

Investigatory Behavior toward Surface Objects and Nonconsumptive Strikes on Seabirds by White Sharks, *Carcharodon carcharias*, at Seal Island, South Africa (1997–2010)

Neil Hammerschlag*

University of Miami

R. Aidan Martin

University of British Columbia

Chris Fallows

Apex Expeditions

Ralph S. Collier

Shark Research Committee

Rob Lawrence

African Shark Eco-Charters

ABSTRACT

Investigation of any unfamiliar object carries inherent risks but can also provide significant benefits, including the discovery of new food sources. White Sharks (*Carcharodon carcharias*) combine numerous characteristics (e.g., large body, developed senses, broad prey spectrum, and few natural enemies) that should foster investigation of novel objects. Over a 13-year period (1997–2010), we observed White Shark investigatory behavior toward 26 floating objects and 61 strikes on seabirds at Seal Island in False Bay, South Africa. Attacks on seabirds were typically forceful and could have resulted from mistaken identity or been stimulated by contest competition from

* Corresponding author (nhammerschlag@rsmas.miami.edu).

conspecifics. Nonconsumption of captured seabirds may also represent food rejection because of unpalatability or low fat content; however, we provide evidence that rejection of low-fat foods by White Sharks is inconsistent with quantitative studies of this species' diet and with available data on dietary thermogenesis. The adaptive value of White Sharks' observed behavior of biting objects that they do not consume is examined. We also present evidence that White Shark teeth function as mechanosensory structures, fostering tactile investigation.

INTRODUCTION

Investigatory behavior may be classified as extrinsic, as in searching for food or other resources, or intrinsic, as in examining novel objects toward no obvious goal (Berlyne, 1963). Most forms of food selection include some degree of tactile investigation (McFarland, 1987). Thus, it can be difficult to determine whether a predator's tactile exploration of objects or animals is motivated by extrinsic or intrinsic factors. Investigatory behavior is largely characterized by motivational conflict between curiosity and fear, often resulting in vacillation between approach and withdrawal, combined with tentative attempts to manipulate, "sniff," or bite the object of interest (Baerends et al., 1975; McFarland, 1987). The investigation of any unfamiliar object or creature carries inherent risks, including potential injury and (if the object proves inedible) lost foraging time; these risks increase with relative proximity and duration, respectively. However, investigation may also bear significant benefits, including the discovery of new food sources or the ability to recognize and respond appropriately to dangerous or inedible objects/creatures on subsequent encounters (Lima and Dill, 1990).

Investigatory behavior has been documented in a variety of taxa (Verbeek et al., 1994, 1996; Marchetti and Drent, 2000; Mettke-Hoffman et al., 2002; Van Oers et al., 2004), including White Sharks (*Carcharodon carcharias*) (Tricas and McCosker, 1984; Strong, 1996). White sharks are responsive to a wide variety of visual, chemical, mechanical, olfactory, and electrical stimuli, all of which may play a role in mediating investigatory behavior (Strong, 1996; Hueter et al., 2004; Yopak et al., 2007; Kajiura et al., 2010; Gardiner and Atema, 2007, 2010).

White Sharks feed on a wide variety of prey items (Compagno, 2001; Martin, 2003). However, White Sharks frequently mouth or bite objects they do not consume, such as penguins (Randall et al., 1988), sea otters (Ames and Morejohn, 1980; Ames et al., 1996), and other inedible objects (Anderson et al., 1996; Collier et al., 1996). Additionally, individual White Sharks often directly approach submerged and surface-borne objects (Miller and Collier, 1981; Tricas and McCosker, 1984; Strong, 1996; Collier, 2003), but how and why White Sharks investigate novel objects in their environment are not fully understood.

The present paper describes observations of White Shark investigatory behaviors toward various floating objects, including nonconsumptive strikes on six species of seabirds at Seal Island in False Bay, South Africa, over a 13-year period. Observations of nonconsumptive strikes on seabirds are compared with those of predatory strikes on Cape Fur Seals (*Arctocephalus pusillus pusillus*) at this site. The adaptive value of White Sharks' observed behavior of biting objects they do not consume is discussed. The relative costs and benefits to a White Shark of biting edible and nonedible objects is examined, and evidence is presented that White Shark teeth function as mechanosensory structures, fostering tactile investigation.

MATERIALS AND METHODS

Seal Island is situated at the foot of False Bay, with its long axis oriented roughly north-south (Figure 8.1). The islet measures about 400 × 50 m and is centered at latitude 34.1374°S, longitude 18.5825°E. Seal Island is inhabited by about 64,000 Cape fur seals (*Arctocephalus pusillus pusillus*), which feed 12–30+ km offshore, outside the 25-km-wide mouth of False Bay, and return to the

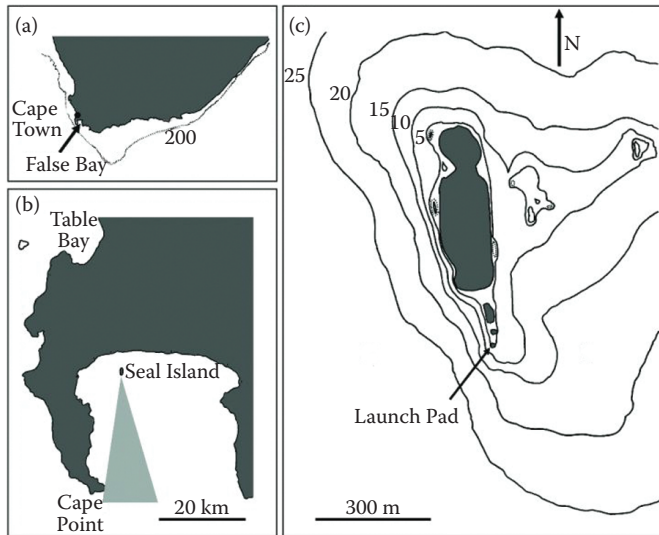


Figure 8.1 Study sites. (a) Location of False Bay, South Africa, with the 200-m depth contour indicated. (b) Location of Seal Island within False Bay, showing the primary path of pinniped movement leaving and returning to the island (gray triangle). (c) Depth contours (meters) around Seal Island.

