

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

Neil Hammerschlag · R. Aidan Martin ·
Chris Fallows

Received: 14 November 2005 / Accepted: 20 March 2006
© Springer Science+Business Media B.V. 2006

Abstract Effects of environmental factors on frequency and success rate of 2,546 natural predatory attacks by white sharks, *Carcharodon carcharias*, on Cape fur seals, *Arctocephalus pusillus pusillus*, were studied over an 8-year period at Seal Island, South Africa. Attacks occurred primarily during winter months (June–August). Attack frequency increased significantly during northerly winds, during high tides, and within 400 m of the island, but predatory success rate decreased with proximity to the island. Attacks occurred over a depth range of 5–31 m, with significantly more occurring at depths of 26–30 m. Attack frequency and success rate increased sig-

nificantly at low light levels. These results are compared with published effects of environmental factors on white shark predation frequency at the Farallon Islands, California, and discussed in terms of the Predation Cycle. Suggestions for future work at this site are offered.

Keywords Elasmobranch · Behavior · Sensory biology · Predation cycle · Ambush · Attack

Introduction

Predation is affected by the environmental conditions under which it occurs. Interactions between a predator and its prey are shaped by their respective sensory capabilities. Sensory performance features two interacting scales: sensitivity, the minimum detectable stimulus, and acuity, discrimination of stimulus characteristics, such as location and type (Hueter et al. 2004). Both sensitivity and acuity of sensory systems depend upon the propagation properties of the transmitting medium, signal strength, and background noise (see MacLeish 1980 for a review of sensory biology of marine animals). Predators and their prey often have different sensory capabilities, with discrete strengths and weaknesses that are called into play within a predatory event (Ellis 1986). A shark's ability to detect and approach prey and the latter's ability to avoid attack and

N. Hammerschlag (✉)
Pew Institute for Ocean Science, Rosenstiel School of
Marine and Atmospheric Science, University of
Miami, Miami, FL 33149, USA
e-mail: nhammerschlag@rsmas.miami.edu

R. A. Martin · N. Hammerschlag
ReefQuest Centre for Shark Research, 595 Burrard
Street, P.O. Box 48561, V7X 1A3 Vancouver, BC,
Canada

R. A. Martin
Fish Museum, Zoology Department, University of
British Columbia, 6270 University Boulevard, V6T
1Z4 Vancouver, BC, Canada

C. Fallows
Apex Expeditions, 14 Thibault Walk, Marina Da
Gama, 7945 Cape Town, South Africa

subjugation are likely affected by environmental factors such as water clarity, ocean depth, tidal height, ambient light levels, current direction and speed. Activity peaks of predators should be correlated with periods when environmental and biological factors are optimal for exploitation of a selected prey item (Rogers et al. 1984; Sundström et al. 2001; Heithaus 2004). Thus, understanding the relative importance of environmental factors to predatory frequency and success is an important component of the sensory ecology of both sharks and their prey.

The Predation Cycle is usually divided into five phases: detection, approach, attack, subjugation, and consumption (Endler 1986). For sharks, least is known about the earliest stages of the Predation Cycle as natural predation by sharks is seldom observed in the wild (Myrberg 1987; Klimley et al. 1992; Bres 1993).

The white shark, *Carcharodon carcharias*, is an expedient species to use as a subject to study shark predation, due to the relative ease with which it can be observed attacking and feeding upon pinnipeds at the surface, especially near rocky islands where they aggregate (Ainley et al. 1981; 1985; Klimley et al. 1992; 1996; 2001). White sharks may detect pinniped haul-out sites by their characteristic odors (Strong et al. 1992). Demski and Northcutt (1996) found that olfactory bulbs of the white shark comprise 18% of total brain mass, the largest proportion of any shark measured to date, suggesting that scent detection is of great importance to these predators. Although other sensory modalities may come into play, individual pinnipeds at the surface are likely detected visually (Strong 1996). Gruber and Cohen (1985) found that the white shark possesses a duplex retina with a low rod-cone ratio (4:1) well suited to acute photopic vision and concluded that this species is primarily a diurnal hunter. White sharks frequently prey upon Cape fur seals, *Arctocephalus pusillus pusillus*, at haul-out sites off southern Africa (Stewardson 1999). Cape fur seals at the surface appear to detect white sharks visually, abruptly suspending travel behavior to assume a head-down posture and engage in subsurface scanning (Martin et al. 2005). Visual acuity and discrimination in Cape fur seals is very good, about 6 min

of arc and difference ratios as small as 1:1.19, respectively (Busch and Dücker 1987). Martin et al. (2005) suggested that under low light conditions, white sharks hunting near the bottom may have a visual and tactical advantage over Cape fur seals at the surface. Thus, abiotic factors that affect chemoreception and vision likely affect white shark–Cape fur seal predator–prey dynamics. Other abiotic factors, such as proximity to pinniped haul-outs, distance from shore or safety, and season also likely affect white shark predatory frequency and success rate.

