by analysis at the species level except for that with white sharks which consume *Sardinops sagax*. Overlaps with other shark species were primarily driven by competition for South African pilchards (*Sardinops ocellatus*). There was also overlap between dolphins and small dusky sharks for Sparidae and Teuthoidea.

The blacktip shark has the greatest overlap with bottlenose dolphins, but this is not a significant interaction (Table 3). This does not mean that there is no competitive interaction. When only the fish portion of the diet was analysed, the overlap is significant in both directions. Differentiation occurs because bottlenose dolphins round out their diet with squid while the sharks take elasmobranchs.

DISCUSSION

Predation pressure on odontocete populations

Very little is known about the influence of predation on odontocete populations. The frequency of scars from shark bites on odontocetes has been used as an indication of predation rate, but there are several problems with this approach. As many authors have pointed out, scars and wounds from shark bites represent failed attempts at predation. There may be a correlation between successful predation and failed attempts, but there are several confounding factors. The ratio between attacks and kills may vary from one shark species to another, or with shark length. For example, large sharks are less likely to fail in predation attempts than smaller sharks. Second, the size (i.e. age or species) of the attacked cetaceans will bias this ratio as smaller individuals, or species, will be taken more often and scarred less frequently than large species or individuals. Therefore, a lack of scars on cetaceans in a population does not necessarily indicate a low predation rate. For example, offshore dolphins seem to have lower scarring frequencies than nearshore dolphins (Wood *et al.*, 1970; Leatherwood *et al.*, 1973). This could indicate a lower predation rate, if large groups of pelagic dolphins are more likely to detect and avoid predators or shark density is lower offshore. However, a predation attempt in such an open environment may be more likely to lead to death. Groups of sharks seem to follow pelagic dolphin schools (Leatherwood, 1977; Au, 1991) and once a single shark has made an attack, others are likely to converge as well. A dolphin, which may have evaded a single shark with just a wound, is likely to be killed if several sharks are involved in an attack. Despite the potential drawbacks of using shark-scarred individuals to assess shark predation, it is still useful for comparisons among relatively similar habitats and species of similar size.

At least 36.6% of the bottlenose dolphins surveyed (both photographically and with field observations) in Moreton Bay, Queensland, exhibit scars from shark bites. Several scars that may have been healed bites were not scored, so an even greater scarring frequency is probable (Corkeron *et al.*, 1987). A higher scarring frequency is also probable because observations were made of free-swimming animals, and photographs of free-swimming animals document only a fraction of the dolphins with scars (Urian *et al.*, 1998).

The frequency of shark bite scars is lower in Sarasota, Florida, where 31% of 151 bottlenose dolphins examined during captures showed signs of healed shark bites or fresh wounds (Urian *et al.*, 1998). Overall, 23% had single scars and 8% had multiple scars.

The frequency of shark scarring suggests that there is little predation pressure on bottlenose dolphins in the Adriatic Sea. No unambiguous shark-inflicted scars were found on >200 dolphins observed, although several individuals bore wounds that may have been inflicted by sharks (Bearzi, Notarbartolo-di-Sciara & Politi, 1997). Conversely, predation pressure on bottlenose dolphins in Shark Bay, Western Australia is probably quite high. Of 128 non-calves surveyed 95 (74.2%) had at least one scar from shark bites and 40 (42.1% of attacked individuals) had multiple scars. Based on the accumulation of fresh bites, 11–13% of the Shark Bay population may be attacked each year (Heithaus, in press).

Scars or recent wounds from shark bites that were not attributable to scavenging were found on 10 of 36 (28%) humpback dolphins caught in shark nets off Natal, South Africa (Cockcroft, 1991). Five of these animals had received multiple bites, and some had obviously been attacked on more than one occasion. This frequency of scarring is greater than that of bottlenose dolphins in the same area (see later) and indicates that the two species are subjected to different predation pressures (Cockcroft, 1991).

Scars and wounds that fit all criteria for non-scavenging shark bites were found on 10.3% (15 of 145) of bottlenose dolphins caught in Natal shark nets. However, the incidence of shark bites may be a high as 19.3% as 13 additional dolphins had scars that may have been inflicted by sharks (Cockcroft *et al.*, 1989). Seven of the 15 animals had multiple scars from shark bites. Based on the stomach contents of predatory sharks, Cockcroft *et al.* (1989) concluded that shark predation may be a significant mortality factor for bottlenose dolphins off the coast of Natal, with up to 2.2% of the population taken annually. If there is a positive relationship between scarring frequency and predation rate, even higher shark mortality would be expected in Shark Bay, Moreton Bay and Sarasota.

Disappearance rates of odontocete calves may also provide insight into predation pressure on populations. In Sarasota, between 1980 and 1984, two dependent bottlenose dolphin calves disappeared and 16 survived beyond 3 years (11% disappearance; Wells *et al.*, 1987). A much higher disappearance rate is found in Shark Bay where *c.* 31% (of 83 newborns) of calves disappear in the first year and 49% have disappeared by age 4 years (Richards, 1993). Both calf mortality and scarring frequency seem to indicate higher shark predation risk in Shark Bay than in Sarasota.