island at irregular intervals (Martin et al., 2005). The primary pinniped entry/exit point, called the “Launch Pad,” is a small craggy outcrop located off the south side of the island (Martin et al., 2005, 2009). At Seal Island, White Shark predatory attacks on Cape fur seals occur primarily between May and August and are concentrated within 2 h of sunrise, which occurs at about 7:30 a.m. during these months (Hammerschlag et al., 2006). For further site details, see Martin et al. (2005).

Between 1997 and 2010, we scanned the waters surrounding Seal Island for White Shark strikes on live, resting seabirds. When a strike on a seabird was observed, at least two observers from the research team were dedicated to guiding our observation vessel to the location of the initial strike, where we recovered and examined bite wounds on the bird. The data recorded included species of bird, date, time, and whether the bird escaped, was killed and consumed, injured and not consumed, or killed and not consumed. Seabird identification and common names follow Sinclair et al. (1993).

Whenever observed, White Shark tactile explorations of inanimate surface-borne objects were recorded. Observational data collected included type of object, date, time, and whether the object was consumed or not.

For the purpose of examining White Shark tooth morphology, we towed behind our vessel a seal-shaped decoy made of soft rubber to elicit a strike by a shark and potentially obtain a shedding tooth. Tooth terminology follows Kent (1994) and Shimada (2002). Tooth measurements follow Chandler (1995).

RESULTS

During the study period, we documented 61 nonconsumptive strikes on six species of seabirds (Table 8.1 and Figure 8.2a and b). Species (and number of times observed in parentheses) of birds attacked but not consumed were as follows: African Penguin, *Spheniscus demersus* (3); Black-Backed Kelp Gull, *Larus dominicanus vetula* (16); Cape Cormorant, *Phalacrocorax capensis* (17); Sooty Shearwater, *Puffinus griseus* (1); Subantarctic Skua, *Catharacta Antarctica* (5); Cape Gannet, *Morus capensis* (15); unidentified bird (1); and White Breasted Cormorant, *Phalacrocorax*

Table 8.1 Descriptions of 61 Nonconsumptive Strikes by White Sharks (WS) on Six Species of Seabirds and One Consumption of a Penguin at Seal Island, South Africa (1997–2010)

Date	Time (h)	Bird Species	Remarks
July 1, 1997	0918	Cape Cormorant (<i>Phalacrocorax capensis</i>)	Shark polaris breach; bird escaped shark strike
July 7, 1999		African Penguin (<i>Spheniscus demersus</i>)	120 m; penguin killed
July 18, 1999	1235	Black-Backed Kelp Gull (<i>Larus dominicanus vetula</i>)	100 m; bird escaped strike
May 24, 2000	1050	Sooty Shearwater (<i>Puffinus griseus</i>)	Bird escaped strike
June 5, 2000	1420	Black-Backed Kelp Gull	150 m; bird escaped strike
June 21, 2000	0930	Cape Cormorant	Bird killed by shark
July 17, 2000		Subantarctic Skua (<i>Catharacta antarctica</i>)	100 m; bird escaped strike
September 3, 2000		Black-Backed Kelp Gull	Bird escaped strike
August 14, 2001	0854	Cape Cormorant	150 m; bird escaped strike
April 5, 2002		Cape Cormorant	Bird escaped strike
May 5, 2002		Black-Backed Kelp Gull	Bird escaped strike
July 21, 2002	0731	African Penguin	Kill, carcass found floating on very calm day with WS bite; shark not seen
August 20, 2002		African Penguin	150 m; bird killed and consumed (whole carcass); male shark
June 12, 2003	0927	Cape Cormorant	150 m; bird killed; carcass found with WS bite
June 13, 2003	1200	Cape Cormorant	60 m; bird escaped; shark lunged at bird at surface
June 27, 2003	903	Cape Cormorant	100 m; bird escaped; shark performed polaris breach
July 1, 2003	0923	Unidentified bird	750 m; bird escaped
July 17, 2003		Black-Backed Kelp Gull	Bird escaped; shark made single strike with upper anterior teeth; calm water, no wind, 8–10-m visibility
July 23, 2003	0959	Cape Cormorant	Dead bird found with WS bite; calm day, great visibility
July 23, 2003	1257	Black-Backed Kelp Gull	Bird escaped
July 29, 2003	1047	Cape Cormorant	Dead bird found with WS tooth marks; calm water, 16-m visibility
June 23, 2004	1044	White Breasted Cormorant (<i>Phalacrocorax lucidus</i>)	200 m; bird escaped
June 30, 2004	0902	Black-Backed Kelp Gull	200 m; shark breach; bird escaped
September 14, 2004	0932	Black-Backed Kelp Gull	250 m; shark breach; bird escaped
April 21, 2004	0732	Black-Backed Kelp Gull	200 m; shark killed bird
May 24, 2005	0732	Black-Backed Kelp Gull	Bird killed
June 16, 2005	0825	Black-Backed Kelp Gull	80 m; bird killed
June 23, 2005		White Breasted Cormorant	80 m; shark breach; bird escaped
August 23, 2005	0930	Black-Backed Kelp Gull	Bird killed by WS
September 2, 2005	0748	Cape Cormorant	100 m; shark breach; bird escaped
June 2, 2006		Cape Gannets (<i>Morus capensis</i>) (×8)	300 m; shark breach on eight birds sitting on surface; birds escaped strike
June 18, 2006	0726	Cape Gannet	600 m; polaris strike on bird

