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TWO SHARK SPECIES INVOLVED IN PREDATION ON SEALS AT SABLE ISLAND, NOVA SCOTIA, CANADA

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Between 1993 and 2001, 4906 seal corpses bearing wounds likely inflicted by sharks were examined on Sable Island, Canada. Five seal species were involved: grey (*Halichoerus grypus*), harp (*Pagophilus groenlandica*), harbour (*Phoca vitulina*), hooded (*Cystophora cristata*), and ringed (*Phoca hispida*) seals. Flesh wounds on seal corpses indicated that two or more shark species prey on seals in waters around Sable Island. Wounds were categorized as either slash or corkscrew, with different predators identified for each type. Wound patterns, tooth fragments, and marks on bones indicated that white sharks (*Carcharodon carcharias*) were involved in the slash wounds, which comprised a small proportion of attacks. Ninety-eight percent of seal corpses, however, bore the corkscrew wounds that could not be attributed to shark species identified in attacks on pinnipeds in other regions and these wounds are previously unreported in the literature. Circumstantial evidence indicates that attacks by Greenland sharks (*Somniosus microcephalus*) were responsible for the clean-edged encircling corkscrew wounds seen on seal corpses washed ashore on Sable Island.

KEY WORDS: Shark Seal, Sable Island, Greenland shark, *Somniosus microcephalus* predation

INTRODUCTION

Shark predation on pinnipeds is well documented for the waters off South Africa (Ebert 1991), Australia (Shaughnessy et al. 2007), Hawaii (Hiruki et al. 1993, Lowe et al. 1996), and California (Ainley et al. 1985). White *Carcharodon carcharias* and tiger *Galeocerdo cuvier* sharks are the species most often involved. Shark predation on pinnipeds in northern waters has been seldom noted. Although shark predation has been suggested as a possible cause of the decline in harbour seals *Phoca vitulina* in Alaska (Taggart et al. 2005), there is no direct evidence of shark predation on any pinniped species in Alaskan waters (K. Goldman 2006 pers. comm.). Where shark predation on northern pinnipeds has been mentioned, species of the genus *Somniosus* (sleeper sharks) are most often

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suspected (Popov 1982). Shark predation on seals near Sable Island was reported by Brodie & Beck (1983) and Lucas & Stobo (2000), however the shark species involved were not identified.

Sable Island, located at the outer edge of the continental shelf approximately 160 km southeast of mainland Nova Scotia, Canada, is a breeding and pupping ground for harbour seals (Bowen et al. 2003a), and is now the world's largest grey seal *Halichoerus grypus* breeding colony (Bowen et al. 2003b). Prior to the early 1990s, shark predation on seals near Sable was sporadic (Brodie & Beck 1983). An increase in predation was first noted in January 1993 (Lucas & Stobo 2000). During 1993-1997 shark predation accounted for high mortality in harbour seals, particularly adult females and pups, and was partly responsible for a marked decline in harbour seal pup production on Sable Island (Lucas & Stobo 2000).

Our objectives here were to document shark-inflicted wounds observed on seals on Sable Island between 1993 and 2001, and to determine which shark species were responsible for the wounds.

MATERIALS AND METHODS

Sable Island, off the coast of Nova Scotia at 44ºN, 60ºW, is 45km long and <1.5km wide with long uninterrupted sand beaches on both the north and south sides (Fig 1). The west and east ends of the island come to a point and curve northwards. Maximum elevation is 30m, but most areas of the island are only 5-15m above sea level.

Beach searches for corpses were conducted year-round during January 1993 to December 2001 by the first author who was resident on the island. In this report, "corpse" refers to dead seals bearing wounds presumed to be inflicted by sharks. We did not observe the attacks nor were we able to recover physical evidence (such as teeth) that could confirm the predator involved in all cases. The number of search days per year averaged 154, with an overall monthly mean of 12.8 days. The fewest search days per month were in March (mean = 9.4), November (mean = 3.6) and December (mean = 6.6) because of weather and beach conditions. Although the search effort was uneven, the persistence of marked corpses on the beach (e.g. Lucas & Daoust 2002) indicated that varying length of intervals between surveys had little impact on monthly number of corpses found. Data recorded for seal corpses included number, species, age class, date, wound characteristics and amount of tissue missing from the corpse. Missing tissue was recorded as a percentage of the body surface area of the corpse. Age was categorized as pup, immature and adult, and was determined on the basis of one or more of the following variables: size (standard

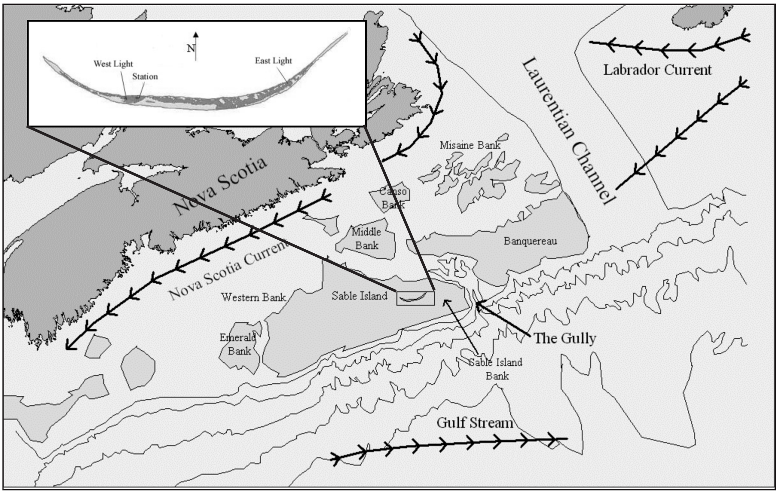

Fig 1 Nova Scotia and Sable Island, Canada

length, McLaren 1993); presence of lanugo; pelage pattern, colour and wear; and tags or brands applied by researchers with Fisheries and Oceans Canada. Month of death used in reporting results and analyses was estimated based on degree of scavenging and decomposition (e.g. a partly decomposed corpse washed ashore in the first week of June was considered a May kill).