Odontocete behavioural responses to shark predation risk

There is much literature on how animals minimize predation risk and make trade-offs between predation risk and, for example, energy intake and reproduction (see Lima & Dill, 1990 for a review of behavioural decisions made under the risk of predation). Predation attempts do not have to occur frequently or always have to be successful to have a major influence on the behaviour of prey species (e.g. shifts in habitat use or activity budgets; Lima, 1998). Unsuccessful predation attempts may have a significant detrimental effect on individual prey. Pinnipeds that survive attacks by white sharks have significantly reduced reproductive success. Most injured female elephant seals *Mirounga angustirostris* at Año Nuevo, California, do not succeed in pupping (Le Boeuf, Reidman & Keyes, 1982). Furthermore, none of the shark-bitten females was observed to copulate before returning to sea. Therefore, a shark bite resulted in a loss of 2 years of reproduction. A similar pattern was found at the Farallon Islands, where only *c.* 10% of mother elephant seals injured by sharks were able to wean their pups, and these individuals did not copulate (Ainley *et al.*, 1981). A similar cost would probably be incurred by odontocetes that survive shark attacks. Shark-attacked individuals would have to devote energy to recuperation and wound healing, and wounded females would not be able to invest as much energy in rearing their calves. Males might also incur reproductive losses if they are wounded, especially in odontocete species with high male–male competition for females. Therefore, odontocetes should employ strategies to reduce shark encounters even if sharks are successful predators only occasionally.

Dolphin behavioural responses provide evidence that they view sharks as a risk. The responses of dolphins to an encounter with sharks will depend on factors such as the species and size of the shark they encounter. Dolphins show species-specific reactions to sharks, and seem to distinguish between predatory species and those that pose no threat. For example, a captive bottlenose dolphin that was trained to repel large sharks, harassed sharks that were not predation threats. When bull sharks were introduced, the dolphin became agitated, avoided the sharks and refused to respond to commands (Irvine *et al.*, 1973).

Close encounters between dolphins and predatory sharks often result in an evasive response by the dolphins. Bottlenose and humpback dolphins have been observed passively avoiding hammerhead *Sphyrna zygaena*, white and either a bull or dusky shark (Tayler & Saayman, 1972; Saayman & Tayler, 1979; Corkeron *et al.*, 1987). An extreme evasive response was observed when resting bottlenose dolphins were startled by the approach of a white shark (Connor & Heithaus, 1996).

Not all encounters between predatory sharks and dolphins result in avoidance, and predator mobbing of sharks has been observed several times. A school of common dolphins sought refuge next to a fisheries research vessel while sharks were attacking the group. The young dolphins were herded next to the boat while adults seemed to chase the sharks away whenever one approached (AIBS, 1967). In another observation, humpback dolphins were seen chasing a large white shark (4–5 m) (Saayman & Tayler, 1979).

Group formation is one way animals can reduce predation risk, but groups may form for other reasons (e.g. food acquisition, reproduction; see Bertram, 1978 for detailed discussion of the benefits of group living, with examples). There are numerous examples of group formation successfully reducing predation in the terrestrial environment, and predation has been suggested as an important determinant of group size in some odontocetes (e.g. Norris & Dohl, 1980*b*; Wells, Irvine & Scott, 1980; Wells, Scott & Irvine, 1987).

Another way to reduce predation risk is to avoid encounters with predators, and many species select habitats where predation risk is relatively low. Predation risk is determined by more than the number of predators in a location. The ability of predators and prey to detect each other and the probability of capture after detection can be influenced by habitat attributes such as substrate colour, water clarity, water depth and light level (intrinsic habitat risk, e.g. Gotceitas & Colgan, 1989; Hugie & Dill, 1994; Miner & Stein, 1996). In some predator–prey interactions, intrinsic habitat risk can be a primary determinant of habitat selection by prey species (Hugie & Dill, 1994). As with group size, habitat use is influenced by factors other than predation risk (e.g. food distribution and abundance, social considerations) and many animals make trade-offs between safety and energy intake (e.g. desert baboons, Cowlishaw, 1997; African hunting dogs, Mills & Gorman, 1997).

Fission–fusion societies allow individuals or subgroups to select their habitat and group size based on ecological conditions and their current activity. This social organization allows individuals to balance conflicting demands such as energy intake, safety and reproduction. The size and habitat use of primate subgroups are responsive to food availability, predation risk and current activity (e.g. macaques, van Schaik & van Noordwijk, 1985; desert baboons, Cowlishaw, 1997). Some dolphin fission–fusion societies are probably influenced mainly by reproductive and foraging considerations (e.g. in the Adriatic Sea), but both food resources and predation risk probably drive other odontocete fission–fusion dynamics. Relationships between group size and habitat use of bottlenose dolphins in Sarasota seem to be a tactic for coping with predation pressure (mainly from bull sharks) balanced with prey availability (Wells, Irvine & Scott, 1980; Wells, Scott & Irvine, 1987; Wells, 1991). In Shark Bay, bottlenose dolphins trade-off food and predation risk from tiger sharks (Heithaus & Dill, 1999). During times of the year when tiger sharks are present, dolphins largely avoid productive shallow areas that are favoured by tiger sharks, but use this habitat extensively when sharks are absent (Heithaus & Dill, 1999).