Table 8.1 (Continued) Descriptions of 61 Nonconsumptive Strikes by White Sharks (WS) on Six Species of Seabirds and One Consumption of a Penguin at Seal Island, South Africa (1997–2010)

Date	Time (h)	Bird Species	Remarks
June 23, 2006	0732	Cape Gannet	800 m; strike on bird (survived)
July 4, 2006		Cape Gannet	800 m; bird found with fatal WS bite
June, 2, 2007		Cape Cormorant group	150 m; shark surface attack on group; birds escaped
July 10, 2007		Cape Cormorant	100 m; shark breach; bird escaped
July 24, 2007	1218	Cape Cormorant	150 m; bird found with fatal WS bite
August 4, 2007		White Breasted Cormorant	100 m; dead bird found floating with fatal WS bite
August 12, 2007	0758	African Penguin	1800 m; WS strike on penguin; escaped
August 19, 2007	0722	Black-Backed Kelp Gull	50 m; WS shark fatal attack on bird
August 20, 2007	0742	Black-Backed Kelp Gull	450 m; WS fatal strike on bird
May 3, 2008		Cape Gannet	WS fatal strike on bird
May 13, 2008	0810	Cape Cormorant	100 m; WS breach; bird escaped
May 18, 2008	0830	Cape Cormorant	100 m; fatal strike
July 12, 2008	0845	Cape Cormorant	600 m; WS breach; bird escaped
July 13, 2008	0830	Subantarctic Skua (x4)	400 m; WS breach; birds escaped
July 19, 2008	0823	Black-Backed Kelp Gull	30 m; WS fatal strike
July 28, 2008	0804	Black-Backed Kelp Gull	150 m; WS breach (outcome unknown)
June 29, 2009	1604	Cape Gannet	80 m; bird found with WS bite
July 21, 2009	1544	Cape Gannet	250 m; bird found with fatal WS bite
August 2, 2010	0845	Cape Cormorant	Bird found with nonfatal shark bite

The distance from the island (in meters) is noted when possible.

lucidus (3). Nonconsumptive strikes on seabirds occurred predominantly within an hour of sunrise. We also observed a single consumption of an African Penguin (Figure 8.2c).

Twenty-six instances of White Sharks investigating floating novel objects, resulting in contact, were also observed (Table 8.2). These objects ranged in shape from spherical to conical to rectangular to irregular and in length from 20 to 250 cm. Object colors included white, yellow, blue, green, and brown. These items were composed of kayaks, apple cores, oranges, cuttlebones, foam mats, brown kelp (*Laminaria* sp.), plastic bags, mesh bags, packets, towed cameras, floats, and buoys (Table 8.2 and Figure 8.2d).

Throughout the course of the study, we towed a seal decoy on 121 occasions around the Island. On September 7, 2000 at 8:56 a.m., a 3.2-m White Shark attacked our decoy, leaving a lower left anterior tooth embedded in it. The tooth was damaged, the distal blade bearing a spall fracture that was not caused by the relatively soft material of the decoy. The tooth measured 42.4 mm in slant height and 22.9 mm in enamel height. A large nutritive pore was apparent near the centre of the lingual surface of the root, around which were scattered four smaller foramina (Figure 8.3). The root of the fresh tooth bore a distinct pink blush and, from two of the small foramina extended about 4 mm of tissue that did not resemble a blood vessel in general aspect, most notably in its apparently solid cross-section and pale yellow color. Examination of cleaned and dried White Shark teeth revealed a common pattern of a large, centrally located nutritive pores surrounded by two to five scattered small foramina (Figure 8.3). We suggest that the yellow soft material removed from the root of the tooth recovered from the decoy was nerve tissue and that the small foramina scattered near the nutritive pore in each White Shark tooth are the openings through which tiny nerves pass into the living root.

