

## CHAPTER 9

# Comparisons between White Shark–Pinniped Interactions at Seal Island (South Africa) with Other Sites in California

7c1b105e3147afedaba950ac2d96cfe9  
ebruary

**Chris Fallows**

Apex Expeditions

**R. Aidan Martin**

University of British Columbia

**Neil Hammerschlag\***

University of Miami

### ABSTRACT

The spatiotemporal patterns of nearly 2,600 predatory interactions between White Sharks and Cape Fur Seals at Seal Island, South Africa were studied. These data, in addition to previously reported data from this site, were compared against published patterns of White Shark–pinniped interactions at sites in California. In the present study, similarities between Seal Island and Californian sites identified included pinniped age class (juvenile), highest attack frequency versus distance from island (<400 m), tidal state (high), and depth range (5–50 m). However, many factors significantly affecting White Shark frequency and success rates of attack differed between Seal Island versus California sites, including seasonal distribution (winter versus autumn), mean frequency of attacks (6.7 per day versus 0.7 per day), prey capture success rate (48% versus 64%), size of attacking sharks (2.1–4.5 m versus 3.5–5.9 m), prey mass (low versus high), timing of attacks (frequency greatest early morning versus all day), wind direction (Northerly versus not significant), and light levels (low versus indiscriminate). The factors affecting White Shark predatory success have been reported from Seal Island, but not from the California sites. These similarities and differences are discussed in terms of prey characteristics and environmental factors at each site. Our results suggest that factors affecting White Shark predatory behavior and success rate are likely prey- and site-specific.

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

## INTRODUCTION

Predator-prey interactions are of central importance in ecology, with important implications for population dynamics, management, and conservation (Walters, 1997; Musick, 1999). However, natural predation is rarely documented, in part because of the inherent difficulties of observing such behavior in the wild, which is especially true for predation in the marine environment (Busse, 1980; Lind and Cresswell, 1995). Thus, how marine predators select a specific prey animal from a group of apparently similar prospects is not fully known (Strong, 1991). Understanding prey selection processes of predators incorporates the antipredatory tactics of their prey. This aspect of predator-prey interaction involving elasmobranchs with mobile prey remains poorly understood (Heithaus, 2004). White Sharks (*Carcharodon carcharias*) aggregate seasonally at pinniped colonies, where they can be observed attacking seals and sea lions at the surface (Compagno, 2001). One such site is Seal Island, in False Bay, South Africa, where White Sharks actively prey upon Cape Fur Seals (*Arctocephalus pusillus pusillus*) during winter months, with up to 42 attacks recorded on a single day (Martin et al., 2005; Hammerschlag et al., 2006). The high frequency of predatory attacks on Cape Fur Seals at Seal Island provides an exceptional opportunity to examine predator-prey interactions between an apex predator and its prey.

White Shark predation on pinnipeds has been studied extensively off California, at the Farallon Islands (Klimley et al., 1992, 1996; Pyle et al., 1996) and at Año Nuevo Island (Le Boeuf and Crocker, 1996; Klimley et al., 2001). Juvenile Northern Elephant Seals (*Mirounga angustirostris*) are the principal pinniped prey at the Farallon Islands (Ainley et al., 1981, 1985) and at Año Nuevo Island (Le Boeuf and Crocker, 1996; Klimley et al., 2001). Klimley et al. (1992) found that attacks on pinnipeds at the South Farallon Islands occur during autumn (late August to early December) at similar times and locations on consecutive days. They also found that attacks were equally distributed throughout daylight hours in a "high-risk zone," concentrated near pinniped entry and exit points, between 25 and 450 m offshore at depths of 5–50 m, with a decrease in attack frequency with increasing depth. Significantly more White Shark attacks were on juvenile pinnipeds along the coast of central California (Long et al., 1996). Frequency of White Shark attacks on Northern Elephant Seals at South Farallon Islands was greatest during high tides, possibly because competition for reduced space on the island forced concentrations of seals into the water (Anderson et al., 1996). Pyle et al. (1996) found that wind direction, air temperature, barometric pressure, swell direction, and sea surface salinity showed no significant correlation with frequency of White Shark predatory attacks at South Farallon Islands; however, attack frequency increased significantly with swell height and decreased with water clarity, factors that likely affect the ability of a pinniped to detect and respond to a stalking White Shark. Pyle et al. (1996) found that the duration of predatory attacks on pinnipeds lasted more than 5 min. White Sharks at California pinniped colonies appear to spend most of their time swimming near the bottom (Goldman and Anderson, 1999). Thus, factors affecting White Shark predatory behavior have been identified based on the Farallon Island studies, but the importance of these factors have not been compared with other sites.