White shark-pinniped predator-prey dynamics have been studied off California and some environmental factors affecting frequency of attack have been identified. Klimley et al. (1992) found that attacks on pinnipeds at Southeast Farallon Island (SEFI) occurred during autumn (August to early December), clustered at similar times and locations on consecutive days. 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 on pinnipeds at SEFI. Attacks were clustered in a “high risk zone” near pinniped entry and exit points, between 25 and 450 m from shore at depths of 5–50 m, with a decrease in attack frequency with increasing depth (Klimley et al. 1992). Frequency of attacks on northern elephant seals, *Mirounga angustirostris*, at SEFI is greatest during high tides, possibly because competition for reduced haul-out space forces concentrations of seals into the water (Anderson et al. 1996). Attack frequency increased significantly with swell height and decreased with water clarity, factors which likely affect the ability of a pinniped to detect and respond to an approaching or attacking white shark (Pyle et al. 1996). Klimley et al. (1992) found that attacks on pinnipeds occurred throughout daylight hours at SEFI; however, Klimley et al. (2001) reported circumstantial evidence of nocturnal white shark predation on northern elephant seals at Año Nuevo Island. Overall predatory success rate of white shark attacks on pinnipeds at SEFI was found to be 64% (Klimley et al. 1992), but environmental factors affecting predatory success were not evaluated for either SEFI or Año

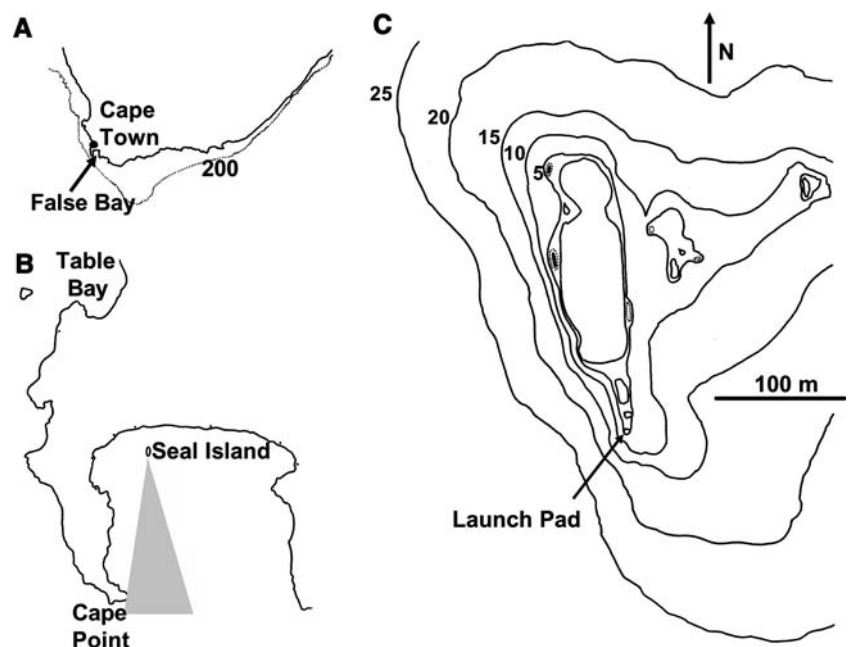
Nuevo Island. Predatory behavior of white sharks has also been studied at Seal Island in False Bay, South Africa by Martin et al. (2005), who concluded that predation is a tactically fluid event that is probably influenced by local environmental conditions. However, they did not evaluate how environmental factors affected white shark predatory success.

The present paper extends previous work at Seal Island and is based on nearly 2,600 natural predations on Cape fur seals documented from observation vessels. Up to 2,400 shark attacks and 700 seal groups leaving and returning from Seal Island were correlated with environmental parameters measured from a land-based weather station and/or onboard vessel sensors. Environmental factors affecting a white shark's ability to successfully detect and approach its pinniped prey and its prey's ability to avoid attack and subjugation are described, including factors not previously described in the literature. These factors affect the sensory ecology of white sharks and Cape fur seals and are most important at the earliest stages of the Predation Cycle (detection, approach, attack), and least significantly influence the later stages (subjugation and consumption). Recommendations for future research at Seal Island are presented.