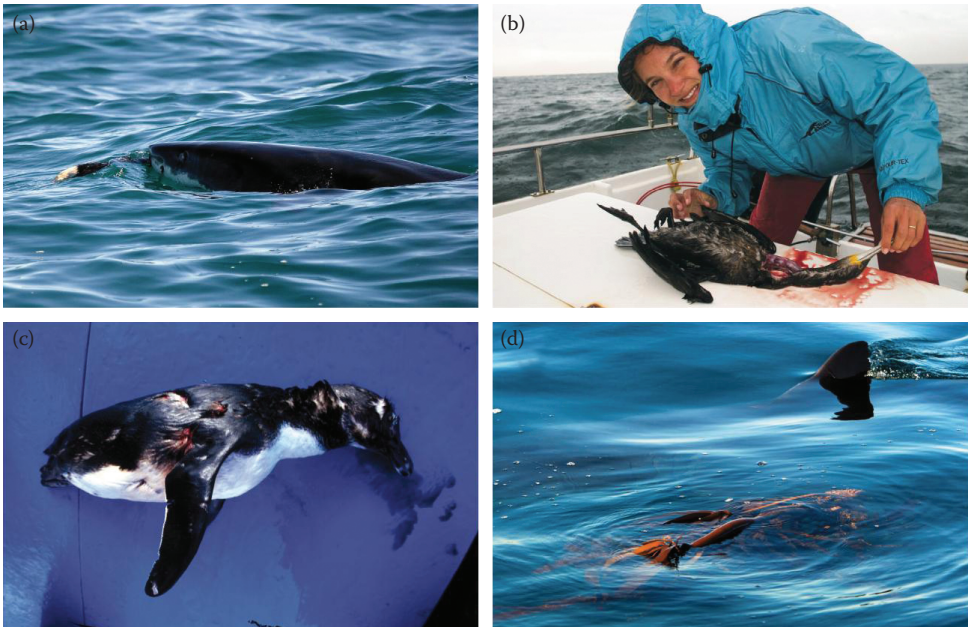


Figure 8.2 Photographic examples of (a) a White Shark performing tactile investigation of a dead seabird, which it killed but did not consume; (b) recovered carcass of a Cape Cormorant and (c) African Penguin following a nonconsumptive strike by a White Shark; and (d) a White Shark tactile investigation of Brown Kelp at Seal Island, South Africa. (Courtesy of Chris Fallows, <http://www.apexpredators.com>.)

DISCUSSION

Why White Sharks attack animals that they do not eat is perplexing. Heithaus (2004) suggested that for ambush predators such as White Sharks, attacking a nonprey item at the surface allows sharks to gather further clues as to its identity. The large number (>5,000) of natural predations by White Sharks on Cape Fur Seals at Seal Island recorded during the study period (1997–2010) provides a useful baseline for comparison against strikes on seabirds (Martin et al., 2005, 2009; Hammerschlag et al., 2006; Chapter 9, this book). Initial strikes by White Sharks on seals were typically sudden, forceful, and devastating, lasting <2 min from initial strike to full consumption (Figure 8.4). Our observed initial strikes on seabirds were similarly forceful and brief. However, during the study period, only one seabird (an African Penguin) was observed to be consumed after the initial strike, compared with 61 nonconsumptive strikes (Figure 8.2).

Klimley (1994) and Klimley et al. (1996) hypothesized that manipulation of a potential food item in its jaws enables a White Shark to assess its fat content and proposed that this species preferentially consumes blubber-rich prey, such as juvenile Northern Elephant Seals (*Mirounga angustirostris*), to fuel its elevated metabolic needs. They further proposed that nonconsumptive strikes on sea otters, seabirds, inedible objects, and humans may represent food rejection because of inadequate energy content. In support of this claim, Pratt et al. (1982) found that White Sharks appeared to feed selectively on the blubber but not the underlying muscle layers of the floating carcass of a mysticete whale. Klimley (1987) found that White Sharks consumed offered seal carcasses but rejected sheep carcasses. Similarly, Polar Bears (*Ursus maritimus*) and Leopard Seals (*Hydrurga leptonyx*) often selectively consume only the fatty layer from phocids (D. Siniff, cited in Klimley et al., 1996). The theory that White Sharks selectively consume fat-rich prey and reject low-fat prey has been cited in numerous popular and scientific works (e.g. Burgess and Callahan, 1996; Bright, 1999; Benchley, 2000).

Table 8.2 Description of 26 Investigations of Floating Objects by White Sharks (WS) at Seal Island, South Africa (1997–2010)

Date	Time (h)	Object	Remarks
June 15, 2001		20-cm white cuttlebone	Twice approached on surface and circled object before biting
June, 27, 2001	1115	Large potato chip packet	Surfaced on object before biting
July 12, 2001		Plastic packet	Approached object on surface followed by bite
July 16, 2001	1345	Blue mat (1.5 × 2.5 m)	Left bait, resurfaced 120 m away; approached, snout poked, bit, and nibbled object
July 17, 2001	1025	Buoy	Tactile investigation
August 11, 2001		Brown Kelp	Approached, bumped, and nipped object
May 30, 2002		Mesh bag (empty)	WS surfaced and bit object
July 11, 2002		Two kayaks	Approached objects, circled, bit
July 12, 2002		Yellow buoy	Approached object, poked with snout, bit
July 18, 2002		Brown Kelp	Gaped at object
July 21, 2002		Two white apple cores, orange	WS consumed apple cores; snout poked orange
June 18, 2003	1555	Plastic packet	Approached and bit object in presence of bait
July 25, 2003	0827	Brown Kelp	Broached on and bit object; may have mistaken it for group of seals moving over object at time of strike
July 25, 2003	1121	Brown Kelp	Surfaced and bit on object
August 3, 2003	1134	Yellow buoy	Surfaced and bit on object
July 7, 2004	1256	Brown Kelp	Shark surfaced on kelp
August 16, 2004	1053	Tow camera	Shark followed camera for 15 min
August 22, 2004	1240	Tow camera	Shark followed camera
July 8, 2005	1330	Brown Kelp	Visual and tactile investigation floating kelp; two more sharks followed within the hour
July 31, 2005	0825	Brown Kelp	200 m; shark circled and contacted surface kelp
June 20, 2005		Yellow buoy	Visually inspected and consumed by 3.7-m female WS
July 7, 2009	1037	White foam float	3.2-m female WS visually inspects and consumes float
June 30, 2010		Yellow buoy	4-m female consumed float
July 4, 2010	1145	Potato chip packet	3.5-m female visually inspected and nibbled package
July 12, 2010	1057	Brown Kelp	Shark visually inspected and contacted kelp
July 15, 2010	1515–1715	Floating black plastic square (1.5 × 1.5 m)	Three sharks visually inspected and bit plastic; one shark exhibited a startle response when plastic folded because of swell

The distance from the island (in meters) is noted when possible.