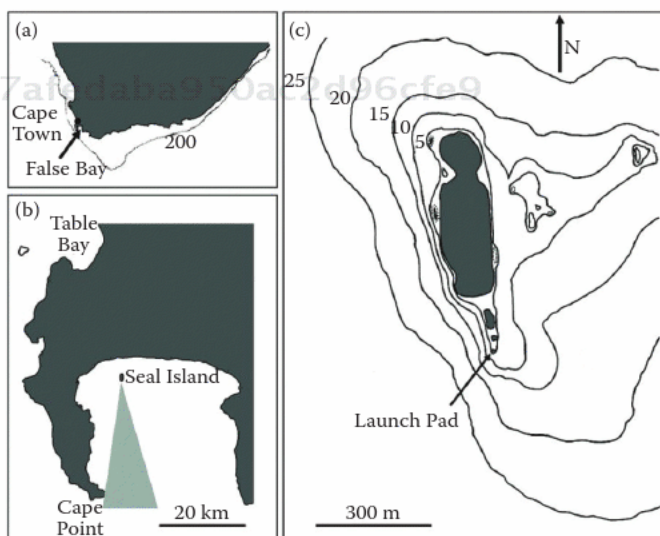
White Sharks are known to attack and consume a wide variety of pinnipeds (Compagno, 2001), but these powerful carnivorous prey are far from defenseless. It is not uncommon to see White Shark snouts and heads bearing patterns of four punctures or four parallel gashes, corresponding to the canine teeth or flipper nails, respectively, of pinnipeds (Martin et al., 2005; Domeier and Nasby-Lucas, 2007; see Figure 9.5). Active antipredator defense by pinnipeds has been reported in the form of juvenile and adult female and male Galapagos Sea Lions (*Zalophus californianus wolfebaeki*) mobbing sharks (Barlow, 1972; Eibl-Eibesfeldt, 1984; Trillmich, 1996). Similar mobbing of White Sharks by adult male Fur Seals has been reported in Australian Fur Seals (*Arctocephalus pusillus doriferus*) and Cape Fur Seals (Stewardson and Brett, 2000; Kirkwood and Dickie, 2005). In theory, mobbing may drive off a hunting shark or alert other group members to it as a potential

predator (Stewardson and Brett, 2000). Grouping can also reduce the probability that an individual pinniped is attacked, through the “selfish herd” (“dilution” or “swamping”) effect, as has been described for other animals (Hamilton, 1971; Ims, 1990). Group living may also confer predator-avoidance advantage through increased overall vigilance (Pulliam and Caraco, 1984). For example, Terhune (1985) and da Silva and Terhune (1998) reported a reduction in scanning or vigilance behavior of individual Harbor Seals (*Phoca vitulina concolor*) in large groups compared with those in small groups, but overall group vigilance increased in larger groups. Le Boeuf and Crocker (1996) suggested that Northern Elephant Seals (*Mirounga angustirostris*) may reduce their vulnerability to attack by White Sharks by minimizing surface intervals.

This chapter presents spatiotemporal patterns of more than 2,600 natural predations by White Sharks on Cape Fur Seals studied at Seal Island in False Bay, South Africa and compares these patterns with those reported from California sites. Specific attention has been paid to the significance of attack locations and prey behaviors on frequency and success rate of White Shark predation on Cape Fur Seals at Seal Island. In addition to data collected in the present study, we also incorporate data from published reports at this site. Although some similarities between White Shark–pinniped interactions at Seal Island and California sites exist, factors affecting White Shark predatory behavior and success rate appear to be prey- and site-specific.

## MATERIALS AND METHODS

Predator-prey interactions between White Sharks (*Carcharodon carcharias*) and Cape Fur Seals (*Arctocephalus pusillus pusillus*) were studied between 1997 and 2004 at Seal Island in False Bay, South Africa, and the site descriptions and methodologies described below are paraphrased from Martin et al. (2005) and Hammerschlag et al. (2006). The island is an elongated rocky islet at the foot of False Bay, centered at latitude 34.1374°S, longitude 18.5825°E, with its south end facing the 25-km-wide mouth of False Bay (Figure 9.1a). The bottom topography of Seal Island features a



**Figure 9.1** Study sites. (a) Location of False Bay, South Africa, with the 200-m depth contour displayed. (b) Location of Seal Island within False Bay, showing the main path of pinniped movement leaving and returning to the island (gray triangle). (c) Depth contours (meters) with location of the Launch Pad indicated.

steep drop-off along most of the western side of the islet, where the water depth reaches 20 m within 50 m of the island and a wide, shallow shelf along the northeastern side, where the water does not reach similar depths until 400 m or more from the island (Hammerschlag et al., 2006). Seal Island is inhabited by over 60,000 Cape Fur Seals, which typically leave the island in coordinated groups of 5–20 to feed in False Bay or up to 12–30 km or more offshore, outside of the bay, returning to the island at irregular intervals as solitary individuals or in groups of two or three (Figure 9.1b). The primary pinniped entry/exit point, called the “Launch Pad,” is a distinguishable spot seaward of a small craggy outcrop situated off the south end of the island (Figure 9.1c). Seals travel to and from the island via porpoising at the surface, where they are attacked.

Observations were made at Seal Island during every month, weather permitting, by groups of two to eight from a single 8-m Butt Cat powered by two 90-horsepower outboards from 1997 to 2000 and by teams of 4–16 from two such boats from 2001 to 2003. At least part of the research team averaged some 200 days per year surveying the island, although most predatory activity occurs from late May to late August (winter). Arrival at Seal Island was before sunrise at about 7:30 a.m., sea conditions permitting. Predations occurred at the surface on porpoising seals and were focused on the southern end of the island, close to shore (within 2 km) and primarily when seals are traveling to and from the Launch Pad (Hammerschlag et al., 2006; Martin et al., 2009). By stationing at either end of the island, a single vessel can survey approximately 270° uninterrupted to a distance of at least 3.5 km. With two vessels, nearly all the water surrounding Seal Island could be surveyed to a similar distance.

