

Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa

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Between 1997 and 2003, there were 2088 natural predations by white sharks (*Carcharodon carcharias*) on Cape fur seals (*Arctocephalus pusillus pusillus*) and 121 strikes on towed seal-shaped decoys were documented from observation vessels at Seal Island, South Africa. White sharks at Seal Island appear to selectively target lone, incoming young of the year Cape fur seals at or near the surface. Most attacks lasted <1 min and consisted of a single breach, with predatory success rate decreasing rapidly with increasing duration and number of subsequent breaches. A white shark predatory ethogram, composed of four phases and 20 behavioural units, is presented, including four varieties of initial strike and 11 subsequent behaviour units not previously defined in the literature. Behaviour units scored from 210 predatory attacks revealed that, for both successful and unsuccessful attacks, Polaris Breach was the most commonly employed initial strike, while Surface Lunge was the most frequent second event, closely followed by Lateral Snap. Examination of video footage, still images, and tooth impressions in decoys indicated that white sharks at Seal Island bite prey obliquely using their anterolateral teeth via a sudden lateral snap of the jaws and not perpendicularly with their anterior teeth, as previously supposed. Analysis of white shark upper tooth morphology and spacing suggest the reversed intermediate teeth of white sharks occur at the strongest part of the jaw and produce the largest wound. White shark predatory success at Seal Island is greatest (55%) within one hour of sunrise and decreases rapidly with increasing ambient light; the sharks cease active predation on seals when success rate drops to $\pm 40\%$; this is the first evidence of cessation of foraging at unproductive times by any predatory fish. At Seal Island, white shark predatory success is significantly lower at locations where frequency of predation is highest, suggesting that white sharks may launch suboptimal strikes in areas of greatest intraspecific competition; this is the first evidence of social influence on predation in any elasmobranch. Idiosyncratic predatory behaviours and elevated success rates of known individual white sharks at Seal Island suggest some degree of trial-and-error learning. A hypothetical decision tree is proposed that models predatory behaviour of white sharks attacking Cape fur seals at the surface.

INTRODUCTION

Predation is a tactically fluid event, the outcome of which depends upon the behaviour of both prey and predator. Behaviour imposes costs in terms of energy, time, and risks that must be balanced against survival benefits, such as resources needed for self maintenance and reproduction (Ellis, 1986). Since a prey animal has everything to lose in a predation event, one would expect it to be willing to commit any amount of energy toward escape. Conversely, if the energetic cost of a predation attempt is too high or the likelihood of capture too low, one would expect a predator to abandon the attempt (Bennett, 1986). Foraging models comprise three elements: (1) decisions made by a predator to attack or not attack a prospective prey; (2) currency, such as energy costs or gains; and (3) constraints, or the factors defining the relationship between decision and currency (Gerking, 1994). Behaviours reflecting predatory choices can be better

understood by dividing predation events into component parts. The predation sequence is usually divided into five stages: detection, identification, approach, subjugation, and consumption (Endler, 1986). Optimal foraging theory (OFT) predicts that a predator should exploit the prey type most energetically advantageous in terms of net energy content minus search and handling costs (Gerking, 1994). The OFT further predicts that predators should be selective when high-quality food is abundant (Helfman et al., 1997). Learning appears to be the underlying mechanism for adaptive behavioural responses in fish foraging (Dill, 1983). The high level of development of the elasmobranch brain (Northcutt, 1977, 1978) implies that sharks ought to be capable of the types of foraging decisions predicted by Dill (Bres, 1993).