Methods

Predatory behavior of the white shark, *Carcharodon carcharias*, was studied between 1997 and 2004 at Seal Island, South Africa. Seal Island is an elongated rocky islet at the foot of False Bay, centered at approximately 35° 8'6"S, 18° 35'00"E, with its south terminus facing the 25-km-wide mouth of False Bay (Fig. 1A). The underwater topography of Seal Island features a sharp drop-off along most of the western side of the islet, where the water depth reaches 20 m within 50 m of shore, and a broad, shallow shelf along the north east side, where the water does not reach comparable depths until 400 m or more from shore. Seal Island is inhabited by some 64,000 Cape fur seals, *Arctocephalus pusillus pusillus*, which feed in False Bay or up to 12–30+ km offshore, outside of the Bay, returning to the island at irregular intervals (Fig. 1B). The primary pinniped entry/exit point, termed the "Launch Pad", is an identifiable spot seaward of a small craggy outcrop located off the south terminus of the island (Fig. 1C). Further site details as well as methodologies relating to predatory event detection, approach and documentation follows Martin et al. (2005). Measurements of environmental parameters, quantification of seal movement, and

Fig. 1 Study site: (A) location of False Bay, South Africa, with the 200 m depth contour indicated; (B) location of Seal Island within False Bay, showing the main path of pinniped movement leaving and returning to the Island (grey triangle) and (C) depth contours (meters) with location of the Launch Pad indicated



statistical methodology used in the present study is described below.

Wind direction, wind speed and ambient light intensity were recorded during the 2003 field season from an erected land-based weather station. Seal Island is inhabited by protected species, making it unavailable for placement of environmental sensors. Since the South African Navy's weather station at Roman Rock is 9 km west of Seal Island and in the lee of the Western Cape mountains, a remote weather station (*Hobo* Weather Logger [H21-001]) was erected on the rooftop of the National Ski and Rescue Institute station (NSRI), on Strandfontein beach. Strandfontein is the closest land point to Seal Island (4.6 km due north) and NSRI's roof top is the highest point in the area and isolated from buildings, trees, mountains or other structures that may be likely to affect readings. Wind direction (in degrees) and speed (in meters per second) was recorded over a 1-min interval, averaged and logged every 30 min from the weather station anemometer (Part # 662491-3). Water clarity was measured to the nearest 0.5 m with a Secchi disc, but could not be used consistently due to surface glare, shadow cast by the observation vessel, and strong currents which pulled the disc out of plumb. Underwater light intensity was measured using a submersible photosynthetically active radiation (PAR) sensor, but sampling depth could not be standardized due to variable current which likewise pulled the apparatus out of plumb. As a default, atmospheric light intensity (micromoles per meter squared per second = μE) was recorded over a 1-min interval, averaged and logged every 30 min from the weather station light sensor (Part # 655641). It stands to reason that light levels in the water column were dependent upon the atmospheric light intensity measured by the sensor on the weather station.

When an attack occurred, at least two observers from the research team were dedicated to guiding our observation vessel to the location of the initial strike, to the best of their abilities (generally within 15 m). Because bottom slope of the central part of False Bay 100–2,000 m from Seal Island is very uniform and gradual (Southern Africa Directorate of Hydrography Marine Chart

SAN 1016), an error in location of the initial strike of as much as 250 m would result in an error in depth of <1.5 m. Thus, when depth was not measured directly via onboard echosounder, GPS location could be used to estimate this parameter to a high degree of accuracy. Distance of the attack from Seal Island and ocean depth (meters) at the locations where attacks took place was measured using on-board depth sensor/GPS locators (Furuno model 1870 color echo locator) from 1997 to 2004. False Bay tidal height data (referenced to Mean Sea Level) for 2003 were provided by the South African Navy, Hydrographic Office.

The time, number of seal groups and number of individuals in the groups leaving from and returning to Seal Island per day was recorded from 21 days between 07:30 and 13:30 h during the 2003 field season.

Chi-squared analysis was used to compare the frequency of observed versus expected (if random) predation for each level of wind direction, wind speed, tidal height and light intensity. The level of each factor for which frequency of attack was significant with respect to wind direction, wind speed, distance from Seal Island, ocean depth and light intensity, was determined according to Martin et al. (2005) using two-way analysis of variance (type I error = 0.05) with replication and Tukey–Kramer comparisons. Data on white shark attack success with respect to month, wind direction, wind speed, distance from shore, ocean depth, tidal height and light intensity were compared using a contingency table χ^2 -analysis. Each factor under investigation was recorded only when it could be clearly identified. Due to 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.