The activity state of odontocetes should influence their responsiveness to food distribution and risk of predation. Foraging is the activity most likely to be seen in dangerous habitats as the energetic benefits may counterbalance predation risk (e.g. desert baboons, Cowlishaw, 1997). Conversely, dolphins would be expected to select safe habitats during resting since the energetic costs of moving to safe habitats is low (Williams *et al.*, 1992) and the benefit of spending time in low-risk habitats can be high. Comparing the habitat use and group sizes of dolphins engaged in resting relative to foraging may provide an index of habitat-specific predation risk. To test this, information about habitat use by sharks should be collected concurrently with data on activity specific habitat use of odontocetes.

Social considerations may complicate studies of odontocete habitat selection and group size as individuals of different age/sex classes may respond differently to predation risk, resource distribution and reproductive concerns. For example, Urian *et al.* (1998) provide evidence that male dolphins are more willing to risk shark predation than females. In Sarasota, these authors found that male bottlenose dolphins had a significantly higher frequency of scarring than did females, and that males seemed to take risks more consistently throughout their lives as they accumulated scars as they matured, while females did not.

To understand group sizes and habitat use of dolphins, it is important to understand the relative risk to an individual odontocete from predators, particularly sharks, in different habitats. It is difficult to compare vastly different habitats because many factors can influence risk. One habitat attribute that will affect predation risk is water depth, but there is probably not a simple relationship between depth and intrinsic risk making comparisons between nearshore and pelagic waters difficult.

In nearshore waters, the shark species present, shark density, water depth, water clarity and substrate colour

Table 4. Distribution and habitats of sharks thought to be predators on cetaceans. Data are based on references cited in text and from Last & Stevens (1994). C, coastal; P, pelagic (including continental shelves and open ocean); F, fresh water; S, surface (generally < 50 m); D, deep ocean (generally > 200 m); Tr, tropical; CTr, cold tropical; Tp, temperate; WTp, warm temperate; CTp, cold temperate; Ar, arctic. Codes in parentheses indicate occasional only

Species	Habitat	Depth	Latitude
White shark *Carcharodon carcharias*	C	S	Tp, CTr, (Tr)
Tiger shark *Galeocerdo cuvier*	C, P	S, (D)	Tr, WTp
Bull shark *Carcharhinus leucas*	C, F	S	Tp, WTp
Sixgill shark *Hexanchus griseus*	C, P	D, (S)	Tp, Tr
Sevengill shark *Notorynchus cepedianus*	C	S	Tp, Tr
Dusky shark *Carcharhinus obscurus*	C, P	S, (D)	Tr, WTp
Oceanic whitetip shark *Carcharhinus longimanus*	P	S	Tr, WTp
Shortfin mako shark *Isurus oxyrinchus*	P	S	Tp, Tr
Pacific sleeper shark *Somniosus microcephalus*	C, P	D	Tp
Greenland shark *Somniosus microcephalus*	C, P	D, (S)	CTp, Ar
Cookie-cutter shark *Isistius brasiliensis*	P	D	Tp, Tr
Portugese dogfish *Centroscymnus coelolphis*	P	D	Tp, Tr

will influence predation risk. White, tiger, bull and sevengill sharks are probably the major predators on nearshore cetaceans, but dusky sharks may also represent a risk (Table 4). The risk that nearshore cetaceans face from sharks will vary with location. For example, the risk of shark predation is probably higher in tropical waters than in higher latitudes because of the diversity and abundance of large, predatory sharks in warm waters (Table 4). Turbidity and substrate colour also contribute to habitat risk. Tiger sharks and white sharks are well camouflaged against dark backgrounds, and some sharks (e.g. sevengill sharks, Ebert, 1991*b*) prefer turbid waters. This may be one reason that odontocetes in some areas avoid turbid waters and dark substrates (e.g. Hawaiian spinner dolphins, Norris & Dohl, 1980*a*; Würsig *et al.*, 1994; bottlenose dolphins, Ross, 1977).

In the open ocean, the only defence against predation is to form groups, and pelagic dolphins consistently form much larger groups than their coastal counterparts (e.g. Saayman, Bower & Tayler, 1972). One interesting possibility in the pelagic environment is for predation risk to be vertically stratified because of changes in light level and the vertical stratification of shark species. In the upper water layers, dolphins would be at risk from oceanic whitetip and mako sharks, and occasionally tiger, dusky and white sharks. (Table 4). Deep-diving cetaceans would face a different suite of sharks while at their foraging depth (Table 4), including ectoparasitic sharks. Large deep water sharks (e.g. sleeper and sixgill sharks) would pose a much greater threat. These sharks, which grow to well over 4 m, are capable of killing adult odontocetes, and the primary depths at which Ebert (1986) found sixgill sharks (100–200 m) coincides with the feeding depth of many pelagic dolphin species (e.g. Fitch & Brownell, 1968; Crovetto *et al.*, 1992).

Competition

Data on the feeding habits of odontocetes and sharks have been collected in various ways which may have different biases associated with them. The protective shark nets of South Africa provide data on the feeding habits of dolphins and sharks in the same area. Because most species were caught by incidental entanglement, biases among species should be minimized and comparisons meaningful. Analyses of dietary overlap showed significant competition between several shark species and common dolphins. This level of overlap suggests that interspecific competition among these species could be an important factor determining group size, habitat use and ranging patterns. In addition to interactions between common dolphins and sharks, moderate levels of overlap were found between sharks and both humpback and bottlenose dolphins. Little is known about how species with a moderate overlap might influence each other, but it seems unlikely that there is no interaction at all, and interactions may become significant at times when certain prey species are scarce.