However, very large White Sharks routinely consume low-fat food items, such as a 4.4-m male specimen captured off Washington state that contained, in addition to a few seal remnants, teleost remains and 150 cancrid crabs (Le Mier, 1951). In the diets of three South African White Sharks examined, Hussey et al. (Chapter 3, this book) found 300, 300, and 477 Sardines (*Sardinops sagax*) in each and suggested that these feeding events were linked to the annual sardine run off the South

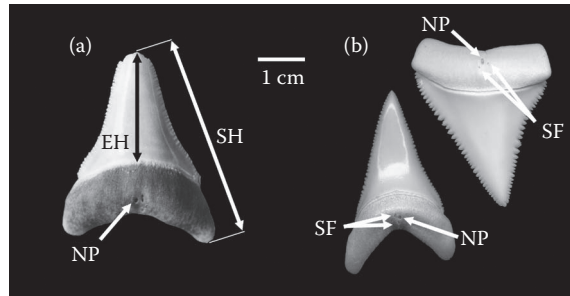


Figure 8.3 Lingual surfaces of representative White Shark teeth. (a) Lower left anterior tooth removed from a seal-shaped decoy towed at Seal Island, South Africa. (b) Upper and lower teeth from a ± 4 -m TL White Shark captured in Natal Sharks Board mesh nets set off Natal, South Africa in June 1986. EH, enamel height; NP, nutritive pore; SF, small foramina; SH, slant height; O, foramina from which putative nervous tissue was removed.



Figure 8.4 Attacks by White Sharks. (a and b) White Shark breach attack on a Cape Fur Seal at Seal Island in False Bay, South Africa. (c and d) Attacks by White Sharks on seals were forceful and devastating, lasting <2 min. from initial strike to full consumption. (Courtesy of Chris Fallows, <http://www.apexpredators.com>.)

African coast (Cliff et al., 1996; Dudley and Cliff, 2010). They also found squid, loligo squid, chiroteuthid squid, and cuttlefish in the stomachs of both small and large White Sharks. Smale and Cliff (Chapter 4, this book) repeatedly found large numbers of cephalopod beaks in the stomachs of African White Sharks.

Pop-up satellite archival transmitting tags have revealed that adult White Sharks of the north-eastern Pacific occupy an entirely pelagic habitat, called the Shared Offshore Foraging Area (SOFA), for 4–6 months of the year where they appear to exhibit vertical diving behavior indicative of active foraging (Weng et al., 2007; Domeier and Nasby-Lucas, 2008; Nasby-Lucas et al., 2009;

Chapter 12, this book). However, small cetaceans and pinnipeds are markedly absent in the SOFA, suggesting that White Sharks likely feed upon nonmammalian (low-fat) prey while occupying this habitat (Chapter 12, this book).

Based on fourteen quantitative studies of White Shark feeding biology ($n = 259$ stomachs, representing all growth stages), Cortés (1999) found that almost 75% of this species' diet consists of low-fat food categories (teleosts, cartilaginous fishes, and cephalopods), whereas only slightly more than 20% consists of marine mammals. Similarly, White Shark diet studies from South Africa (Cliff et al., 1989) and South Australia (Bruce, 1992) indicate that the majority of the diet at both localities consisted of fishes. Based on stomach content analysis of 255 South African White Sharks, Hussey et al. (Chapter 3, this book) found White Sharks consumed a large number of prey items from several functional prey categories. At Gudalupe Island, Mexico, Domeier (2009) documented a White Shark preferentially feeding on tuna bait over an adjacent seal carcass. Additionally, while conducting feeding studies on captive juvenile White Sharks, Ezcurra et al. (Chapter 1, this book) observed one individual consistently feeding on energy-poor items from an array of energy-rich prey from which the shark could have selected.

So do White Sharks at Seal Island refrain from consuming seabirds that they have already killed because the birds lack the fat needed to fuel the shark's elevated body temperatures? In nutrition experiments, fat contains 9 kilocalories per gram, whereas protein contains only 4 kilocalories per gram (Whitney and Hamilton, 1984). Thus, on a per unit mass basis, fat-rich, protein-poor foods would seem more than twice as energy-rich as protein-rich, fat-poor foods. However, animals are not bomb calorimeters. Because of recent research into the claimed weight-loss benefits of high-protein, low-fat diets, precise measurements of physiological responses in humans to both food types are available (Halton and Hu, 2004). Fat and protein servings of equivalent energy content differ greatly in postprandial thermogenesis (specific dynamic action), with protein generating 200% more heat than fat within 2.5 h of consumption (Johnston et al., 2002). Another study allowing *ad libitum* food intake found that dietary thermogenesis of protein was 17% more than that of fat 5 h after consumption (Raben et al., 2003). Thus, protein is significantly more effective than fat at maintaining elevated body temperature in humans. Gut secretion and digestion in elasmobranchs is similar to that of other vertebrates, including mammals (Holmgren and Nilsson, 1999). White Shark stomach temperature is relatively constant at about 26°C (Lowe and Goldman, 2001), and intestinal valve temperatures of other lamnid sharks are 40–56% higher than their stomach temperatures (Carey et al., 1985). Because gut physiology and operating temperatures of White Sharks are similar to those of humans, it is likely that dietary thermogenesis of fats versus proteins is also similar. Therefore, we suggest that the theory that White Sharks selectively reject low-fat foods and consume fat-rich foods to facilitate maintaining elevated body temperature is inconsistent with quantitative studies of this species' diet and with the available data on dietary thermogenesis.