Results

A total of 2,546 natural predatory interactions between white sharks, *Carcharodon carcharias*, and Cape fur seals, *Arctocephalus pusillus pusillus*, were documented at the study site between 1997

and 2004. Up to 43 predatory interactions were observed in a single day. Predations peaked from May through August, averaging 6.68 per day during the winter months (Fig. 2); however, success rate was not significantly different between months ($n = 2,507$, $P > 0.284$; Fig. 2). Mean predatory success rate over the 8-year study was about 48%.

Up to 2,369 shark attacks and 645 seal groups leaving from and returning to Seal Island were correlated with environmental conditions. Predations occurred during all wind directions, but attack frequency was greatest during northerly winds ($n = 366$, $P < 0.002$; Fig. 3A); however, sharks were equally successful at prey capture during different wind directions ($n = 366$, $P > 0.198$; Fig. 3A). Observed attacks were not significantly different than if random with respect to seal availability at different wind speeds ($n = 366$, $P < 0.326$). Attacks occurred between

0 and 2,000 m from Seal Island, with a higher mean number of daily predations recorded between 0 and 400 m from the island, but significantly higher predatory success recorded at distances greater than 800 m from the island ($n = 2,369$, $P < 0.001$; Fig. 3B).

Attacks occurred at the surface over water with depths ranging between 5 and 39 m, with significantly higher mean number of daily attacks recorded where depths ranged from 26 to 30 m ($n = 309$, $P < 0.001$; Fig. 4A). However, sharks were equally successful at prey capture at each depth range ($n = 745$, $P > 0.087$; Fig. 4A). Attacks were recorded during tidal heights ranging from 1 to 3,374 cm above Mean Sea Level (MSL), but significantly fewer attacks occurred at low tidal heights (< 500 cm above MSL) and more at high tides (> 1,500 cm above MSL) ($n = 381$, $P < 0.005$; Fig. 4B). Sharks were

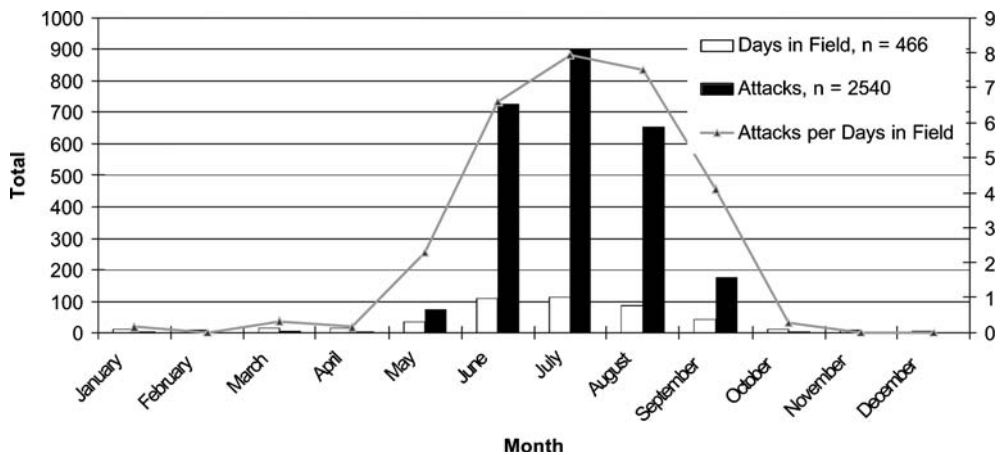


Fig. 2 Number of attacks documented per total days spent in the field during each month over the 8 year study period

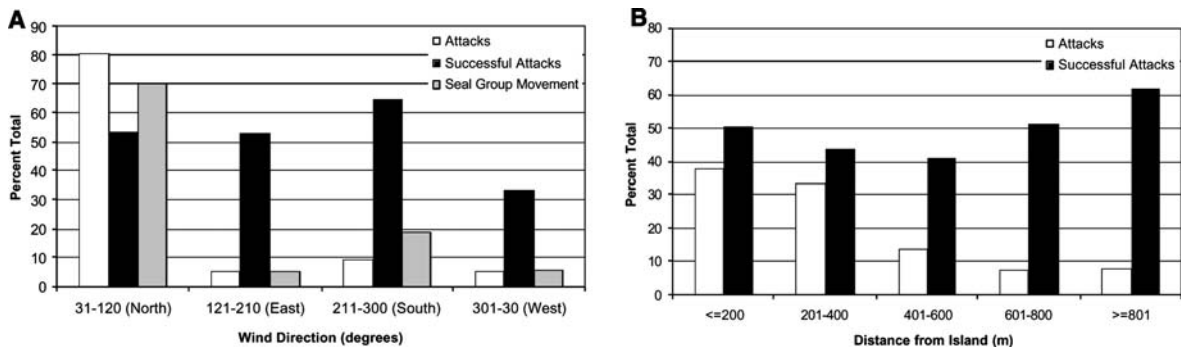


Fig. 3 (A) Percent of total ($n = 366$) and successful ($n = 196$) predatory attacks by white sharks on Cape fur seals and percent of total seal group movement about the