These results are only instructive for South Africa. Competitive interactions are likely to be highly variable geographically because of the dietary flexibility of both dolphins and sharks. Further investigations into competition between sharks and dolphins in other areas of the world will provide insights into the generality of these results.

Resource competition among sharks and odontocetes is likely to be non-aggressive. On four occasions, Leatherwood (1977) witnessed groups of bottlenose dolphins and sharks feeding from the same school of fish with no aggressive interactions, and sharks and dolphins feed together behind trawlers in Australia (Corkeron *et al.*, 1987). The lack of aggression is not surprising given that the time spent defending resources would significantly decrease the feeding times of defending individuals. Also, individuals that did not participate in resource defence would gain an advantage over those that did. Aggression or avoidance was probably not observed on these occasions because sharks were not a predatory threat, given that abundant and more easily captured teleost prey were available to them.

Seasonal variation in food resources may influence shark–odontocete interactions. There may be a large overlap in shark and odontocete prey species, but, if resources are abundant, competition will be unimportant and coexistence may be expected. However, when resources are limiting, increased competition may lead to niche divergence or non-tolerant interactions. During these times, some shark species may switch to preying upon dolphins. If this were the case, dolphins should not show a reaction to the presence of sharks when other shark food resources are abundant, but change their habitat use or show strong evasive responses to the presence of predatory sharks during food-limited seasons.

One interesting possibility raised by the competition analyses is that shark and dolphin species that engage in predator–prey interactions may also compete for food (intraguild predation). Intraguild predation among dolphins and sharks also occurs between killer whales and white sharks (e.g. Pyle *et al.*, 1999). In this situation, both species consume pinniped prey, and killer whales prey upon white sharks. Intraguild predation is a common feature of many communities and may have a major influence on the habitat use of both species even when dietary overlap is not high (e.g. Holt & Polis, 1997). It is possible that intraguild predation may be responsible for the displacement of white sharks by killer whales in the Farallon Islands (Pyle *et al.*, 1999).

Size dependent interactions

Both competitive and predator–prey interactions between sharks and odontocetes will be influenced by their body sizes. White (Tricas & McCosker, 1984; Klimley, 1985; Cliff, Dudley & Davis, 1989), tiger (Simpfendorfer, 1992; Lowe *et al.*, 1996), sixgill (Ebert, 1994) and bull sharks (Cliff & Dudley, 1991*a*) all show marked changes in diet with increasing size. Small sharks of each species tend to feed on teleost fishes, but as shark size increases, so does the number of prey groups and size of prey.

Odontocetes represent a high-energy food source, and once sharks are large enough to capture them, they should include dolphins and porpoises in their diet, at least opportunistically. Large tiger, bull, white and sixgill sharks increase their predation rate on odontocetes as predator size increases (Cliff, Dudley & Davis, 1989; Cliff & Dudley, 1991*a*; Ebert, 1994; Lowe *et al.*, 1996). However, relatively small sharks are still capable of taking young calves and sick individuals (e.g. Mann & Barnett, 1999).

Ontogenetic shifts in diet lead to size-structured interactions among species (see Werner & Gilliam, 1984 for a review). Shark competition with odontocetes will be size structured. Feeding data for dusky sharks from South Africa show that dietary overlap with all three dolphin species changed with shark size (Table 3). Small dusky sharks always showed a higher overlap with dolphins than did large dusky sharks. Unfortunately, most data that have been collected have been lumped for sharks of all size classes, but if a pattern like that of dusky sharks occurred with other shark species then there should be greater dietary overlap between odontocetes and small- to medium-shark size classes (which are more likely to take prey sizes and species similar to odontocetes).

FUTURE DIRECTIONS

This review of shark–dolphin interactions reveals that there is a lack of quantitative data on the potential influences of shark predation and competition on odontocete populations, habitat use and behaviour. However, several methods have been suggested that will enhance future investigations. If these methods are applied in future studies, a much greater understanding of shark–odontocete interactions will emerge. Although difficult, a significant step toward understanding the nature of these interactions will involve attempts to quantify predation risk and prey availability. Researchers should make use of data available from sport fishing and net catches of sharks to understand the possibility for size-structured competition, predation and intraguild predation. Data on habitat use of predatory sharks must be collected and integrated with habitat characteristics to provide an index of habitat-specific predation risk. By incorporating these data into long-term research projects, it will be possible to investigate more detailed questions about how individual dolphins make decisions about habitat use and group size as well as the fitness consequences of these decisions. Finally, understanding the influences of shark predation on current cetacean populations may enhance our understanding of the pressures leading to the evolution of odontocete group living and sociality.

Acknowledgements

I thank L. Dill, I. Hamilton, R. Connor, R. Heithaus, L. Barre, H. Finn, V. Janik, the late K. Norris, B. Würsig, V. Cockcroft, M. Abrahams, J. Clutton-Brock and an anonymous reviewer for helpful comments on previous versions of this manuscript. Thanks also go to I. Hamilton who provided great assistance in helping me obtain necessary papers. Support was provided by NSERC Canada grant A6869.