Predatory events were detected at the surface by one or more of the following:

1. White Shark breach with a seal in its jaws or a seal leaping away from its mouth (Figure 9.2a and b)
2. An abrupt change in the travel behavior of seals, switching from porpoising at the surface to zigzag evasive movements with a shark in pursuit (Figure 9.2c and d)
3. A large splash accompanied by a blood stain, oil slick, distinctive odor, and any of the following secondary indicators such as a floating seal head, excised heart and/or lungs, entrails floating on the surface or trailing from the gills of a White Shark in the vicinity (Figure 9.2e), and/or focused plunge-diving Black-Backed Kelp Gulls (*Larus dominicanis vetula*) picking up seal entrails (Figure 9.2f)

Any subsurface kills could be detected by the appearance of a blood stain at the surface and floating seal entrails. Evidence of 10 subsurface strikes by White Sharks on Cape Fur Seals were recorded during the study period but were not included in the analysis of nearly 2,600 surface attacks. When a predatory event was observed, at least two researchers from the team were dedicated to guiding our vessel to the site of the initial strike to the best of their abilities using an onboard GPS (generally within 15 m).

Predatory events were classified as unsuccessful, in which the seal escaped, or successful, in which the seal was consumed. Where it could be identified, the following data recorded at each event: time of the predatory event and duration of the predatory event scored and defined as the time from initial White Shark strike to either seal consumption or escape. For the few cases in which a seal was killed but not consumed ( $n = 10$ ), end of the predation event was calculated as the time after which the floating carcass was unattended by a shark for at least 120 s. The size of the seal group attacked was estimated as either solitary, 2–4, 5–10, or >11, and their direction of travel was categorized as either outgoing from or incoming to the island. Cape Fur Seals were divided into four classes that combine their size, maturity state, and sex:

1. Class 1: neonates [black pelt, <70 cm total length (TL)]
2. Class 2: young of the year (YOY, 70–100 cm TL)
3. Class 3: adult females and subadult males (lack of sagittal crest, 1.1–1.5 m TL)
4. Class 4: adult males (pronounced sagittal crest, >2 m TL)





**Figure 9.2** Predatory events were detected by the following: (a and b) White Shark breach with a seal in its mouth or a seal leaping away from its mouth; (c and d) a sudden change in the movements of seals, switching from directional porpoising to zigzag evasive manoeuvres with a shark in pursuit; (e) a large splash in combination with a blood stain, oil slick, distinctive odor, and a floating seal head, excised heart and/or lungs, or seal entrails floating on the surface or trailing from the gills of sharks in the immediate vicinity; and (f) highly focused plunge-diving Black-Backed Kelp Gulls (*Larus dominicanis vetula*) picking up entrails.

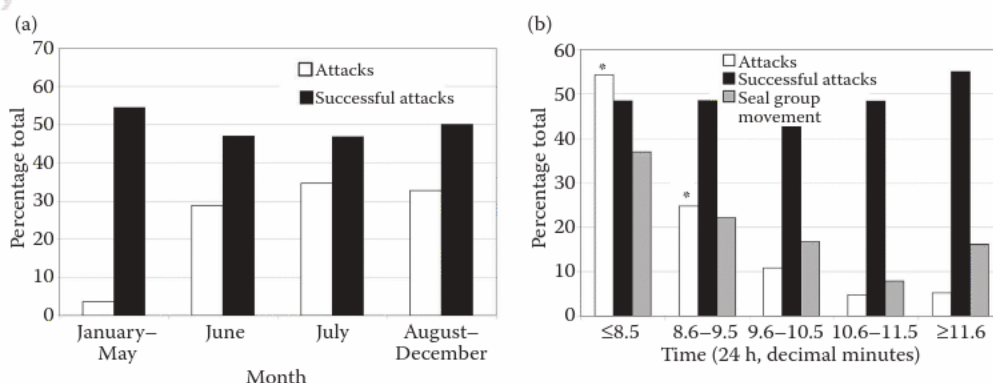
Although we are within close proximity to seals both porpoising and during attacks, our age-class categories are based on a combination of size and distinct characteristics so that we can assign seals to these categories under field conditions. During or after many predatory events, sharks were close enough (<3 m) for sufficient time to permit estimation of size. Estimations were made independently by two trained observers. Shark lengths were estimated to the nearest 0.5 m against known dimensions of the vessel and placed into one of three size categories: small (<3 m), medium (3–3.5 m), or large (>3.5 m). Shark length was only recorded when it could be estimated with confidence by both trained observers. The time and number of seal groups leaving from and returning to Seal Island per day was recorded over 21 days between 7:30 a.m. and 1:30 p.m. Seal swimming behaviors and interactions with sharks were recorded topside by videography and photography, underwater via pole camera, recorded on field data sheets, and documented via Dictaphone.