Wounds were categorized as either slash or corkscrew. The slash wound comprised one or a combination of cuts, punctures and rake marks, on any part of the body, often in a pattern suggesting a bite (Fig 2). The corkscrew wound, which lacked the usual features of shark bites, was typically long and clean-edged, and always found on the front of the seal running diagonally around the body axis from the head to some point between the shoulders and pelvic areas (Figs 3 and 4).

RESULTS

A total of 4906 seal corpses of five species were found on Sable Island during 1993-2001, of which grey seals comprised 76%, and harp *Pagophilus groenlandica*, harbour and hooded *Cystophora cristata* seals comprised 13%, 9% and 1%, respectively. One ringed seal *Phoca hispida* corpse was recovered. The numbers of presumed shark-killed seals reported here are minimums. It is not known what proportion of corpses were unrecorded because they were entirely consumed by the attacking sharks, or the corpse was

Table 1a Numbers of seal corpses found by species and age with a) slash wounds, and b) corkscrew wounds.

Species	**Age group**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**Total**
Grey seal	adult		1	2	3		6		1		13
	immature	2	2	1		3	3	3	2	4	20
	pup		14	8	8	16	13	5	13	9	86
Harbour seal	pup	2	1								3
Total		4	18	11	11	19	22	8	16	13	122

Table 1b

Species	**Age group**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**Total**
Grey seal	immature	1	2	284	2	20	9	23	10	17	368
	pup	65	127	7	360	543	558	579	490	529	3258
Harbour seal	adult	12	51	73	57	31	9	1	7	4	245
	immature	1	12	5	5	1					24
	pup	16	71	42	39	13	1	2		1	185
Total		95	263	411	463	608	577	605	507	551	4080

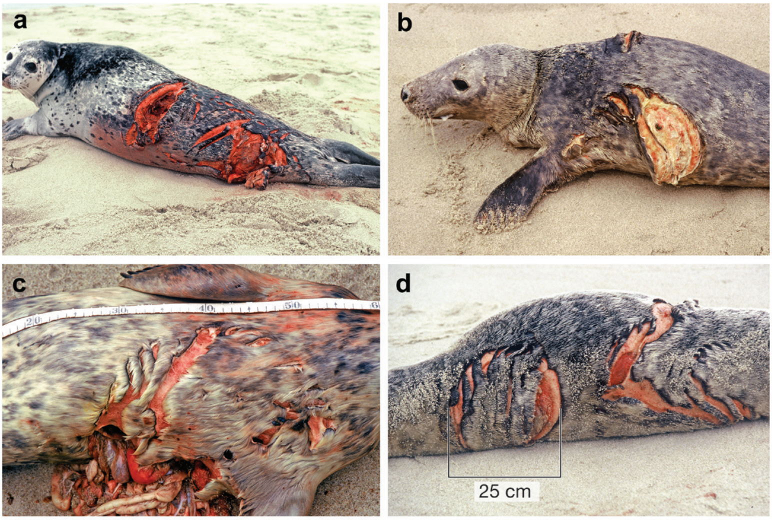

Fig 2 Slash wounds on Sable Island seals
a) An adult harbour seal with slash wounds on back, hip and rump.
b) A juvenile grey seal with wounds on back and shoulders. No tissue is missing. Elasticity in the skin causes the wound edges to pull apart, exposing blubber beneath the skin.
c) Pectoral area of the corpse of a juvenile grey seal (right front flipper at the top of the photo). The wound, roughly 25 cm in width, shows the arc of the bite.
d) The left side of a juvenile grey seal corpse, (shoulder, upper back, and hip). The seal had been bitten at least three times.

not beached or was completely decomposed and/or scavenged while still in the water. Of the 4906 corpses examined, 2% bore slash wounds, and 98% bore corkscrew wounds. For description of wound characteristics and identification of the predator we used observations collected from the island's two breeding species, grey and harbour seals. The other three seal species will not be considered further in this paper.

Slash wounds

Slash wounds (Table 1a and Fig 2) ranged in severity from several score marks and superficial punctures on the hide, to one or more extensive deep cuts. Over 90% of these seals were injured in more than one of the five positions on the body (Table 2), with 31% injured in at least four of the body positions. Fifty-two percent of all wounds were on the hindquarters. The pattern of some slash wounds suggested the arc of teeth in one or both jaws of the attacking shark (Figs 2c and 2d). Where an arc could be discerned and measured,

Table 2 Position of slash injuries attributed to white sharks on 114 corpses (3 harbour seals and 111 grey seals) at Sable Island between 1993 and 2001.

Location of wound on seal's body	Number of records	Percent of 349 location records	Percent of 114 seals*
Head, neck	15	4.3	13.2
Shoulder, chest, foreflippers	64	18.3	56.1
Trunk	88	25.2	77.2
Rump, hips, pelvis	92	26.4	80.7
Tail, hind flippers	90	25.8	78.9
Total	349	100.0	

* The sum of the records expressed as a percentage of 114 seals exceeds 100% because many seals had wounds on more than one part of the body.

bite width ranged from 25-35cm. In 86% of corpses, no tissue was missing, and only one, a female adult grey seal, had lost a limb.