REFERENCES

Ainley, D. G., Strong, C. S., Huber, H. R., Lewis, T. J. & Morrell, S. H. (1981). Predation by sharks on pinnipeds at the Farallon Islands. *Fish. Bull. US* **78**: 941–945.

AIBS (1967). *Conference on the shark–porpoise relationship. Symposium Proceedings*. Washington, DC: American Institute of Biological Sciences.

Arnold, P. W. (1972). Predation on harbour porpoise, *Phocena phocena*, by a white shark, *Carcharodon carcharias*. *J. Fish. Res. Board Can.* **29**: 1213–1214.

Au, D. W. (1991). Polyspecific nature of tuna schools: shark, dolphin, and seabird associates. *Fish. Bull. US* **89**: 343–354.

Baker, A. N. (1981). The southern right whale dolphin *Lissodelphis peronii* (Lacepede) in Australasian waters. *Nat. Hist. Mus. N. Z. Rec.* **2**: 17–34.

Barros, N. B. & Cockcroft, V. G. (1999). Prey resource partitioning between Indo-Pacific hump-backed dolphins (*Sousa chinensis*) and bottlenose dolphins (*Tursiops truncatus*) off South Africa – competitive exclusion or mutual tolerance? Abstracts, Thirteenth Biennial Meeting of the Society for Marine Mammalogy, Maui, HI. 28 November–3 December.

Bass, A. J., D'Aubrey, J. D. & Kistnasamy, N. (1973). Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). *Invest. Rep. Oceanogr. Res. Inst., Durban, S. Afr.* **33**: 1–168.

Baughman, J. L. & Springer, S. (1950). Biological and economic notes on the sharks of the Gulf of Mexico, with especial reference to those of Texas, and with a key for their identification. *Am. Midl. Nat.* **44**: 96–152.

Bearzi, G., Notarbartolo-di-Sciara, G. & Politi, E. (1997). Social ecology of bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). *Mar. Mamm. Sci.* **13**: 650–668.

Beck, B. & Mansfield, A. W. (1969). Observations on the Greenland shark, *Somniosus microcephalus*, in northern Baffin Island. *J. Fish. Res. Board Can.* **26**: 143–145.

Bell, J. C. & Nichols, J. T. (1921). Notes on the food of Carolina sharks. *Copeia* **92**: 17–20.

Benjaminsen, T. & Christensen, I. (1979). The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Forster). In *Behaviour of marine animals* **3**. *Cetaceans*: 143–164. Winn, H. E. & Olla, B. A. (Eds). New York: Plenum Press.

Bertram, B. C. R. (1978). Living in groups: predators and prey. In *Behavioural ecology: an evolutionary approach*: 64–96. 4th edn. Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell.

Bright, D. B. (1959). The occurrence and food of the sleeper shark, *Somniosus pacificus*, in a central Alaskan Bay. *Copeia* **1959**: 76–77.

Brownell, R. L. Jr (1975). Progress report on the biology of the Franciscana dolphin, *Pontoporia blainvillei*, in Uruguayan waters. *J. Fish. Res. Board Can.* **32**: 1073–1078.

Bruce, B. D. (1992). Preliminary observations on the biology of the white shark, *Carcharodon carcharius*, in South Australian waters. *Aust. J. Mar. Freshwater Res.* **43**: 1–11.

Caldwell, M. C., Caldwell, D. K. & Siebenaler, J. B. (1965). Observations on captive and wild Atlantic bottlenose dolphins, *Tursiops truncatus*, in the north-eastern Gulf of Mexico. *Contrib. Sci. Los Angel.* **91**: 3–10.

Carey, F. G., Kanwisher, J. W., Brazier, O., Gabrielson, G. Casey, J. G. & Pratt, H. L. Jr (1982). Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* **1982**: 254–260.

Castro, J. I. (1996). Biology of the blacktip shark, *Carcharhinus limbatus*, off the south-eastern United States. *Bull. Mar. Sci.* **59**: 508–522.

Cawthorn, M. W. (1988). Recent observations of Hector's dolphin *Cephalorhynchus hectori*, in New Zealand. *Rep. Int. Whaling Comm. Spec. Issue* **9**: 303–314.

Clark, E. & Kristof, E. (1990). Deep sea elasmobranchs observed from submersibles off Bermuda, Grand Cayman, and Freeport Bahamas. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries*: 269–284. Pratt, H. L., Gruber, S. H. & Taniuchi, T. (Eds). *NOAA Tech. Rep. NMFS* **90**: 269–284.

Clarke, M. R. & Merrett, N. (1972). The significance of squid, whale and other remains from the stomachs of bottom-dwelling deep-sea fish. *J. Mar. Biol. Assoc. UK* **52**: 599–603.

Cliff, G. (1995). Sharks caught in the protective gill nets off Kwazulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rüppell). *S. Afr. J. Mar. Sci.* **15**: 105–114.

Cliff, G. & Dudley, S. F. J. (1991*a*). Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* (Valenciennes). *S. Afr. J. Mar. Sci.* **10**: 253–270.