We suggest that most studies of White Shark feeding are biased toward over-reportage of marine mammal remains because of (1) the relative ease of sampling White Sharks near pinniped colonies or floating whale carcasses and (2) the greater durability in the gut of marine-mammal bones and fur compared with fish bones, skin, scales, or invertebrate skeletons. Accordingly, White Sharks may consume an even higher percentage of low-fat food items than present data indicate. Thus, the diet of the White Shark may be characterized best as highly euryphagous and opportunistic locally (Chapter 3, this book). In his review of shark foraging behavior, Bres (1993) found that numerous shark species shift their diet to whatever prey is locally most abundant.

In their discussion of nonconsumptive attacks by White Sharks on African Penguins, Randall et al. (1988) refrained from speculating as to why the birds were attacked or why they were not consumed. Most of the nonconsumptive seabird strikes reported in the present study occurred during winter months under conditions of moderate to high sea chop and low ambient-light levels, including periods of intense competition among White Sharks for seals (Hammerschlag et al., 2006; Martin et al., 2009). Under these environmental conditions, seabirds may have simply been attacked

by White Sharks because they were mistaken for pinnipeds. It is also plausible that under high levels of competition, attacks on seabirds may have occurred to prevent conspecifics from usurping feeding opportunities. Unpalatable chemical (uropygial secretions) or tactile (feathers) cues exuded by seabirds may also lead White Sharks to reject and not consume seabird prey. Dense mats of feathers are likely also difficult to digest such that cost of consumption outweighs the benefits of a small meal. Similarly, Sea Otters (*Enhydra lutris*) have dense fur and secrete pungent oil from their anal glands (C. Harvey-Clark, personal communication). It has been suggested that White Sharks may reject sea otters as food because of their strong smell as well as their dense fur and its batting-like texture (Limbaugh, 1963).

White sharks at Seal Island investigated a wide variety of floating objects (Table 8.2 and Figure 8.4). These objects ranged in shape from spherical to rectangular to irregular; they ranged in size from 20 to 250 cm in length and were white, yellow, blue, and brown in color. These parameters do not closely resemble Cape Fur Seals or other prey known from South African White Sharks. In at least one case, a White Shark left bait apparently to investigate a novel object. At 1:45 p.m. on July 16, 2001, a 2.8-m White Shark had been orbiting the tuna bait at the stern of our observation vessel, when a sudden gust of wind blew from the bow a 1.2×2.5 -m pale-blue foam-rubber mat onto the water surface some 120 m away. The shark immediately dived and then reappeared a minute or so later at the surface next to the mat, where it began to repeatedly bite the mat. This lasted for 25 min. until we retrieved the mat.

So why do White Sharks frequently bite novel floating objects or creatures? Investigation of unfamiliar objects by animals can result in injury, which may negatively impact future foraging and/or reproductive success (Vermeij, 1987). Thus, animals must weigh potential benefits against potential risks when deciding whether to investigate a novel object or not. White Sharks are exceptionally large among elasmobranchs and have very few natural predators (Taylor et al., 1983; Compagno, 2001). Further, White Sharks are fast, maneuverable, well armed, and protected by a tough, armored hide that heals remarkably quickly (Reif, 1978; Kemp, 1999; Compagno, 2001; Chapter 6, this book). Thus, for White Sharks, the risks of exploring novel objects or creatures may be low. Thus, we propose that if energy cost and risk of injury are minimal, a White Shark's best strategy is to bite any novel object or creature, regardless of whether or not it proves edible.

Although much work has been done on mechanoreception in sharks, including the acoustico-lateralis system and cutaneous mechanosensitivity (Bleckmann and Hofmann, 1999), relatively less attention has been given to studying mechanoreception in shark jaws. Roberts and Witkovsky (1975) used microelectrodes to record electrical activity in peripheral branches of the trigeminal (V) nerves caused by direct mechanical deflection of the teeth and gums in two species of carcharhinoid shark (*Scyliorhinus canicula* and *Mustelus canis*). They concluded that sensory endings located in the jaws of these sharks behave as high threshold mechanoreceptors. White Sharks are members of the order Lamniformes, which is believed to be the primitive sister taxon to the carcharhinoids (Compagno, 1999). Thus, the mechanoreceptive abilities of the teeth and gums of the carcharhinoid sharks tested by Roberts and Witkovsky (1975) are likely shared by White Sharks.

White Sharks are well known to be able to protrude their jaws with astonishing dexterity (Tricas and McCosker, 1984; Martin, 2003). Moreover, our findings suggest that nerves penetrate the roots of living White Shark teeth until they are shed (Figure 8.3). The combination of likely mechanoreceptive abilities of White Shark teeth and gums, jaw protrusibility, and the innervation of the teeth and gums may provide White Sharks with tactile information from objects held in their jaws. Thus, based on our observations of White Sharks biting floating objects, we propose that teeth and gums are important sensory structures for this species. With this being said, future studies are needed to fully understand the sensory modalities employed, as well as the adaptive costs and benefits of White Shark investigation. However, White Shark jaws can do far more than gouge flesh from prey too large to swallow whole. In addition to enabling feeding, a White Shark's jaws may function as remarkably dexterous tactile sensory and manipulative structures used in investigation.

ACKNOWLEDGMENTS

For their invaluable assistance and ongoing support both in and out of the field, we thank M. Fallows, P. Jacobs, M. Bright, K. Cooper, and A. Barron. Thanks to M. Domeier, A. Gallagher, C. M. Hammerschlag, and the anonymous referees whose comments helped strengthen this chapter. For sharing data and ideas, thanks to B. Bruce of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) of Australia and C. Harvey-Clark of the University of British Columbia. Thanks also to A. E. Martin, who prepared the line figures.