Most (99%) of the corpses with slash wounds were observed during July through October, with 44% found in August. Only one slash-wounded corpse was found in June; none were found in November through May. Seventy-three percent of corpses with slash wounds were pups (Table 1a). Although few corpses were examined for score marks on bone and tooth fragments, a tooth fragment identified as shortfin mako (D. Long 1996 pers. comm.), was found embedded in a hind limb bone that was also scored by white shark teeth. Fragments and score marks of white shark teeth were found on the bones of two other corpses (D. Long 1996 pers. comm.).

Although it was impossible to determine how far offshore seals were attacked, there were indications that some seals had been attacked close to the beach. On several occasions live wounded seals were observed coming ashore with arterial blood spurting from wounds.

Corkscrew wounds

Corkscrew wounds (Fig 3) were recorded for 3626 grey seals and 454 harbour seals (Table 1b and Fig 5). Although corpses bearing fresh corkscrew injuries occurred throughout the year (Fig 6), there was a significant difference in numbers per month for both grey $\chi 2(11, N = 3626) = 3127.1, p = 0<0.05$) and harbour seals $\chi 2(11, N = 454) = 209.5, p = 0<0.05$). Seventy-nine percent of grey seals were found in January and February, while most (88%) of the harbour seals were found in April through September peaking in June.

Fig 3 Corkscrew wounds on Sable Island seals

a) Ventral view of the upper body of a juvenile grey seal. The wound runs between chin and pectoral area in a counterclockwise path across the throat and around to just below the right front flipper. No tissue is missing.

b) Dorsal view of a harbour seal pup. Parallel tears run in a counterclockwise direction around the body, showing the lighter-coloured ventral pelage at the end of each strip. Such complex wound patterns were seen most often in harbour seal pups. No tissue is missing.

c) The right and left front flippers and scapulas (jacket), have been removed from the upper body of an adult harbour seal, but remain attached by a strip of skin on the snout. A chevron is present on the corpse's back. No tissue is missing.

d) Three harbour seal pups with jackets missing. Although gulls have scavenged soft tissues, the spine and ribcage in each corpse is intact, and except for the jacket, the skeleton is complete. With further scavenging and decomposition, the remaining connective tissue ceases to hold the corpse together.

e) An adult harbour seal with the jacket attached to the body by a shred of tissue at the right scapula. The jacket includes the snout (nostrils and vibrissae, in the lower left corner), and the alternating light ventral and dark dorsal pelage shows how the fragment came off in a helical tear around the body. When fitted to the body, the fragment indicates a counterclockwise path.

f) Ventral view of the lower half of an adult harbour seal showing the chevron wound edge pattern on the dorsal surface. In the past, such corpses were described as being "bitten in half by a white shark", however, the clean-edged chevron is diagnostic of a jacket removal, and confirms that the partial corpse is a remnant of the corkscrew kill.

All grey seal corpses were young animals, with pups comprising 89.9% of the total. However, in harbour seals, the majority of corpses were adults (Table 1b).

The fresh condition of some seal corpses indicated that they had washed ashore within a few hours of being killed and thus had been attacked close to the beach. Several were still bleeding and had a core temperature that was warm to the bare hand.

All corkscrew wounds were so clean-edged that they appeared to have been made with a sharp instrument. The wound typically penetrated hide and blubber, but did not cut into muscle tissue. Although the bones of face and jaws were sometimes fractured, other skeletal material, trachea, and organs were most often intact (except for damage caused by scavenging gulls). The lack of skeletal damage was evident even in the harbour seal pups, the smallest and most delicate of seal corpses (Fig 3d). Punctures in tissue, if present, were usually small and found on the face. In most corpses in which the head was not lost, the facial-mask (the area between forehead, ears and nostrils) was undamaged. Fresh specimens, before scavengers and decomposition removed tissue and organs, looked skinned (Figs 3c and 3e). In highly scavenged and partly decomposed corpses, corkscrew wounds could be identified on the basis of several characteristics, including the presence of strips of hide showing alternating dorsal and ventral pelage patterns (Fig 3e), which indicated that the strip had encircled the body, and the presence of a chevron-shaped contour along one edge of the remaining tissue (Figs 3d, 4b and 4c).

In July 1994, the carcass of a freshly killed harbour seal pup bearing a time-depth recorder (TDR) was washed ashore. The TDR had been applied by researchers studying diving and foraging behaviour (Bowen et al. 1999). A typical corkscrew wound encircled the body, but its path was unaffected by the presence of a large section of nylon webbing, glued with epoxy to the coat on the seal's back, which served as a mount for the TDR. The webbing, epoxy, and acrylic casing of the instrument were not damaged and showed no sign of having been bitten (i.e. no scratches or punctures), yet the wound ran through the tissue under the webbing. Tissue at one