Cliff, G. & Dudley, S. F. J. (1991*b*.) Sharks caught in the protective gill nets off Natal, South Africa. 5. The Java shark *Carcharhinus amboinensis* (Muller & Henle). *S. Afr. J. Mar. Sci.* **11**: 443–453.

Cliff, G. & Dudley, S. F. J. (1992). Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Gunther). *S. Afr. J. Mar. Sci.* **12**: 663–674.

Cliff, G., Dudley, S. F. J. & Davis, B. (1988). Sharks caught in the protective gill nets off Natal, South Africa. 1. The sandbar shark *Carcharhinus plumbeus* (Nardo). *S. Afr. J. Mar. Sci.* **7**: 255–265.

Cliff, G., Dudley, S. F. J. & Davis, B. (1989). Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *S. Afr. J. Mar. Sci.* **8**: 131–144.

Cliff, G., Dudley, S. F. J. & Davis, B. (1990). Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). *S. Afr. J. Mar. Sci.* **9**: 115–126.

Cliff, G., Dudley, S. F. J. & Jury, M. R. (1996). Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. In *Great white sharks: the biology of Carcharodon carcharias*: 351–362. Klimley, A. P. & Ainley, D. G. (Eds). New York: Academic Press.

Cockcroft, V. G. (1991). Incidence of shark bites on Indian Ocean hump-backed dolphins (*Sousa plumbea*) off Natal, South Africa. *Rep. Int. Whaling Comm. Spec. Issue* **12**: 277–282.

Cockcroft, V. G., Cliff, G. & Ross, G. J. B. (1989). Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. *S. Afr. J. Zool.* **24**: 305–310.

Cockcroft, V. G & Ross, G. J. B. (1990). Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In *The bottlenose dolphin*: 295–308. Leatherwood, S. & Reeves, R. R. (Eds). New York: Academic Press.

Compagno, L. J. V. (1984*a*). FAO species catalogue **4**. Sharks of the world. Part 1 – Hexanchiformes to Lamniformes. *FAO Fish. Synop.* **125**: 1–249.

Compagno, L. J. V. (1984*b*). FAO species catalogue **4**. Sharks of the world. Part 2 – Carchariniformes. *FAO Fish. Synop.* **125**: 250–655.

Connor, R. C. & Heithaus, M. R. (1996). Great white shark approach elicits flight response in bottlenose dolphins. *Mar. Mamm. Sci.* **12**: 602–606.

Corkeron, P. J., Morris, R. J. & Bryden, M. M. (1987). Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquat. Mamm.* **13**: 109–113.

Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**: 667–686.

Crovetto, A., Lamilla, J. & Pequeno, G. (1992). *Lissodelphis peronii* Lacepede 1804 (Delphinidae, Cetacea) within the stomach contents of a sleeping shark, *Somniosus* cf. *Pacificus*, Bigelow & Schroeder 1944, in Chilean waters. *Mar. Mamm. Sci.* **8**: 312–314.

Dudley, S. F. J. & Cliff, G. (1993). Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). *S. Afr. J. Mar. Sci.* **13**: 237–254.

Ebert, D. A. (1986). Biological aspects of the sixgill shark, *Hexanchus griseus*. *Copeia* **1986**: 131–135.

Ebert, D. A. (1990). *The taxonomy, biogeography, and biology of cow and frilled sharks (Chondrichthyes: Hexanchiformes)*. PhD thesis, Rhodes University.

Ebert, D. A. (1991*a*). Diet of the sevengill shark *Notorynchus cepedianus* in the temperate coastal waters of southern Africa. *S. Afr. J. Mar. Sci.* **11**: 565–572.

Ebert, D. A. (1991*b*). Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *S. Afr. J. Mar. Sci.* **11**: 455–465.

Ebert, D. A. (1994). Diet of the sixgill shark *Hexanchus griseus* off southern Africa. *S. Afr. J. Mar. Sci.* **14**: 213–218.

Ebert, D. A., Compagno, L. J. V. & Cowley, P. D. (1992). A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of Southern Africa. *S. Afr. J. Mar. Sci.* **12**: 601–609.

Ebert, D. A., Compagno, L. J. V. & Natanson, L. J. (1987). Biological notes on the Pacific sleeper shark, *Somniosus pacificus* (Chondrichthyes: Squalidae). *Calif. Fish Game* **73**: 117–123.

Ellis, J. R., Pawson, M. G. & Shackley, S. E. (1996). The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. *J. Mar. Biol. Assoc. U.K.* **76**: 89–106.

Fergusson, I. K. (1996). Distribution and autoecology of the white shark in the eastern north Atlantic Ocean and the Mediterranean Sea. In *Great white sharks: the biology of Carcharodon carcharias*: 321–345. Klimley, A. P. & Ainley, D. G. (Eds). New York: Academic Press.

Fertl, D., Acevedo-Guiterrez, A. & Darby, F. L. (1996). A report of killer whales (*Orcinus orca*) feeding on a carcharhinid shark in Costa Rica. *Mar. Mamm. Sci.* **12**: 606–611.

Fitch, J. E. & Brownell, R. L. Jr (1968). Fish otoliths and their importance in interpreting feeding habits. *J. Fish. Res. Board Can.* **25**: 2561–2574.