Statistical analysis was conducted following Hammerschlag et al. (2006), chi-squared analysis was used to compare the frequency of observed attacks versus expected if attacks were random with respect to seal availability. The expected values were calculated by multiplying the proportion of seals available by the total number of attacks on them. For example, the expected number of attacks on different seal age classes if random with respect to their availability was calculated by multiplying the proportion of seals of the different age classes by the total number of attacks on all seals. Data on White Shark attack success with respect to month, time of day, seal group size, age class, seal movement relative to the island, and shark size were compared using a contingency table and chi-squared analysis. Each variable under investigation was recorded only when it could be clearly identified. Because of a lack of all factors being identified at each predatory event, interactions could not be analyzed using applications of multivariate analysis and/or generalized linear models for examining probability of success.

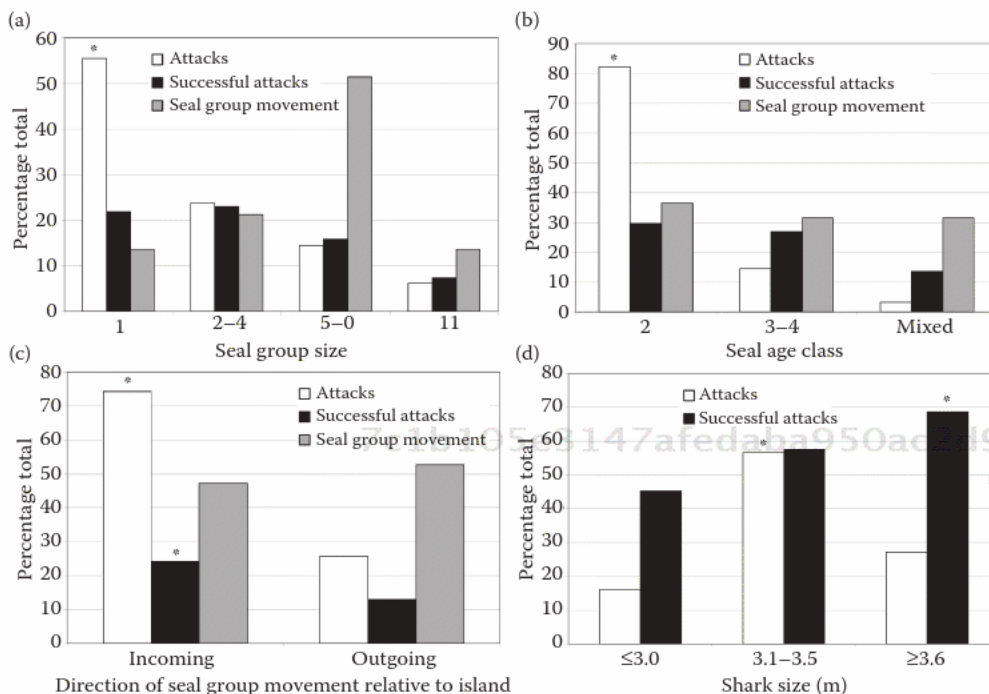
Published data by Hammerschlag et al. (2006) on environmental factors affecting White Shark attack frequency and success rate at Seal Island were incorporated in the discussion of this paper. These factors included: wind direction and speed, tidal height, ocean depth, month of the year, and light intensity.

## RESULTS

Between 1997 and 2004, a total of 2,546 predator-prey interactions between White Sharks (*Carcharodon carcharias*) and Cape Fur Seals (*Arctocephalus pusillus pusillus*) were documented. Predations peaked from June through August; success rates were not significantly different between months ( $n = 2507$ ,  $p > 0.284$ ; Figure 9.3a). Attacks occurred during all daylight hours, but frequency of predations at different times were nonrandom and were influenced by seal availability ( $n = 282$ ,  $p < 0.001$ ; Figure 9.3b). The frequency of attacks was significantly higher within an hour of sunrise, before 8:30 a.m. The second highest frequency of attack occurred between 8:30 and 9:30 a.m., followed by between 9:30 and 10:30 a.m. ( $n = 1948$ ,  $p < 0.001$ ). The success rate did not differ with time of day ( $n = 2482$ ,  $p > 0.213$ ). The group size of seals attacked ranged from 1 to at least 15, but were nonrandom, with most attacks on solitary seals ( $n = 436$ ,  $p < 0.001$ ; Figure 9.4a). Although not significant ( $n = 436$ ,  $p < 0.22$ ), the success rate showed a decreasing trend with increasing seal group size. Seals representing all size classes except Class 1 were attacked, but predations occurring on



**Figure 9.3** (a) Percentage of total ( $n = 2507$ ) and successful ( $n = 1207$ ) predatory attacks by White Sharks on Cape Fur Seals versus months. (b) Percentage of total ( $n = 2482$ ) and successful ( $n = 1194$ ) attacks by White Sharks on Cape Fur Seals and percentage of total seal group movement about the island ( $n = 644$ ) versus time of day. Significance is indicated with an asterisk; see "Results" for further details.