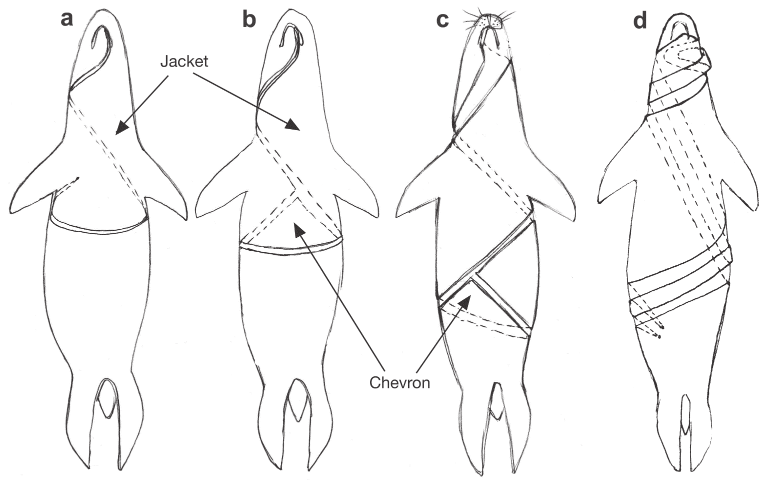

Fig 4 Diagrams of counterclockwise corkscrew wounds on seal corpses found at Sable Island. All are ventral views.

a) The wound runs around the body in a helical path between the left jaw and the right side of the upper back, similar to the wound path shown in Fig 3a.
b) The wound intersects on the upper back, and is similar to the wound in Fig 3c. Although the skin is still attached to the chin and right lower jaw, with such a “completed” tear, the jacket and blubber layer can be torn away from the body. The wound forms the characteristic chevron on the seal’s back.
c) A long single tear line runs around the body twice and intersects on pelvic area of the seal. Ventral chevrons are most often formed by tears that encircle the body two or more times.
d) Parallel tears run around the body but do not intersect. This wound pattern is similar to that shown in Fig 3b.

side of the wound had pulled away from the webbing, indicating that the tissue had been torn, not cut.

Of the 1119 corpses examined for missing tissue, 61% had ≤5% missing. In 53% of the complete corpses examined for wound pattern (924), the corkscrew wound was almost identical: a long, single tear line with no tissue missing (Figs 3a, 4a and 4b). The remaining 47% of complete corpses bore wounds comprised of two or more parallel tears (Figs 3b and 4d) sometimes with a small patch or strip of tissue missing from the face or neck. In the incomplete corpses missing tissue ranged from strips of hide and blubber, to the entire front half or front three-quarters of the body (i.e. all tissue and skeletal material). Most often the missing tissue was a jacket, the section of hide and blubber from the front half of the body, with

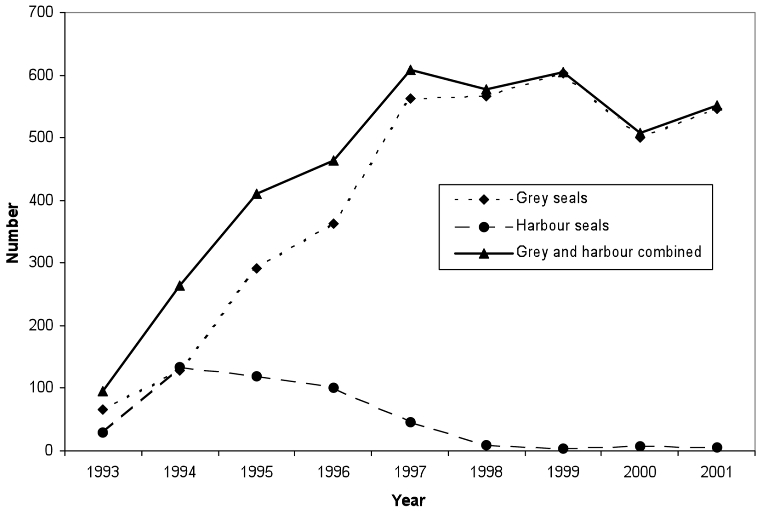

Fig 5 Number of seal corpses with corkscrew wounds by year

both front flippers, and usually scapulas, attached (Figs 3c and 3d). Of the 3004 corpses for which the presence or absence of a jacket was recorded, 5.7% were missing full jackets and 3.9% were missing partial jackets (with only the left or right flipper and scapula). A chevron was present in 39% of the 1314 corpses for which the presence or absence of a chevron was recorded.

DISCUSSION

Characteristics of wounds observed on beached seal corpses indicate that at least two shark species were involved in the predation on seals near Sable Island. The majority of seal corpses bore wounds that could not be attributed to shark species previously identified in attacks on pinnipeds in other regions. Numbers of shark-killed seal corpses recovered reflected seasonal local abundance of grey and harbour seals.

Grey seals are year-round residents on Sable Island, and the island is a major breeding ground for this species (Bowen et al. 2003b). The size of the population increased during the 1980s to present, and in the latter years of the study period, grey seals produced approximately 20,000-25,000 pups during each December to February pupping season (Bowen et al. 2003b). Although large numbers of grey seals are in waters near the island throughout the year, the majority of grey seal corpses were observed in January

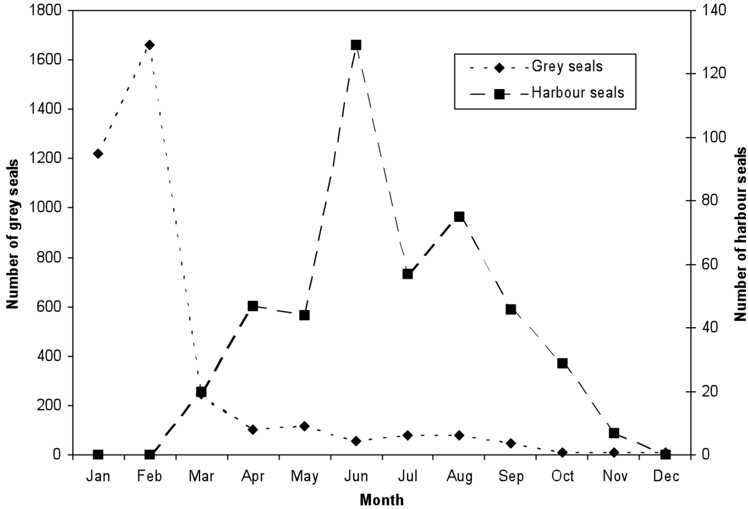

Fig 6 Number of seals corpses with corkscrew wounds by month

and February corresponding with the grey seal breeding season when recently weaned pups enter the water.