Island ($n = 644$) versus wind direction; (B) percent of total ($n = 2,369$) and successful ($n = 1,133$) attacks versus distance from shore

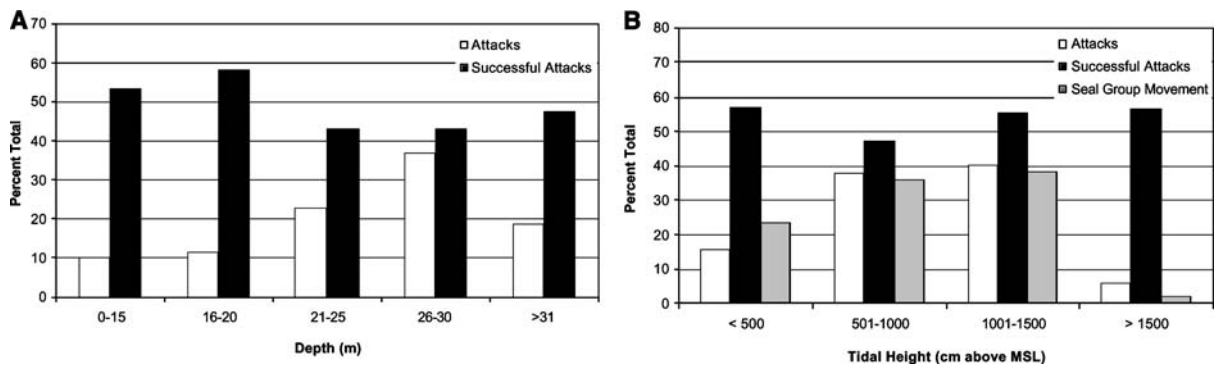


Fig. 4 (A) Percent of total ($n = 745$) and successful ($n = 348$) predatory attacks by white sharks on Cape fur seals versus ocean depth; **(B)** Percent of total ($n = 381$)

and successful attacks ($n = 200$) and percent of total seal group movement about the Island ($n = 616$) versus tidal height

equally successful at prey capture during all tidal heights ($n = 381$, $P > 0.453$; Fig. 4B).

Predations occurred during all light levels, but attacks were not random with respect to seal availability ($n = 366$, $P < 0.001$; Fig. 5A). Predatory frequency ($n = 366$, $P < 0.001$) and success rate (55%, $n = 366$, $P < 0.057$) was significantly higher at light intensities below 300 μE (Fig. 5A). Predation frequency and success rate decreased with increased light and white sharks appeared to cease active predation on Cape fur seals when success rate dropped to about 40% at light levels above 400 μE (Fig. 5B).

Discussion

The present study demonstrates that white shark, *Carcharodon carcharias*, predation on Cape fur

seals, *Arctocephalus pusillus pusillus*, at Seal Island is affected by environmental factors that facilitate a shark’s need for encountering, detecting and remaining cryptic from its prey as well as its prey’s ability to detect its predator prior to attack.

Prey may have differential distribution, abundance and vulnerability at different times of the year and roving elasmobranchs can increase the probability of encountering and capturing prey by selecting the appropriate habitat and time to actively predate (see review by Heithaus 2004). Although white sharks are found in False Bay throughout the year (authors, unpublished data), the onset of active predation by white sharks on seals at Seal Island coincides with when the warm-water predatory fishes leave False Bay for the winter and juvenile Cape fur seals finish weaning and begin foraging away from the Island for the first time. Martin et al. (2005) proposed