**Figure 9.4** (a) Percentage of total ( $n = 436$ ) and successful ( $n = 89$ ) predatory attacks by White Sharks on Cape Fur Seals and percentage of total seal group movement about the island ( $n = 103$ ) versus seal group size. (b) Percentage of total ( $n = 1132$ ) and successful ( $n = 326$ ) attacks by White Sharks on Cape Fur Seals and percentage of total seal group movement about the island ( $n = 41$ ) versus seal age class. (c) Percentage of total ( $n = 390$ ) and successful ( $n = 83$ ) attacks by White Sharks on Cape Fur Seals and percentage of total seal group movement about the island ( $n = 645$ ) versus seal travel direction. (d) Percentage of total ( $n = 669$ ) and successful ( $n = 392$ ) predatory attacks by White Sharks on Cape Fur Seals versus size of attacking shark. Significance is indicated with an asterisk; see “Results” for further details.

different seal age classes was not random ( $n = 1132$ ,  $p < 0.001$ ) with significantly more attacks on Class 2 seals than any other size class ( $n = 1008$ ,  $p < 0.001$ ; Figure 9.3b). Although not significant, the success rate showed a decreasing trend with attacks occurring on increasing seal age class ( $n = 1132$ ,  $p < 0.085$ ). Although both incoming and outgoing seals were attacked, the frequency of predations occurring on incoming versus outgoing seal groups was significantly different from random with respect to their availability ( $n = 390$ ,  $p < 0.001$ ; Figure 9.4c). Frequency ( $n = 287$ ,  $p < 0.001$ ) and success rate ( $n = 390$ ,  $p < 0.019$ ) were significantly higher on incoming seals (Figure 9.4c). Size of attacking sharks ranged from 2.1 to 4.5 m; however, 3.1–3.5-m sharks were responsible for significantly more attacks than any other shark size category ( $n = 632$ ,  $p < 0.001$ ), whereas sharks larger than 3.6 m possessed significantly higher success rates ( $n = 669$ ,  $p < 0.001$ ; Figure 9.4d).

## DISCUSSION

White Shark predation at Seal Island occurs during the winter, peaking from late June to early August, at a time in which YOY Cape Fur Seals have just finished being weaned, have a thick layer of insulating blubber but limited energy stores, and are starting to forage away from Seal Island for the first time (Martin et al., 2005). The seals are likely targeted by White Sharks because they are small, inexperienced, have undeveloped swimming and diving abilities, and are probably easier



to overpower and consume than older, larger seals (Le Boeuf et al., 1982; Brodie and Beck, 1983; Ainley et al., 1985; Le Boeuf and Crocker, 1996). Seals moving about Seal Island range in size and weight from yearlings (70 cm TL and 4.5 kg) to adult bulls (>200 cm TL and 360 kg) (Jefferson et al., 1993; E. Keith, personal communication). Cape Fur Seals possess strong claws and teeth; in many predatory events, seals bite and scratch sharks, even if grasped within the latter's jaws (Figure 9.5a–c). Large seals possess significant mass and represent a challenge, if not a danger, to any pursuing shark. Investigations of shark predation on Cape Fur Seals from the Eastern Cape of South Africa by Stewardson (1999) showed that a large number of adults, as compared with juvenile seals, had old bite wounds, suggesting that predatory attacks on older, more experienced, seals may be less successful than on younger seals.

Although Cape Fur Seals are available in the waters surrounding Seal Island from dawn to at least early afternoon, the documented increase in frequency and success of White Shark predation



**Figure 9.5** (a and b) Cape Fur Seal biting a White Shark. (c) Cape Fur Seal clawing a White Shark. Injuring may cause shark to release seal or otherwise abort attack. (d) Swimming in large groups provides shared vigilance responsibilities, which increases probability of predator detection at reduced costs. (e) A seal swimming upside down within a porpoising group to maintain subsurface shared vigilance. (f) Groups of seals leave the island in coordinated groups traveling via rapid low porpoising (3+ body lengths/second). [(a–e) Courtesy of Chris Fallows, <http://www.apexpredators.com>; (f) courtesy of Neil Hammerschlag, <http://www.neilhammer.com>.]



during the early mornings, within an hour of sunrise, is likely due to low light conditions (Martin et al., 2005). Hammerschlag et al. (2006) concluded that during scotopic conditions at Seal Island, a seal's ability to detect a hunting shark is compromised, whereas White Sharks are at a visual and tactical advantage and as such benefit from higher success rates. Preliminary research indicates a smaller secondary daily peak in predation frequency occurs during dusk. Interestingly, on days that are overcast, predation continues throughout the day, rather than attenuating at midday (Fallows et al., unpublished data). For example, on August 8, 2003, 12 predatory attacks were recorded between 9:30 a.m. and 1:30 p.m., while there was little available ambient light all day because of an overcast sky. At the Farallones, attacks occur during all daylight hours; however, Pyle et al. (1996) reported a significant increase in nonpredatory sighting (including surfacing and breaches) of sharks at Southeast Farallon Island when cloud cover was high.

White Sharks appear to target solitary seals, which are unable to share vigilance or defensive duties and thus may be more vulnerable to ambush attacks by White Sharks than larger groups maintaining shared vigilance (Figure 9.5d and e). Large seal groups experience fewer attacks than solitary individuals, probably because grouping provides early warning of approaching danger and confuses sharks trying to select and attack a particular group member (Caro and Fitzgibbon, 1992; Savino and Stein, 1982). There are no reports from the Farallones showing that single or small groups of seals travelling about the islands are attacked more frequently than large groups of seals (Le Boeuf and Crocker, 1996).