Harbour seals are also year-round residents and breed on the island, although they comprise a far smaller population than grey seals. Harbour seal adults congregate during spring and summer for pupping and breeding. At this time, nursing mothers with pups and recently weaned pups are in the water. Harbour seal pup production declined from 625 pups in 1989 to only 32 in 1997, due primarily to shark-inflicted mortality (Lucas & Stobo 2000). Thus, during the study period, harbour seals on Sable Island were outnumbered by grey seals by >20:1, increasing to >500:1 by the end of the 1990s (Bowen at al. 2003a). However, there were still 300 to 400 adult and immature harbour seals frequenting the island (W.D. Bowen 2006 pers. comm.), particularly during the annual molt in July-August.

Life history information on the various shark species that seasonally inhabit the region provides insight regarding which shark species were responsible for these attacks.

Scotian Shelf Sharks

Few shark species reside year-round in Canadian waters; however, seasonal migrants increase the species composition in the warmer months of summer (Templeman 1963). Twenty shark species have been recorded off Nova Scotia, although many have been seen infrequently (Table 3). Based on size, distribution and/ or feeding ecology, 14 of the 20 species can be ruled out as having

Table 3 Information on twenty shark species reported off Nova Scotia. Species arranged by size. Shaded species are those which, based on size, seasonal distribution and feeding ecology, could be predators on Sable Island seals.

Species	Max size TL (m)	Primary distribution in the western North Atlantic	Food types	Occurrence in Nova Scotia
Rough sagre, *Etmopterus princeps*	0.75	Scotian Shelf to New Jersey	Unknown	Occasional 567-2213m
Black dogfish, *Centroscyllium fabricii*	1	Greenland to Virginia, possibly south in deep water	Invertebrates and small fish	Deepwater ~460m
Portuguese shark, *Centroscymnus coelolepis*	1	Grand Banks to Delaware Bay	Bony fish, squid	Uncommon
Atlantic sharpnose shark, *Rhizoprionodon terraenovae*	1.2	New Jersey to Florida	Bony fish and invertebrates	1 record, very rare
Spiny dogfish, *Squalus acanthias*	1.4	Greenland to Cuba	Small fish and invertebrates	Common seasonal, summer to late fall
Smooth dogfish, *Mustelus canis*	1.5	Massachusetts to Florida Uncommon north of MA	Large crustaceans, small fish	Northern limit, rare
Deepsea catshark, *Apristurus profundorum*	~1.6	Atlantic coast?	Bottom and midwater fish and invertebrates	Not uncommon, distribution unknown but deep 1300-1600m
Sand tiger, *Carcharias taurus*	3.2	Gulf of Maine to Florida, poleward migrations in summer	Bony fishes, small sharks, invertebrates	Observed rarely

Table 3 *Cont'd*

Species	**Max size TL (m)**	**Primary distribution in the western North Atlantic**	**Food types**	**Occurrence in Nova Scotia**
Oceanic whitetip, *Carcharhinus longimanus*	3.5	Maine to Argentina	Bony fish and cephalopods, mammal carrion, birds, turtles and invertebrates	Northern limit, uncommon in EEZ
Porbeagle, *Lamna nasus*	3.7	Newfoundland to New Jersey	Schooling fish and squid	Common, year round
Dusky shark, *Carcharhinus obscurus*	3.7	Cape Cod and Georges Bank to Florida	Bony and cartilaginous fish, whale meat uncommon	Northern limit, rare
Blue shark, *Prionace glauca*	3.8	Newfoundland to Argentina	Fish and squid, scavenge on marine mammal	Primarily summer but all months except January and December
Shortfin mako, *Isurus oxyrinchus*	4	Newfoundland to Brazil	Pelagic fish, including swordfish, some marine mammal	Summer
Smooth hammerhead, *Sphyrna zygaena*	4	Nova Scotia to Florida	Bony and cartilaginous fish, invertebrates	Occasional, summer only
Bluntnose six gill shark, *Hexanchus griseus*	4.8	North Carolina to Florida	Fish, invertebrates, carrion, seals	Rare, 2 juveniles collected in 1989
Thresher shark, *Alopias vulpinus*	5.5	Newfoundland to Cuba	Bony fish, squid, crustaceans	Summer to November, peak in August/September

Table 3 *Cont'd*

Species	**Max size TL (m)**	**Primary distribution in the western North Atlantic**	**Food types**	**Occurrence in Nova Scotia**
Tiger shark, *Galeocerdo cuvier*	5.5	Cape Cod, MA to Uruguay	Fish, turtles, birds, marine mammals	Probably northern limit, rare, only small specimens reported
White shark, *Carcharodon carcharias*	6.4	Newfoundland to Cuba	Fish, marine mammals	Sporadic, April-November, peak in August
Greenland shark, *Somniosus microcephalus*	6.4-7.3	Arctic to Cape Cod, further south in deeper water	Fish, marine mammal, birds, invertebrates	Reported in spring, winter and fall, deeper in summer
Basking shark, *Cetorhinus maximus*	9.8	Newfoundland to Florida	Plankton	Summer