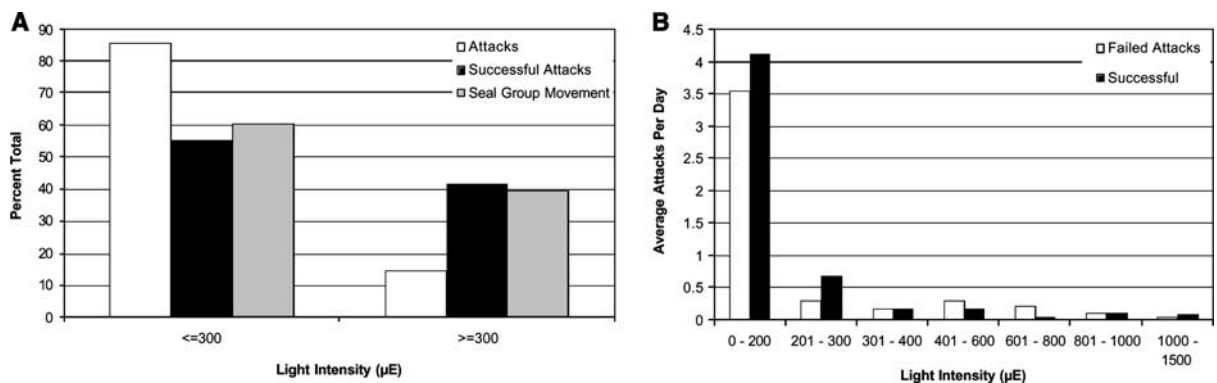


Fig. 5 (A) Percent of total ($n = 366$) and successful ($n = 196$) predatory attacks by white sharks on Cape fur seals and percent of total seal group movement ($n = 644$)

about the Island versus ambient light levels; **(B)** Average number failed ($n = 170$) and successful attacks ($n = 196$) per day versus ambient light levels

that during the winter, white sharks switch from foraging on warm-water fishes to predating on juvenile Cape fur seals at a time when the seals are inexperienced and most vulnerable to predation.

Our findings support the speculation by Strong et al. (1992) that white sharks may locate pinniped rookeries by their distinctive odors. Northerly winds blow from Seal Island and out the mouth of False Bay, propelling chemical stimuli (such as pinniped excreta, blood, and other organic compounds or fractions) that may enable white sharks to locate the Island, where opportunities to predate upon pinnipeds are likely more concentrated than in the open sea. Northerly winds predominate during South African winter storms and directly following such weather, new sharks are found patrolling Seal Island that were not present before (authors, unpublished data).

Northerly winds may also render Cape fur seals more conspicuous visually. During northerly winds, seals must return to Seal Island by locomoting against the current, resulting in enhanced water disturbances around the seal's outline. Such disturbances likely compromise a seal's ability to maintain subsurface vigilance and possibly detect its predator. Seals locomoting against the current also visually highlights their location at the surface and produces sound, either or both of which may aid in prey detection. This is further borne out by results of experimental decoy tows conducted at Seal Island. Between 1997 and 2003, 121 strikes were elicited by sharks on seal-shaped decoys towed at 2.5 km h^{-1} around the Island. Decoy sizes and shapes were varied experimentally. Relatively thick decoys (16–35 cm) created more disturbance around their anterior margins and elicited significantly more strikes per unit tow-duration than did thinner decoys (0.3–5 cm; authors, unpublished data). In contrast to our findings, wind direction showed no effect on white shark predation at the Farallon Islands (Pyle et al. 1996).

Stalking and ambush are important for successful prey capture in many predacious fishes (Strong 1996). Stalking undetected from depth and then rushing to the surface to capture prey is a predatory tactic that has been proposed for sevengill sharks (Ebert 1991), tiger sharks

(Heithaus et al. 2002), blue sharks (Carey and Scharold 1990) and white sharks (Tricas and McCosker 1984; Strong 1996; Goldman and Anderson 1999). Although it is not known if at Seal Island sharks are stalking seals from depth as has been shown at the Farallons (Goldman and Anderson 1999), a depth range of 26–30 m may be optimal for sharks to remain undetected while stalking seals from below, with enough vertical distance to build up momentum required for launching a debilitating strike at the surface. This could be further explored with telemetric measurements of shark swimming depth and speed.

During high tides, the critical minimum depth from which sharks can approach seals undetected is closer to shore, possibly reflecting the decrease and increase in predations documented during low and high tides, respectively. Preliminary results suggest that on spring high tides there is a higher frequency of attacks occurring closer to the Island as well as at the Launch Pad and off the northwest corner of the Island: sites where seals tend to gather in large numbers over shallow reefs. At the Farallons, white shark predatory frequency similarly increased with tidal height (Anderson et al. 1996; Pyle et al. 1996). However, Anderson et al. (1996) suggested that an increase in tidal height likely reduced haul-out area for elephant seals, forcing them into the water and, in effect, increasing prey availability and thus predation.