Differences in swimming behavior, physical condition, and vigilance capabilities of seals returning to versus leaving from the island likely resulted in the documented difference in attack frequency and success. When leaving the island, Cape Fur Seals travel in large coordinated groups, locomoting via low porpoising at high speeds in the direction of the mouth of the bay, increasing shared subsurface vigilance (Figure 9.5f). Cape Fur Seals spend an average of 2.3 days at sea foraging (David and Rand, 1986), and YOY seals often return to the island as lone individuals or in small groups that are unable to benefit from shared vigilance and are likely also tired and affected by postprandial torpor, which may further decrease vigilance and make them more susceptible to attack (Martin et al., 2005). No comparison of attacks on incoming versus outgoing seals has been reported from the Farallones. Although White Sharks appear to target individual or small groups of seals returning to Seal Island, it should be noted that periods occur during which most seals return to the island in larger groups, and attack frequency on such groups increases, which is likely a reflection of prey availability.

Between 1998 and 2003, length range of attacking sharks at Seal Island ranged from 2.2 to 4.6 m, whereas at the Farallon Islands, sharks observed feeding between 1988 and 1992 ranged from 3.46 to 5.86 m. The occurrence of larger sharks feeding on seals in California sites, compared with Seal Island may be related to differences in pinniped prey size and a sharks' subsequent ability to incapacitate and subjugate prey accordingly. Northern Elephant Seals at the Farallones are massive (30–2200 kg). In comparison, Cape Fur Seals at Seal Island are relatively small (4.5–360 kg) (Jefferson et al., 1993; E. Keith, personal communication). It is logical that small sharks (<4 m) probably cannot subjugate large Elephant Seals; however, it stands to reason that larger sharks (>5 m) should still visit Seal Island to predate on relatively small Cape Fur Seals. The reason that latter is not observed may be related to locomotor performance of both predators and prey. Our data suggest that a 1.1-m-long Cape Fur Seals can reverse direction in about the same amount of time as a 3.5-m-long White Shark but in only 10–35% the distance. Thus, during secondary pursuit of a Cape Fur Seal by a White Shark, superior agility favors the former (Fallows et al., unpublished data). Thus, the lack of large (>5 m) White Sharks observed hunting at Seal Island may be because it is both difficult and energy-inefficient to leap out of the water in pursuit of an agile small prey. Further evidence to support this hypothesis comes from data collected when whale carcasses have been found at Seal Island. During the peak of the hunting season (May–August), the average shark size at Seal Island is 3.5 m, with sharks in excess of 4 m being a relatively rare occurrence, comprising 11% of the population observed (Fallows et al., unpublished data). However, during the three occasions

that a whale carcass was found at Seal Island, in less than 24 h, we have observed over two dozen White Sharks feeding on the carcasses, mostly animals exceeding 4 m, including individuals over 5 m. The speed at which large White Sharks came to feed on the carcasses leads us to hypothesize that larger sharks are relatively nearby but choose not to hunt Cape Fur Seals. Over the course of 13 yrs., we have documented numerous individuals returning to feed at Seal Island on an annual basis, but when they grow in excess of 4 m, they disappear. For example, we first documented a female White Shark in 1997, measuring 2.5 m. This individual returned to the island annually, until 2004, when the shark measured 4.2 m in length. This shark has yet to return over the past 6 yrs. (Fallows et al., unpublished data). One slight exception to this general pattern was a large female that was first observed at 2.9 m, which grew to over 5 m in a period of 10 yrs. Upon reaching 4.2 m, she only returned to Seal Island every second year up until 2008, after which she never seen again at the island. With this being said, we cannot discount the possibility that size of sharks at these sites may be independent from the size of their prey. Particularly, emerging evidence suggests that large, sexually mature White Sharks in the eastern Pacific are aggregating at seal rookeries to mate (Chapter 11, this book).

Similarities and differences in White Shark–pinniped interactions at Seal Island and the Farallon Islands are summarized in Table 9.1. Similarities between the two sites include most frequently

Table 9.1 A Comparison of Factors Affecting Predation at Seal Island and the Farallon Islands

Factors	Seal Island	Farallon Islands	Similar
Frequency of attacks	High (6.68 per day)	Low (0.7 per day) (Klimley et al., 1992)	No
Mean predatory success rate	48%	64%*	Yes
Time of year in which attack frequency is highest	Winter (June to August)	Autumn (August to December) (Klimley et al., 1992)	No?
Time of day in which attack frequency is highest	Early morning (7:30–10:30 a.m.)	Frequency is high all day (Klimley et al., 1992)	No
Prey age class on which attack frequency is highest	Juvenile	Juvenile (Ainley et al., 1981, 1985; Long et al., 1996)	Yes
Prey mass	Low (4.5–360 kg)	High (30–2200 kg)	No
Location of attack relative to the island in which attack frequency is highest	Entry and exit points on southern side of Seal Island	All around island (Klimley et al., 1992)	No
Distance from island where attack frequency is highest	Near island (<400 m) (Martin et al., 2005; Hammerschlag et al., 2006)	Near island (<400 m) (Klimley et al., 1992)	Yes
Size of shark responsible for the highest frequency of attacks	Small (3.1–3.5 m TL)	Large (3.46–5.86 m TL)	No
Tidal height during which attack frequency is highest	High (>1500 cm above mean sea level) (Hammerschlag et al., 2006)	High (Anderson et al., 1996)	Yes
Depth range of in which attacks take place	Deep (5–46 m) (Hammerschlag et al., 2006)	Deep (5–50 m) (Klimley et al., 1992)	Yes
Wind direction in which attack frequency is highest	Northerly (Hammerschlag et al., 2006)	Not significant (Pyle et al., 1996)	No
Affect of light levels on attack frequency	Highest during low light levels (0–200 $\mu$ E) (Hammerschlag et al., 2006)	Occur during all light levels	No