References: Scott & Scott 1988; Compagno 1984; Joyce et al. 2002; Stillwell & Kohler 1982; Stevens 1973, 1984; Stillwell & Kohler 1982; Gilhen & Coad 1989.

caused the types of wounds observed on seals at Sable Island. While porbeagle *Lamna nasus* distribution and size suggest it as a possible predator, an extensive study on porbeagle in the area indicated no evidence of marine mammals as a food source (Joyce et al. 2002). Of the remaining six species, two, the bluntnose sixgill shark *Hexanchus griseus* and the tiger shark, have been reported in the region only as juveniles, an age group that would not normally be feeding on marine mammals (Ebert 1994, Lowe et al. 1996). The occurrence of two neonatal (60-70cm total length, TL) (Ebert 1986) bluntnose sixgill sharks in waters off Nova Scotia (Gilhen & Coad 1989), suggested the recent presence of a mature female. However, in a compilation of deepwater species caught between 38°N into the Mid-Atlantic Bight and northwards to the Scotian continental slope from the 1960s to 2002, no other members of this species have been reported (Moore et al. 2003).

Large tiger sharks are known predators of marine mammals in the Pacific (Hiruki et al. 1993, Lowe et al. 1996). Tiger sharks have been reported in waters well south of Sable Island (N. Kohler 2006 pers. comm.); however, the largest was 155cm fork length (FL), which is well below the size that usually preys on marine mammals (Lowe et al. 1996). Large tiger sharks have been captured in the Canyons off the US East Coast and it is possible that some could move into waters near the island from the offshore warmer waters during the late summer or when Gulf Stream eddies move warm water masses toward the Sable Island Bank (Zwanenburg et al. 2002). Lowe et al. (1996) suggest that tiger sharks are opportunistic feeders, thus they may migrate to take advantage of seasonally abundant prey. Despite the potential for consumption of marine mammals by large members of this species, the rarity of sightings, and the small sizes of those sighted, indicates that Nova Scotia is probably the extreme northern limit of their range and it is unlikely that a large enough population existed in the area to account for the number of attacks near Sable Island.

The four remaining species are shortfin mako, and blue, white and Greenland sharks. Diet and temperature preferences rule out the shortfin mako, blue and white sharks for the majority of the attacks that occur in January and February. Beached specimens of both blue shark and shortfin mako have been found on Sable Island during the last 20 years (Z. Lucas unpub. data). Four blue sharks were found in July, August, and late October, and two shortfin makos occurred in August and late October. Blue sharks are found in these waters during most of the year, but are infrequent or absent in December and January (Templeman 1963, Campana et al. 2006a). Shortfin makos in Atlantic Canada are generally associated with the warm waters of the Gulf Stream (Campana et al. 2006b) and are primarily reported during summer and early autumn in the Scotian Shelf region (Campana et al. 2005). The limited occurrence of marine mammal tissue in the stomach contents of blue sharks and shortfin makos worldwide (Stevens 1973, Cliff et al. 1990, Cortes 1999, Henderson et al. 2001) and specifically in the northwest Atlantic (Kohler & Stillwell 1981, Stillwell & Kohler 1982, McCord & Campana 2003) suggests that these species only consume marine mammals opportunistically and are not likely to be major predators on seals. While it is possible that these species switch prey in this area of high marine mammal concentration, the size of the bite of a slash wound, when present, was too large for the blue shark and unlike the ragged edged bite that is caused by the pointed teeth of the shortfin mako. Additionally, seasonal distribution ruled out these species for the corkscrew wounds.

White sharks are not common, but range between the Gulf of Mexico and Newfoundland (Templeman 1963, Casey & Pratt 1985). The white shark is found in temperatures of 11-24ºC but most occurrences (75%) are in the range of 15-22ºC (Casey & Pratt 1985). Distribution studies have indicated that the larger whites (>200cm TL) occur over the whole geographical range, whereas the smaller white sharks are more confined to the Mid-Atlantic Bight area due to a limited temperature tolerance (Casey & Pratt 1985). In the region of the Gulf of Maine and Nova Scotia, there is a peak in sightings of white sharks in the months of July and August, and these are mostly larger individuals whose primary prey are marine mammals (Casey & Pratt 1985, Estrada et al. 2006). Since 1800, only one white shark has been reported between December and June in Atlantic Canada (T. Curtis 2010 pers. comm.).

The Greenland shark *Somniosus microcephalus* is common in Arctic waters from Eurasia to North America. Cape Cod, Massachusetts in the west, and the British Isles in the east, are considered the southern extremes of its known normal range (Benz et al. 2007); however, large Greenland sharks have been caught as far south as Cape Hatteras, North Carolina (J. Casey 1994 pers. comm.). In many portions of its range, the Greenland shark is abundant and has been both target and by-catch of fisheries. Greenland sharks have been found in temperatures ranging from polar extremes up to 10-12ºC (Compagno 1984). This species tracked off northern Baffin Island (Skomal & Benz 2004) showed no apparent depth or temperature preference and was found to move into shallower waters at night. Results indicated that this species is not exclusively benthic and suggested that the Greenland shark may actively hunt ringed seals under landfast sea ice (Skomal & Benz 2004).