Gotceitas, V. & Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia (Berl.)* **80**: 158–160.

Gunter, G. (1942). Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montagu), on the Texas coast, with particular reference to food habits. *J. Mammal.* **23**: 267–276.

Heithaus, M. R. (In press). Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies and attack seasonality. *Mar. Mamm. Sci.* **17**.

Heithaus, M. R. & Dill, L. M. (1999). Influence of prey availability and tiger shark predation risk on bottlenose dolphin habitat use. Abstracts, Thirteenth Biennial Meeting of the Society for Marine Mammalogy, Maui, HI. 28 November–3 December.

Holt, R. D. & Polis, G. A. (1997). A theoretical framework for intraguild predation. *Am. Nat.* **149**: 745–764.

Hugie, D. M. & Dill, L. M. (1994). Fish and game: a game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.* **45**(suppl. A): 151–169.

Irvine, A. B., Wells, R. S. & Gilbert, P. W. (1973). Conditioning an Atlantic bottle-nosed dolphin to repel various species of sharks. *J. Mammal.* **54**: 503–505.

Jones, E. C. (1971). *Isistius brasiliensis*, a squalioid shark, the probable cause of crater wounds on fishes and cetaceans. *Fish. Bull. US* **69**: 791–798.

Klimley, A. P. (1985). The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. South. *Mem. Calif. Acad. Sci.* **9**: 15–40.

Klimley, A. P. (1994). The predatory behavior of the white shark. *Am. Sci.* **82**: 122–133.

Last, P. R. & Stevens, J. D. (1994). *Sharks and rays of Australia*. Australia: CSIRO.

Leatherwood, S. (1977). Some preliminary impressions of the numbers and social behavior of free-swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the north-eastern Gulf of Mexico. In *Breeding dolphins: present status, suggestions for the future*: 143–167. Ridgway, S. H. (Ed.). Report to the US Marine Mammal Commission MM6AC009.

Leatherwood, S., Perrin, W. F., Garvie, R. & LaGrange, J. (1973). Observations of sharks attacking porpoises (*Stenella* spp. and *Delphinus* cf. *D. delphis*) Nav. *Undersea Center Tech. Note* **908**: 1–7.

Le Boeuf, B. J., Reidman, M. & R. S. Keyes, (1982). White shark predation on pinnipeds in California coastal waters. *Fish. Bull. US* **80**: 891–895.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *BioScience* **48**: 25–34.

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.

Long, D. J. & Jones, R. E. (1996). White shark predation and scavenging on cetaceans in the eastern north Pacific Ocean. In *Great white sharks: the biology of Carcharodon carcharias*: 293–307. Klimley, A. P. & Ainley, D. G. (Eds). New York: Academic Press.

Lowe, C. G., Wetherbee, B. M., Crow, G. L. & Tester, A. L. (1996). Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ. Biol. Fishes* **47**: 203–211.

Macpherson, E. (1981). Resource partitioning in a Mediterranean demersal fish community. *Mar. Ecol. Prog. Ser.* **4**: 183–193.

Mann, J. & Barnett, H. (1999). Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: defense and reactions by the mother. *Mar. Mamm. Sci.* **15**: 568–575.

Mauchline, J. & Gordon, J. D. M. (1983). Diets of the sharks and chimaeroids of the Rockall Trough, north-eastern Atlantic Ocean. *Mar. Biol.* **75**: 269–278.

McBride, A. F. & Hebb, D. O. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. *J. Comp. Physiol. Psychol.* **41**: 111–123.

Mead, G. M. & Potter, C. W. (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In *The bottlenose dolphins*: 165–195. Leatherwood, S. & Reeves, R. R. (Eds). New York: Academic Press.

Mills, M. G. & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol.* **11**: 1397–1406.

Miner, J. G. & Stein, R. A. (1996). Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. *Trans. Am. Fish. Soc.* **125**: 97–103.

Norris, K. S. (1994). Predators, parasites, and multispecies aggregations. In *The Hawaiian spinner dolphin*: 287–300. Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M. (Eds). Berkeley: University of California Press.

Norris, K. S. & Dohl, T. P. (1980*a*). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull. US* **77**: 821–849.

Norris, K. S. & Dohl, T. P. (1980*b*). The structure and function of cetacean schools. In *Cetacean behavior: mechanisms and functions*: 211–261. Herman, L. M. (Ed.). New York: Wiley.

Paterson, R. A., Quayle, C. J. & Van Dyck, S. M. (1993). A humpback whale calf and two subadult dense-beaked whales recently stranded in southern Queensland. *Mem. Queensl. Mus.* **33**: 291–297.

Pyle, P., Schramm, M. J., Keiper, C. & Anderson, S. D. (1999). Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. *Mar. Mamm. Sci.* **15**: 563–568.

Randall, J. E. (1973). Size of the great white shark. *Science* **181**: 169–170.

Randall, J. E. (1992). Review of the biology of the tiger shark (*Galeocerdo cuvier*). *Aust. J. Mar. Freshwater Res.* **43**: 21–31.

Richards, A. F. (1993). *Reproductive parameters of bottlenose dolphins in Shark Bay, Western Australia*. Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, TX, Abstracts: 91.