\* Methodology may result in an under-representation of failed predation by White Sharks on juvenile elephant seals. Klimley et al. (1992) observed predatory events from a tower 102 m above sea level, where attention was first drawn to predatory attack by the appearance of blood, an oil slick, or an explosive splash where the initial bite was not usually seen (Ainley et al., 1981, 1985; Klimley, 1994; Klimley et al., 1996), and thus they were more likely to notice successful predations.

attacked prey age class (juvenile), most frequent attack distance from the island (<400 m), most frequent attack depth range (<50 m), and most frequent attack tide state (high). Juvenile prey are naïve and have less-developed defensive capabilities (diving and fighting) and thus may require less effort for a predator to subjugate. Distance from the island and depth range are inherently linked, and tide state also affects depth at a given distance from shore. These variables may reflect prey availability, which is greatest close to the island and when haul-out space is reduced (Anderson et al., 1996; Hammerschlag et al., 2006). Differences in such interactions at Seal Island and the Farallones include attack frequency (high versus low, respectively), mean predatory success rate (48% versus 64%), most frequent attack time of day and light levels (dawn versus all day), peak attack season (winter versus autumn), most frequent prey mass and shark length (small versus large, for both), and most frequent attack wind direction (westerly versus no significant difference). Differences in attack frequency may be attributable to concentration of prey near the Launch Pad at Seal Island compared with lack of such an aggregating point at the Farallones. Differences in success rate may not be significant or may reflect a logistically imposed bias toward conspicuous successful attacks at the Farallones, where predations events are typically detected by the appearance of blood, an oil slick, or an explosive splash and are spotted from atop a 102-m-tall observation point (Klimley et al., 1992). Time of day and light levels are causally related. Differences between Seal Island and Farallones may reflect relative heights of these islands, the former being low and the latter being high, thus casting a directional shadow that may prolong shark crypsis within its influence. Further data from the Farallon Islands are needed to test this idea. Differences in prey mass and attacking-shark size may be related, because it is unlikely that a 2-m White Shark could subjugate a 1.5-m Northern Elephant Seal pup as reliably as it could a 60-cm Cape Fur Seal pup. Differences in the significance or nonsignificance of wind direction may reflect the fact that Seal Island is located at the foot of False Bay, so northerly winds transport surface-borne scents seaward, whereas the Farallones are isolated offshore islands, essentially surrounded by open ocean on all sides.

The present study suggests that predation at Seal Island is significantly affected by factors that influence a shark's ability to encounter, ambush, and subjugate its pinniped prey and its prey's ability to detect, avoid, and injure its predator as proposed by Hammerschlag et al. (2006). Specific factors affecting the frequency of White Shark predation at Seal Island (prey age class, distance from island, tidal height, and depths at which attacks range) are similar to those identified at the Farallon Islands, off California; however, most (time of year, time of day, prey group size, prey mass, location of attacks relative to the island, distance from island, depth, wind direction, light intensity, and shark size) are different or have not been reported. Factors significantly affecting predatory success rate were identified at Seal Island (location of attacks relative to island, distance from island, seal direction of travel, tidal height, light intensity, and shark size); factors significantly affecting White Shark predatory success have not been reported from the Farallones. Therefore, factors affecting White Shark predatory behavior and success rate are likely prey- and site-specific.

## ACKNOWLEDGMENTS

We would like to thank M. Fallows for her ongoing support, tremendous help, skill in field observations, data recording, and sensitive boat handling, without which most of this project could not have been accomplished. We would also like to thank R. Lawrence for his ongoing efforts to help in data collection and also for his respect of the area as a sensitive ecosystem. Thanks also to R. Strong for helping in the initial phases of setting up methodology for data collection as well as many of the film crews, including the BBC, Discovery, National Geographic, and many others who have allowed us to review footage shot with us and confirm observed behavior. We thank our corporate sponsors Canon South Africa and Fuji South Africa, YSI Environmental, Oregon Scientific, Li-Cor Biosciences, and Ben Meadows for generous donation of environmental sensor equipment. Thanks



to all volunteer research assistants during the study period. Thank you to R. Farre, S. Gildenhuys, and the South African Navy: Hydrographic Office via the Institute for Maritime Technology for providing hydrographical data.