Little is known about the migratory movements of the Greenland shark. Historically, this species is known to be in Scotian Shelf waters in autumn and winter (Templeman 1963), and has been reported on Georges Bank on the Scotian Shelf in summer (J. Conway 1996 pers. comm.). In October, there is a large increase in numbers of Greenland sharks in the northern section of the Davis Strait, and the sharks appear to be moving down from north at that time (J. Pedersen 1994 pers. comm.) The Greenland shark appears to be a generalist predator; its diet includes a wide variety of fishes and elasmobranchs (Bigelow & Schroeder 1948, Templeman 1963). Also listed as food items are seabirds, squids, crabs, large snails, medusae and entire reindeer (without horns) (Bigelow & Schroeder 1948). Greenland sharks are reported to be carrion feeders, tending to gather around whaling stations to obtain offal (Bigelow & Schroeder 1948) and entering shallow water to feed on camp garbage (Beck & Mansfield 1969).

Recent evidence indicates that the trophic level of the Greenland shark increases with size and that seals may be a common food item of some large Greenland sharks (Fisk et al. 2002, Yano et al. 2007). Yano et al. (2007) found that marine mammals (at least three species of pinniped) were the second most common prey item in terms of frequency of occurrence and index of relative importance. Whole and portions of harbour, ringed, harp and hooded seal have been found in the stomachs of Greenland shark from many locations (Bigelow & Schroeder 1948, Ridoux et al. 1998, Orlov 1999, Fisk et al. 2002, Yano et al. 2007), but it was unknown whether the seals were consumed as live prey or were scavenged. Recently, however, Yano et al. (2007) found freshly dead pinnipeds in the stomach contents of Greenland sharks, suggesting that the sharks captured active prey.

Slash wounds

Based on the seasonality of the slash wounds and the behaviour, range and temperature tolerances of the sharks in the region, the white shark and shortfin mako were the most likely species responsible for the slash wounds. In many regions, pinnipeds appear to be a major source of food for white sharks (Ainley et al. 1985, Long et al. 1996, Shaughnessy et al. 2007). Slash wounds coincided with the summer and early autumn occurrence of white sharks in the Scotian Shelf region (Casey & Pratt 1985, Casey & Kohler 1992). Additionally, the slash wounds were generally similar to injuries inflicted on seals elsewhere by white sharks (Long et al. 1996). Score marks made by white shark teeth on the bones of several fresh corpses bearing slash wounds indicated that white sharks were near Sable Island when they attacked the seals. The location of Sable Island and its use by thousands of seals makes it a likely site for large white sharks to feed during summer migration. It is hypothesized that white shark distribution is related to prey availability within thermal limits and, on the West Coast, that they time their movements to those of breeding pinnipeds (Long et al. 1996). Since Sable Island is the only consistent source of congregated prey in the region, it is likely that white sharks would utilize this food source during the months that the water temperature is in a tolerable range.

The shortfin mako tooth fragment embedded in seal bone also scored by white shark teeth, suggested that the shortfin mako may be responsible for some attacks or may be scavenging on the corpses of seals killed by white sharks. While the shortfin mako cannot be excluded as the possible cause of some of the injuries, based on wound characteristics, it is probable that most, if not all, of the slash wounds seen on seal corpses at Sable Island were inflicted by white sharks. Slash wounds were observed on grey seals of all ages indicating no prey size limitation.

Corkscrew wounds

The unusual nature of the long clean-edged corkscrew wounds, which are atypical of well documented shark-inflicted injuries, suggested causes including manmade hazards, ice, and other predators such as killer whales *Orcinus orca*. The corkscrew wounds, however, are markedly different from the wounds seen on manatees injured by ship propellers (Hare & Mead 1987), and the evidence that some kills had occurred close to the beach further rules out propellers since Sable's shoreline is not accessible to ships. Wounds also bore no similarity to entanglement injuries caused by net, rope, or strapping, all of which have been observed on Sable Island during marine litter and entanglement studies (Lucas 1992). Access to Sable Island is restricted and activities monitored, thus it is not possible that the wounds could have been deliberately inflicted by humans. Killer whales are uncommon in the Scotian Shelf region (Lucas & Hooker 2000), and the clean-edged wounds are not consistent with the dentition and feeding behaviour of these cetaceans (R. Baird 2008 pers. comm.). Pack ice does not normally occur within 200 km of Sable Island (G. Forbes 2010 pers. comm.).

Attributes of the life history of the Greenland shark suggest it was the predator causing the corkscrew wounds. The teeth of Greenland sharks are markedly dissimilar in the two jaws. The upper teeth are small and thorn-like; the lower teeth are subquadrate, about half as broad as high, each overlapping the next outermost and forming a continuous saw-like or bread knife-like cutting edge. Wound patterns found on seal corpses on Sable Island suggest that the Greenland shark grasps the live seal front first; the lower teeth cut into the hide, and the upper teeth, which are not cutting teeth, may help to hold and manipulate the prey. Greenland sharks have many of the modifications for a suction-feeding elasmobranch, including a small mouth laterally enclosed by modified labial cartilages, small teeth (Motta et al. 2002), and a large long pharynx (buccal cavity, Ebert 1994). Wilga and Motta (1998) concluded that spiny dogfish *Squalus acanthias* which is in the same family as the Greenland shark, use suction and ram mechanisms for prey capture and suction for prey transport, and that the species is capable of using a wide variety of food capture strategies on a single food type. Head shaking in the spiny dogfish was used to cut and subdue prey, and to gouge pieces from large prey. Wilga & Motta (1998) suggest that tooth morphology is an important component of the head shaking cutting behaviour. This method of holding the prey with the teeth in both jaws and cutting tissue with the sharp lower teeth is described as the typical “clutching-cutting” method of Squaloids (Shirai & Nakaya 1992). The lack of skeletal damage to seal corpses on Sable Island suggests that the shark in question does not bite down with much pressure. Assuming the prey is captured by suction, the upper teeth may hold the prey in place during a lateral head shaking that would allow the lower teeth to make a sharp cut. In conjunction with prey response and/or head shaking by the shark, the hide tissue with blubber attached is held and pulled by both teeth and suction, and then is torn off the body and the jacket is pulled free of the seal carcass. The helical path of the tear may be explained by the characteristics of collagen fibres present in the skin and blubber of marine mammals. These fibres wind around the body and are oriented in two directions at roughly 45 degrees to the body axis (Brodie 2001). As the tissue is pulled off the seal’s body, the tear runs diagonally around the torso and intersects with the tear running in the other direction, thus forming the diagnostic chevron pattern (Fig 3d).