REFERENCES

- Ames, J. A., and Morejohn, G. V. (1980). Evidence of white shark, *Carcharodon carcharias*, attacks on sea otters, *Enhydra lutris*. *California Fish and Game* 66: 196–209.
- Ames, J. A., Geibel, J. J., Wendell, F. E., and Pattison, C. A. (1996). White shark-inflicted wounds of sea otters in California, 1968–1992. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 309–316.
- Anderson, S. D., Henderson, R. P., Pyle, P., and Ainley, D. G. (1996). White shark reactions to unbaited decoys. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 223–228.
- Baerends, G., Beer, C. and Manning, A. (1975). *Function and Evolution in Behavior: Essays in Honor of Professor Niko Tinbergen*. Oxford, UK: Clarendon Press.
- Benchley, P. (2000). Great white sharks. *National Geographic* 197: 2–29.
- Berlyne, D. E. (1963). Motivational problems raised by exploratory and epistemic behaviour. In *Psychology: A Study of a Science, Vol. 5*. (S. Koch, ed.). New York, NY: McGraw-Hill. pp. 284–364.
- Bleckmann, H., and Hofmann, M. H. (1999). Special senses. In *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes* (W. C. Hamlett, ed.). Baltimore, MD: Johns Hopkins University Press. pp. 300–328.
- Bres, M. (1993). The behaviour of sharks. *Reviews in Fish Biology and Fishes* 3: 133–159.
- Bright, M. (1999). *The Private Life of Sharks: The Truth Behind the Myth*. London, UK: Robson Books.
- Bruce, B. D. (1992). Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. *Australian Journal of Marine and Freshwater Research* 43: 1–11.
- Burgess, G. H., and Callahan, M. (1996). Worldwide patterns of white shark attacks on humans. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 457–469.
- Carey, F. G., Casey, J. G., Pratt, H. L., Jr., Urquhart, D., and McCosker, J. E. (1985). Temperature, heat production, and heat exchange in lamnid sharks. *Memoirs of the Southern California Academy of Sciences* 9: 92–108.
- Chandler, R. (1995). *Cretaceous and Paleogene Fossils of North Carolina: A Field Guide*. Durham, NC: North Carolina Fossil Club.
- Cliff, G., Dudley, S. F. J., and Davis, B. (1989). Sharks caught in the protective nets off Natal, South Africa: 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science* 8: 131–144.
- Cliff, G., Dudley, S. F. J., and Fry, M. R. (1996). Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 351–362.
- Collier, R. S. (2003). *Shark Attacks of the Twentieth Century from the Pacific Coast of North America*. Chatsworth, CA: Scientia Publishing.
- Collier, R. S., Marks, M., and Warner, R. W. (1996). White shark attacks on inanimate objects along the Pacific Coast of North America. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 217–222.
- Compagno, L. J. V. (1999). Systematics and body form. In *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes* (W. C. Hamlett, ed.). Baltimore, MD: Johns Hopkins University Press. pp. 1–42.

- Compagno, L. J. V. (2001). *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date: Volume 2. Bullhead, mackerel, and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO species catalogue for fishery purposes, No. 1, Vol. 2. Rome: FAO.
- Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56: 707–717.
- Domeier, M. L. (2009). Experimental scavenging preference for the adult white shark, *Carcharodon carcharias*. *California Fish and Game* 95: 140–145.
- Domeier, M. L., and Nasby-Lucas, N. (2008). Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series* 370: 221–237.
- Dudley, S. F. J., and Cliff, G. (2010). Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. *African Journal of Marine Science* 32: 383–397.
- Gardiner, J. M., and Atema, J. (2007). Sharks need the lateral line to locate odor sources: Rheotaxis and eddy chemotaxis. *Journal of Experimental Biology* 210: 1925–1934.
- Gardiner, J. M., and Atema J. (2010). The function of bilateral odor arrival time differences in olfactory orientation of sharks. *Current Biology* 20: 1187–1191.
- Halton, T. L., and Hu, F. B. (2004). The effects of high protein diets on thermogenesis, satiety and weight loss: A critical review. *Journal of the American College of Nutrition* 23: 373–385.
- Hammerschlag, N., Martin, R. A., and Fallows, C. (2006). Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environmental Biology of Fishes* 76: 341–350.
- Heithaus, M. R. (2004). Predator-prey interactions. In *Biology of Sharks and Their Relatives* (J. C. Carrier, J. A. Musick, and M. R. Heithaus, eds.). Boca Raton, FL: CRC Press. pp. 487–521.
- Holmgren, S., and Nilsson, S. (1999). Digestive system. In *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes* (W. C. Hamlett, ed.). Baltimore, MD: Johns Hopkins University Press. pp. 144–173.
- Hueter, R. E., Mann, D. A., Maruska, K. P., Sisneros, J. A., and Demski, L. S. (2004). Sensory biology of elasmobranchs. In *Biology of Sharks and Their Relatives* (J. C. Carrier, J. A. Musick, and M. P. Heithaus, eds.). Boca Raton, FL: CRC Press. pp. 325–368.
- Johnston, C. S., Day, C. S., and Swan, P. D. (2002). Postprandial thermogenesis is increased 100% on a high-protein, low-fat diet versus a high-carbohydrate, low-fat diet in healthy, young women. *Journal of the American College of Nutrition* 21: 55–61.
- Kajiura, S. M., Cornett, A. D., and Yopak, K. E. (2010). Sensory adaptations to the environment: Electroreceptors as a case study. In *Biology of Sharks and Their Relatives* (J. C. Carrier, J. A. Musick, and M. P. Heithaus, eds.). Boca Raton, FL: CRC Press. pp. 393–429.
- Kemp, N. E. (1999). Integumentary system and teeth. In *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes* (W. C. Hamlett, ed.). Baltimore, MD: Johns Hopkins University Press. pp. 43–68.
- Kent, B. W. (1994). *Fossil Sharks of the Chesapeake Bay Region*. Columbia, MD: Egan Rees & Boyer.
- Klimley, A. P. (1987). Field studies of the white shark, *Carcharodon carcharias*, in the Gulf of the Farallones National Marine Sanctuary. In *Current Research Topics in the Marine Environment* (M. Croom, ed.). San Francisco, CA: Gulf of the Farallones National Marine Sanctuary. pp. 33–36.
- Klimley, A. P. (1994). The predatory behavior of the white shark. *American Scientist* 82: 122–133.
- Klimley, A. P., Pyle, P., and Anderson, S. D. (1996). The behavior of white sharks and their pinniped prey during predatory attacks. In *great white sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). San Diego, CA: Academic Press. pp. 175–191.
- Le Mier, E. H. (1951). Recent records of the great white shark, *Carcharodon carcharias*, on the Washington coast. *Copeia* 1951: 259.
- Lima, S. L., and Dill, L. M. (1990) Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- Limbaugh, C. (1963). Field notes on sharks. In *Sharks and Survival* (P. W. Gilbert, ed.). Boston, MA: D.C. Heath. pp. 63–94.
- Lowe, C. G., and Goldman, K. J. (2001). Thermal and bioenergetics of elasmobranchs: Bridging the gap. *Environmental Biology of Fishes* 60: 251–266.
- Marchetti, C., and Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour* 60: 131–140.