Strong (1996) suggested that a pinniped at the surface is at a visual disadvantage to a white shark hunting beneath. White shark predatory frequency and success at low ambient light levels is likely reflective of this discrepancy. The large quantity of seal excreta released continually by the Island's resident colony of 64,000 contributes to the murkiness of the waters (average $\pm 7 \text{ m}$ horizontal visibility). In conjunction with low light levels, the seal's ability to detect the darkly pigmented dorsum of a white shark stalking from deep below is probably compromised. Conversely, a hunting shark has a visual and tactical advantage. White sharks are able to stalk seals from below, searching the surface for its prey's silhouette, backlit against Snell's window (Strong 1996), and can launch a brief vertical attack, minimizing strike distance and attack duration

while the seal has limited option for escape at the surface. The documented cease in white shark predatory activity when capture success rate drops to about 40% at high light levels, suggests that sharks at Seal Island may be making foraging decisions that optimize probability of prey capture.

Significant differences were apparent in effects of environmental factors on frequency and success rate of predatory attacks on pinnipeds at Seal Island and SEFI (Table 1), supporting the conclusion of Martin et al. (2005) that white shark predation is tactically fluid and influenced by local environmental conditions. A white shark’s probability of successful prey capture is greatest if the targeted Cape fur seal is incapacitated in the initial strike and the present paper describes six environmental conditions that appear to affect white shark ambush at the surface. Eleven secondary pursuit white shark behaviors have been described by Martin et al. (2005); however, these do not appear to be influenced by environmental conditions. In general, environmental factors—especially those affecting sensory performance—are most influential during the earliest stages of the Predation Cycle (detection, approach, and attack) and less so at later stages (subjugation and consumption).

It is likely that not all significant environmental factors affecting white shark predation were identified. For example, preliminary data suggest that just prior to a storm striking the Cape Peninsula, frequency of attacks increases. Although this needs to be further explored, we hypothesize

that the observed increase in attack frequency may be a result of an increase in seals, which having detected the pressure system, return to Seal Island ahead of the storm to haul-out during the bad weather. Further studies should examine the effects of barometric pressure on seal activity and predation frequency.

Circumstantial evidence from Año Nuevo Island (Klimley et al. 2001) suggests that white sharks prey on pinnipeds at night and it is possible that attacks may be occurring at Seal Island at night. Additionally, a full moon may silhouette a seals location against the surface, making it more visible to its predator. Experiments by Fouts and Nelson (1999) have shown that the Pacific angel sharks, *Squatina californica*, feed at night and that their attacks may be facilitated by turbulence-generated bioluminescence. Trips made to Seal Island at night demonstrated that seals could be detected visually by turbulence-generated bioluminescence. Experiments using infrared video thermography (FLIR Systems ThermoCAM E4 infrared camera equipped with a 12° telescopic lens) at night revealed that both seals and white sharks could be detected by their thermal signatures. Preliminary results suggest that the number of seal groups departing the Island at night is far greater than during the day, possibly reflecting a decrease in predation risk; however, this needs to be further explored. Video sequences using infrared thermography, depicting white sharks breaching and nightly seal group movement about the Island is available as supplementary material to this paper.

Table 1 Effects of environmental factors on predatory frequency and success at Seal Island and Southeast Farallon Island (SEFI) (see Discussion for details)

Factor	Seal island	SEFI	Similar
Season	Winter	Autumn	No
Wind direction	Increased frequency during northerly winds	Wind direction not significant	No
Distance from seal haul-out	Increased frequency and decreased success rate near island	Increased frequency near island (success rate not measured)	Yes
Depth	5–31+ m (increased success 26–30 m)	5–50 m (success rate not measured)	Yes
Tides	Increased frequency during high tides	Increased frequency during high tides	Yes
Swell height	(Not measured)	Increased frequency with increased swell	N/A
Water clarity	(Not measured)	Decreased frequency with increased clarity	N/A
Light intensity	Increased frequency and success under low light conditions	Attacks under all light conditions (success rate not measured)	No

Conclusion

Environmental factors affecting a white shark's ability to successfully detect and approach its pinniped prey and its prey's ability to avoid attack and subjugation are most important during the earliest stages of the Predation Cycle. Many aspects of white shark predatory behavior at Seal Island resemble those of other predatory fishes (Martin et al. 2005) and as a consequence, environmental factors affecting white shark–Cape fur seal interactions and the sensory modalities involved may be applicable to predator–prey interactions involving other predatory fishes.