Ridgway, S. H. & Dailey, M. D. (1972). Cerebral and cerebellar involvement of trematode parasites in dolphins and their possible role in stranding. *J. Wildl. Dis.* **8**: 33–43.

Ross, J. G. B. (1977). The taxonomy of bottlenose dolphins, *Tursiops* species in South African waters, with notes on their biology. *Ann. Cape Prov. Mus. Nat. Hist*. **11**: 135–194.

Ross, G. J. B., Heinsohn, G. E. & Cockcroft, V. G. (1994). Humpback dolphins *Sousa chinensis* (Osbeck 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii* (Kukenthal 1892). In *Handbook of marine mammals* **5**. *The first book of dolphins*: 23–42. Ridgway, S. H. & Harrison, R. (Eds). New York: Academic Press.

Saayman, G. S., Bower, D. & Tayler, C. K. (1972). Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. *Koedoe* **15**: 1–24.

Saayman, G. S. & Tayler, C. K. (1979). The socioecology of humpback dolphins (*Sousa* sp). In *Behaviour of Marine animals* **3**. *Cetaceans*: 165–226. Winn, H. E. & Olla, B. A. (Eds). New York: Plenum Press.

Simpfendorfer, C. (1992). Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. *Aust. J. Mar. Freshwater Res*. **43**: 33–43.

Simpfendorfer, C. A., Goodreid, A. B. & McAuley, R. B. (In press). Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Env. Biol. Fish*.

Smale, M. J. (1991). Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus*, and *Sphyrna zygaena*, on the eastern Cape coast of South Africa. *S. Afr. J. Mar. Sci*. **11**: 31–42.

Stevens, J. D. (1973). Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. *J. Mar. Biol*. Assoc. U.K. **53**: 357–361.

Stevens, J. D. (1984). Biological observations on sharks caught by sport fishermen off New South Wales. *Aust. J. Mar. Freshwater Res*. **35**: 573–590.

Stevens, J. D. & McLoughlin, K. J. (1991). Distribution, size, and sex composition, reproductive biology and diet of sharks from northern Australia. *Aust. J. Mar. Freshwater Res*. **42**: 151–199.

Stillwell, C. E. & Kohler, N. E. (1982). Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the north-west Atlantic. *Can. J. Fish. Aquatic Sci*. **39**: 407–414.

Stillwell, C. E. & Kohler, N. E. (1992). Food habits of the sandbar shark *Carcharhinus plumbeus* off the US north-east coast, with estimates of daily ration. *Fish. Bull. US* **91**: 138–150.

Tayler, C. K. & Saayman, G. S. (1972). The social organization and behavior of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. *Ann. Cape Prov. Mus. Nat. Hist*. **9**: 11–49.

Terborgh, J. W. (1983). *Five new world primates: a study in comparative ecology*. Princeton, NJ: Princeton University Press.

Tricas, T. C. & McCosker, J. E. (1984). Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc. Calif. Acad. Sci*. **43**: 221–238.

Urian, K. W., Wells, R. S., Scott, M. D., Irvine, A. B., Read, A. J. & Hohn, A. A. (1998). *When the shark bites: an analysis of shark bite scars on wild bottlenose dolphins (Tursiops truncatus) from Sarasota, Florida*. The World Marine Mammal Conference, Monaco 20–24 January, 1998, Abstracts: 139.

van Schaik, C. P. & van Hoff, J. A. R. M. (1983). On the ultimate causes of primate social systems. *Behaviour* **85**: 91–117.

van Schaik, C. P. & van Noordwijk, M. A. (1985). Evolutionary effects of the absence of felids on the social organization of the macaques on the island of Simeulue (*Macaca fasicularis fusca*, Miller 1903). *Folia Primatol*. **44**:138–147.

Wells, R. S. (1991). Bringing up baby. *Nat. Hist*. August: 56–62.

Wells, R. S., Irvine, A. B. & Scott, M. D. (1980). The social ecology of inshore odontocetes. In *Cetacean behavior: mechanisms and functions*: 263–317. Herman, L. M. (Ed.). New York: Wiley.

Wells, R. S., Scott, M. D. & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In *Current mammalogy* **1**: 247–305. Genoways, H. H. (Ed.). New York: Plenum Press.

Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst*. **15**:393–425.

Wetherbee, B. M., Lowe, C. G. & Crow, G. L. (1994). A review of shark control in Hawaii with recommendations for future research. *Pac. Sci*. **48**: 95–115.

Williams, T. M., Friedl, A. W., Fong, M. L., Yamada, R. M., Sedivy, P. & Haun, J. E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature (Lond.)* **355**: 821–823.

Williamson, G. R. (1963). Common porpoise from the stomach of a Greenland shark. *J. Fish. Res. Board Can*. **20**: 1085–1086.

Wood, F. G. Jr, Caldwell, D. K. & Caldwell, M. C. (1970). Behavioral interactions between porpoises and sharks. *Invest. Cetacea* **2**: 264–277.

Würsig, B., Wells, R. S., Norris, K. S. & Würsig, M. (1994). A spinner dolphin's day. In *The Hawaiian spinner dolphin*: 65–102. Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M. (Eds). Berkeley: University of California Press.

Young, D. D. & Cockcroft, V. G. (1994). Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialization? *J. Zool. (Lond.)* **234**: 41–53.