- Martin, R. A. (2003). *Field Guide to the Great White Shark*. Vancouver, Canada: ReefQuest Centre for Shark Research. Special Publication No. 1.
- Martin, R. A., Hammerschlag, N., Collier, R. S., and Fallows, C. (2005). Predatory behavior of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom* 85: 1121–1135.
- Martin, R. A., Rossmo, D. K., and Hammerschlag, N. (2009). Hunting patterns and geographic profiling of white shark predation. *Journal of Zoology* 279: 111–118.
- McFarland, D. (1987). Exploratory behaviour. In *The Oxford Companion to Animal Behaviour* (D. McFarland, ed.). Oxford, UK: Oxford University Press. p. 159.
- Mettke-Hoffman, C., Winkler, H., and Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108: 249–272.
- Miller, D. J., and Collier, R. S. (1981). Shark attacks in California and Oregon, 1926–1979. *California Fish and Game* 67: 76–104.
- Nasby-Lucas, N., Dewar, H., Lam, C. H., Goldman, K. J., and Domeier, M. L. (2009). White shark offshore habitat: A behavioral and environmental characterization of the eastern Pacific shared offshore foraging area. *PLoS ONE* 4: e8163.
- Pratt, H. L., Jr., Casey, J. G., and Conklin, R. B. (1982). Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York. *Fisheries Bulletin* 80: 153–156.
- Raben, A., Agerholm-Larsen, L., Flint, A., Holst, J. J., and Astrup, A. (2003). Meals with similar energy densities but rich in protein, fat, carbohydrate, or alcohol have different effects on energy expenditure and substrate metabolism but not on appetite and energy intake. *American Journal of Clinical Nutrition* 77: 91–100.
- Randall, B. M., Randall, R. M., and Compagno, L. J. V. (1988). Injuries to jackass penguins (*Spheniscus demersus*): Evidence for shark involvement. *Journal of the Zoological Society of London* 214: 589–599.
- Reif, W.-E. (1978). Wound healing in sharks: Form and arrangement of repair scales. *Zoomorphologie* 90: 101–111.
- Roberts, B. L., and Witkovsky, P. (1975). A functional analysis of the mesencephalic nucleus of the fifth nerve of the selachian brain. *Proceedings of the Royal Society of London – B* 190: 473–495.
- Shimada, K. (2002). Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). *Journal of Morphology* 251: 38–72.
- Sinclair, I., Hockey, P., and Tarboton, P. (1993). *Birds of Southern Africa*. Cape Town, South Africa: Struik.
- Strong, W. R., Jr. (1996). Shape discrimination and visual predatory tactics in white sharks. In *Great White Sharks: The Biology of Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.). Academic Press: San Diego, CA. pp. 229–240.
- Taylor, L. R., Compagno, L. J. V., and Struhsaker, P. J. (1983). Megamouth: A new species, genus, and family of lamnoid shark (*Megachasma pelagios*, family Megachasmidae) from the Hawaiian Islands. *Proceedings of the California Academy of Sciences* 43: 87–110.
- Tricas, T. C., and McCosker, J. E. (1984). Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proceedings of the California Academy of Science* 43: 221–238.
- van Oers, K., Drent, P. J., de Goede, P., and van Noordwijk, A. J. (2004). Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London – B* 271: 65–73.
- Verbeek, M. E. M., Drent, P. J., and Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* 48: 1113–1121.
- Verbeek, M. E. M., Boon, A., and Drent, P. J. (1996). Exploration, aggressive behavior and dominance in pairwise confrontations of juvenile male great tits. *Behaviour* 133: 945–963.
- Vermeij, G. J. (1987). *Evolution and Escalation: An Ecological History of Life*. Princeton, NJ: Princeton University Press.
- Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A., and Block, B. A. (2007). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* 152: 877–894.
- Whitney, E. N., and Hamilton, E. M. N. (1984). *Understanding Nutrition* (3rd edition). St. Paul, MN: West Publishing.
- Yopak, K. E., Lisney, T. J., Collin, S. P., and Montgomery, J. C. (2007). Variation in brain organization and cerebellar foliation in chondrichthyans: Sharks and holocephalans. *Brain Behavior and Evolution* 69: 280–300.