Acknowledgements Thanks to Herman Oosthuizen and South Africa's Marine and Coastal Zone Management for permitting us to do this work. For their invaluable assistance and ongoing support both in and out of the field, we especially thank R. Lawrence, M. Fallows and M. Bright. Thanks to all volunteer research assistants during the study period; especially C. Peyer, C. Meyers, D. Washington, D. Atagöksel, G. Sure, C. Voltaire, B. Jasinsky, B. Kilbride, A. Currie, G. Gurman, K. Hodgson, M. Hawksworth, J. Northey, B. Bray, H. Brown, B. Lindl, C. Black, B. Gonzalez, R. Flores, A. Barron, G. Markham, J.N. & D. Allinson, K. & G. Foster. We thank our corporate sponsors, YSI, Oregon Scientific, Li-Cor Biosciences, and Ben Meadows for generous donation of environmental sensor equipment. Thank you to Ruth Farre, Sanette Gildenhuys and the South African Navy: Hydrographic Office via the Institute for Maritime Technology for providing hydrographical data. Thank you to NSRI for permitting us to erect a weather station on their facility. We thank J.N. Allinson Associates, Inc. for supplying infrared thermography equipment. Thanks to the SeaStar foundation for financial support. We thank M. Farber and E. Keith of Nova Southeastern University's Oceanographic Center for technical advice and encouragement; we also thank E. Taylor of the UBC Fish Museum, the Zoology Department at University of British Columbia, and the Pew Institute for Ocean Science, Rosenstiel School of Marine and Atmospheric Science at the University of Miami for continued support. For their technical and statistical assistance, special thanks to J. Serafy and E. Babcock. Thanks to our families for their ongoing care and perpetual support, especially A.E. Martin, who also prepared the figures. Thanks also to A.P. Klimley, whose review enabled us to strengthen and shorten this paper.

References

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

- Ainley DG, Henderson RP, Huber HR, Boekelheide RJ, Allen SG, McElroy TL (1985) Dynamics of white shark/pinniped interactions in the Gulf of the Farallons. *Memories Southern California 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
- Bres M (1993) The behaviour of sharks. *Rev Fish Biol Fisher* 3:133–159
- Busch H, Dücker G (1987) Das visuelle Leistungsvermögen der Seebären (*Arctocephalus pusillus* und *Arctocephalus australis*). *Zool Anz* 219:197–224
- Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar Biol* 106:329–342
- Demski LS, Northcutt RG (1996) The brain and cranial nerves of the white shark: an evolutionary perspective. In: Klimley AP, Ainley DG (eds) *Great white sharks: the biology of *Carcharodon carcharias**, Academic Press, San Diego, pp 121–130
- Ebert DA (1991) Observations on the predatory behavior of the sevengill shark *Notorynchus cepedianus*. *South African J Mar Sci* 11:455–465
- Ellis DV (1986) *Animal behaviour and its applications*. Lewis Publishers, Inc., Chelsea, p 329
- Endler JA (1986) Defence against predators. In: Feder ME, Lauder GV (eds) *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*, University of Chicago Press, Chicago, pp 109–134
- Fouts WR, Nelson DR (1999) Prey capture by the Pacific angel shark, *Squatina californica*: visually mediated strikes and ambush-site characteristics. *Copeia* 1999:304–312
- 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
- Gruber SH, Cohen JL (1985) Visual system of the white shark, *Carcharodon carcharias*, with emphasis on retinal structure. *Memoirs Southern California Acad Sci* 9:61–72
- Heithaus MR (2004) Predator–prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives*, CRC Press, Boca Raton, pp 488–512
- Heithaus MR, Dill LM, Marshall GJ, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Mar Biol* 140:237–248
- Hueter RE, Mann DA, Maruska KP, Sisneros JA, Demski LS (2004) Sensory biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives*, CRC Press, Boca Raton, pp 325–368
- Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* 3:680–690

- 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
- Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Sommeran SV, Kelly JT (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar Biol* 138:617–636
- MacLeish WH (1980) Senses of the sea. *Oceanus* 23:1–76
- Martin RA, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of White Sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J Mar Biol Assoc UK* 85:1121–1135
- Myrberg AA Jr (1987) Understanding shark behavior. In: Cook S (ed) *Sharks: an inquiry into biology, behavior, fisheries and use*. Oregon State University Extension Service, Portland, pp 41–83
- 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
- Rogers SC, Church DW, Weatherly AH, Pincock DG (1984) An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging trout, *Salmo gairdneri* Richardson. *J Fish Biol* 25:697–710
- Stewardson CL (1999) Preliminary investigations of shark predation on Cape fur seals *Arctocephalus pusillus pusillus* from the Eastern Cape coast of South Africa. *Trans Roy Soc South Africa* 54:191–203
- Strong WR Jr (1996) Shape discrimination and visual predatory tactics in white sharks. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*, Academic Press, San Diego, pp 229–240
- Strong WR Jr, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. *Aust J Mar Freshw Res* 43:13–20
- Sundström LF, Gruber SH, Clermont SM, Correia JPS, de Marniac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environ Biol Fish* 60:225–250
- Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc California Acad Sci* 43(14):221–238