## REFERENCES

- Ainley DG, Henderson RP, Huber HR, Boekelheide RJ, Allen SG, McElroy TL (1985) Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *Mem South Calif Acad Sci* 9: 109–122.
- Anderson SD, Klimley AP, Pyle P, Henderson RP (1996) Tidal height and white shark predation at the Farallon Islands, California. In: Klimley AP, Ainley DG (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 275–279.
- Ainley DG, Strong CS, Huber HR, Lewis TJ, Morrell SJ (1981) Predation by sharks on pinnipeds at the Farallon Islands. *Fish Bull* 78: 941–945.
- Barlow GW (1972) A paternal role for bulls of the Galapagos sea lion. *Evolution* 26: 307–310.
- Brodie P, Beck B (1983) Predation by sharks on the grey seal (*Halichoerus grypus*) in eastern Canada. *Can J Fish Aquat Sci* 40: 267–271.
- Busse C (1980) Leopard and lion predation upon chacma baboon living in the Moremi Wildlife Reserve. *Botswana Notes Rec* 12: 15–21.
- Caro TM, Fitzgibbon CD (1992) Large carnivores and their prey: The quick and the dead. In: Crawley MJ (ed), *Natural enemies: The population biology of predators, parasites and diseases*. Blackwell Scientific Publications, London. pp. 117–142.
- Compagno LJ (2001) Sharks of the world. *FAO species catalogue for fishery purposes*, No. 1, Vol. 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes, and Orectolobiformes). FAO, Rome.
- da Silva J, Terhune JM (1988) Harbour seal grouping as an anti-predator strategy. *Anim Behav* 36: 1309–1316.
- David JHM, Rand RW (1986) Attendance behavior of South African fur seals. In: Gentry RL, Kooyman GL (eds), *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ. pp. 126–141.
- Domeier ML, Nasby-Lucas N (2007) Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Mar Biol* 150: 977–984.
- Eibl-Eibesfeldt I (1984) The Galapagos seals: Part 1. Natural history of the Galapagos sea lion (*Zalophus californianus wollebaek*, Sivertsen) In: Perry R (ed), *Key environments: Galapagos*. Pergamon Press, Oxford, UK. pp. 207–214.
- Goldman KJ, Anderson SD (1999) Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environ Biol Fish* 56: 351–364.
- Hamilton WD (1971) Geometry of the selfish herd. *J Theor Biol* 31: 295–311.
- Hammerschlag N, Martin RA, 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. *Environ Biol Fish* 76: 341–350.
- Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds), *Biology of sharks and their relatives*. CRC Press, Boca Raton, FL. pp. 488–512.
- Ims RA (1990) On the adaptive value of reproductive synchrony as a predator swamping strategy. *Am Nat* 136: 485–498.
- Jefferson TA, Leatherwood S, Webber MA (1993) *Marine mammals of the world*. FAO species identification guide. FAO, Rome.
- Kirkwood R, Dickie J (2005) Mobbing of a great white shark (*Carcharodon carcharias*) by adult male Australian fur seals (*Arctocephalus pusillus doriferus*). *Mar Mamm Sci* 21: 336–339.
- Klimley AP (1994) The predatory behaviour of the white shark. *Am Sci* 82: 122–133.
- Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* 1992: 680–690.
- Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Sommerer SV, Kelly JT (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology* 138: 617–636.
- Klimley AP, Pyle P, Anderson SD (1996) Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 365–373.

- Le Boeuf BJ, Crocker DE (1996) Diving behavior of elephant seals: Implications for predator avoidance. In: Klimley AP, Ainley DG (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 193–205.
- Le Boeuf BJ, Riedman M, Keyes RS (1982) White shark predation on pinnipeds in California coastal waters. *Fish Bull* 80: 891–895.
- Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. *Behav Ecol* 16: 945–956.
- Long DJ, Hanni KD, Pyle P, Roletto J, Jones RE, Bandar R (1996) White shark predation on four pinniped species in central California waters: Geographic and temporal patterns inferred from wounded carcasses. In: Klimley AP, Ainley DG (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 263–274.
- Martin RA, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J Mar Biol Ass UK* 85: 1121–1135.
- Martin RA, Rossmo DK, Hammerschlag N (2009). Hunting patterns and geographic profiling of white shark predation. *J Zool* 279: 111–118.
- Musick JA (1999) Ecology and conservation of long-lived marine animals. *Am Fish Soc Symp* 23: 1–10.
- Pulliam HR, Caraco T (1984) Living in groups: Is there an optimal group size? In: Krebs R, Davies NB (eds), *Behavioural ecology*, 2nd ed. Blackwell Scientific, Oxford, UK. pp. 122–147.
- Pyle P, Anderson SD, Klimley AP, Henderson RP (1996) Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. In: Klimley AP, Ainley DG (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 281–291.
- Savino JF, Stein RA (1982) Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. *Trans Am Fish Soc* 11: 255–266.
- Stewardson CL (1999) Preliminary investigations of shark predation on Cape Fur seals *Arctocephalus pusillus pusillus* from the Eastern Cape coast of South Africa. *Trans R Soc S Afr* 54: 91–203.
- Stewardson CL, Brett M (2000) Aggressive behaviour of an adult male Cape fur seal (*Arctocephalus pusillus pusillus*) towards a great white shark (*Carcharodon carcharias*). *Afr Zool* 35: 147–150.
- Strong WR (1991) Instruments of natural selection: How important are sharks. In: Gruber SH (ed), *Discovering sharks*. American Littoral Society, Highlands, NJ. pp. 70–73.
- Terhune JM (1985) Scanning behavior of harbor seals on haul-out sites. *J Mamm* 66: 392–395.
- Trillmich F (1996) Parental investment in pinnipeds. *Adv Study Behav* 25: 533–577.
- Walters C (1997) Challenges in adaptive management of riparian and coastal ecosystems. *Conserv Ecol* 1:1 (<http://www.consecol.org/vol1/iss2/art1>).