The Greenland shark may selectively feed on the most energy-rich portion of the seal prey. In more than half of the corpses examined, very little to no tissue was missing indicating that, following some attacks, the shark did not feed on the corpse because it was either not a feeding event or that it was a failed feeding attempt. Where tissue was missing, however, it was a section of hide with the blubber layer attached. The energy content of blubber is roughly twice that of muscle tissue (Stirling & McEwan 1975). In young grey seals in good body condition, the blubber comprises 25-40% of total body weight (Addison & Stobo 1993). The fat content of ringed seals in good body condition accounts for 50-85% of the caloric value of the whole corpse (Stirling & Oritsland 1995). It is not unprecedented for predators to selectively consume this layer: in the Canadian Arctic, polar bears *Ursus maritimus* eat mainly the blubber layer of ringed seals (Stirling & Oritsland 1995), and white and blue sharks have been observed to strip the blubber layer off cetacean corpses (Pratt et al. 1982).

Based on current information on distribution, prey preference, foraging behaviour, jaw and tooth morphology, the Greenland shark is the most likely species responsible for the corkscrew wounds. This species is the only large predator known to occur year-round in the Sable Island area and to consume marine mammals as a common part of its diet.

Responses to photographs and diagrams of the corkscrew wounds sent to researchers studying pinnipeds and/or sharks in other regions, including Norway, Iceland, Greenland, Great Britain, California, Alaska and the northeast United States, South Africa and Australia, indicated that such wounds had not been observed elsewhere during this study (1993-2001). However, reports in the British media (e.g. BBC 2010) suggest that similar injuries have been seen recently along the North Sea coastline. Thus it is likely that the Sable Island situation is not unique, and that the Greenland shark similarly preys on seals in other regions where it coexists with pinnipeds. However the scarcity of reports suggests that (a) such predation has not occurred until recently in other regions; (b) it has occurred but the corpses have not been observed or reported because the breeding colonies may be away from land and on ice (Sergeant 1991) making corpses unlikely to wash ashore; and/or (c) similar wounds have been seen but the damage has been attributed to some other agent such as entanglement, ships' propellers, rafting ice, or deliberate mutilation. This type of wound occurred in Atlantic Canada when more than a thousand harp seal pup corpses washed ashore on Prince Edward Island in April 1998 and gave rise to a controversy (Toughill 1998) with claims that a large proportion of the seals had been deliberately mutilated by fishermen or sealers, and counter-claims that the seals had been caught and cut in ice. These wounds, however, were very similar to those on the corpses found on Sable Island and, thus, it is possible that such predation on harp seal pups is not uncommon, but is normally miss-classified.

Our data suggest a prey size limitation for the predator inflicting the corkscrew wounds. Young seals predominated in the corpse totals in all months, peaking during the January-February grey seal pupping season. Most grey seal corpses were pups. In addition to being present in large numbers near the island during much of the year, these young animals, being small and naïve, are likely the most vulnerable. Ainley et al. (1985), Long et al. (1996), and Shaughnessy et al. (2007) also reported that young pinnipeds were more susceptible to attack by sharks. In harbour seals, however, more adults than pups were killed. The adult harbour seal is smaller than the adult grey seal, and thus may represent the upper limit of prey size range for corkscrew predation. Adult male and female harbour seals are 157cm and 149cm in length, respectively, compared with 231cm and 201cm for adult grey seals (McLaren 1993).

The warm and bleeding condition of some beached corpses, and data from TDRs suggest that corkscrew wounds can occur close to shore. In June 1996, two harbour seal pups bearing TDRs (Bowen et al. 1999) were attacked. The data from the TDRs showed that the pups had been killed at midnight, in approximately 2m of water at the north side of the island (W.D. Bowen 1996 pers. comm.). Based on the slope of the island, the pups would have been less than 30m from shore at the time of death (G. Forbes 2006 pers. comm.).

In summary, the patterns and seasonality of shark-inflicted injuries on seals washed ashore on Sable Island indicate that two or more shark species were involved. There is direct evidence that white sharks were responsible for a portion of the attacks on seals during summer and early autumn. Identification of the Greenland shark as the predator responsible for >95% of all shark-killed seals seen year-round at Sable Island, is based on data gleaned from a large number of seal corpses, review of existing knowledge of distribution, behaviour, morphology, and diets of sharks, suggested predatory strategy and distribution and behaviour of seals. The unusual and dramatic corkscrew wound, characteristic of corpses attacked by the Greenland shark, is primarily a tear, not a cut. Young animals comprised the majority of seals killed by both shark species, and it is likely that a proportion were killed close to shore.

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