Natural predation by sharks is seldom observed in the wild, due in large part to their high vagility and the visually concealing nature of the marine environment (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 at certain sites (Compagno, 2001). Despite this observability, little is known of the predatory behaviours the white shark employs under natural conditions (Klimley et al., 1996a). To date, most of what is known about the white shark's mode of prey capture and handling has been inferred from bite wounds and scars on pinnipeds surviving attacks (Tricas & McCosker, 1984; Ainley et al., 1985; McCosker, 1985); bite wounds and scars found on dead pinnipeds, dolphins, sea otters, and turtles (Orr, 1959; Ames & Morejohn, 1980; Brodie & Beck, 1983; Corkeron et al., 1987; Cockeroff et al., 1989; Ames et al., 1996; Long, 1996; Long et al., 1996; Long & Jones, 1996); stomach contents of dead sharks (Bonham, 1942; Fitch, 1949; Le Bocuf et al., 1982; Scholl, 1983; Stewart & Yochem, 1985) and limited observations of white sharks preying upon pinnipeds, in which neither shark nor prey was seen before the initial strike (Ainley et al., 1981, 1985; Klimley et al., 1992, 1996a). Tricas & McCosker (1984) proposed the 'bite, spit, and wait' hypothesis, suggesting that white sharks may release and retreat from a stricken prey until it bleeds to death, thereby reducing their risk of injury. Klimley et al. (1996a) found no evidence to support this theory. They also presented an ethogram for white sharks preying on pinnipeds at the Farallon Islands, California, but observation logistics precluded describing the initial strike.

A white shark's principal prey-capture mechanism is its jaws. Kinematics of galeomorph shark jaws, hyoid arches, and associated head movements during biting has been studied via electromyography and analysis of film footage (Moss, 1972, 1977; Motta et al., 1991, 1997, 2002). Tracings from film frames of white sharks feeding on bait have been used to divide this species' bite sequence into four phases and quantify degree of stereotypy of each (Tricas & McCosker, 1984; Tricas, 1985). White sharks exhibit a typical lamnoid dental pattern, with the upper dentition featuring marked heterodonty (Compagno, 2001; Shimada, 2002). Mechanical properties of white shark teeth have been described, including stress distributing and anti-snagging qualities (Preuschoft et al., 1974; Frazetta, 1988). Degree of jaw gape imposes changes in the angles of white shark upper and lower teeth relative to the plane of the jaw (Powlik, 1990, 1995). Observations of white sharks feeding on whale carcasses show that they usually approach perpendicular to the cetacean body axis and initiate contact with the anterior teeth (Pratt et al., 1982; Long & Jones, 1996). However, how white sharks use their jaws and teeth during prey capture has not been described.

Sociobiology of white sharks has received little study, but increasing evidence suggests that this species is socially complex (Compagno, 2001; Martin, 2003). At whale carcasses and feeding stations provided by people, white sharks frequently aggregate and sort themselves into a temporary social ranking based partly on size (Compagno, 2001). At pinniped haul-out sites, white sharks often aggregate after another has made a kill and several discrete categories of social interactions have been defined (Klimley et al., 1996a; Martin, 2003). Tail slap

and breach have been proposed as kill-associated agonistic behaviours in white sharks (Klimley et al., 1996b) and repetitive aerial gaping (RAG) has been proposed as a socially nonprovocative way for white sharks thwarted in attempts to feed on bait to vent their frustration (Strong, 1996a). Based on trackings using a radio acoustic positioning (RAP) system, Klimley et al. (2001) suggested that white sharks at Año Nuevo Island, California, may 'listen in' on one another, possibly in readiness to exploit a pinniped kill made by any of them. But social effects on white shark predatory success have not been described.

The present paper is based on nearly 2100 natural predations on Cape fur seals (*Arctocephalus pusillus pusillus*) and over 120 strikes on towed seal-shaped decoys documented from observation vessels at the study site over a seven-year period. Evidence that white sharks at Seal Island exhibit foraging decisions that optimize probability for prey capture is presented. A white shark predatory ethogram is presented, including four varieties of initial strike. Frequency and event sequence analyses of behavioural units comprising the predatory ethogram are presented. Tactical and biomechanical advantages of white shark use of jaws and teeth during prey capture are described. Evidence of elevated foraging success due to learning and social effects on white shark predatory success is presented. A hypothetical decision tree modelling predatory behaviour of white sharks attacking Cape fur seals at the surface is proposed.

MATERIALS AND METHODS

Natural predatory behaviour of the white shark (*Carcharodon carcharias*) was studied between 1997 and 2003 at Seal Island, South Africa. Seal Island is an elongated rocky islet at the foot of False Bay, with its long axis oriented roughly north-south (Figure 1A,B). The islet measures some 400 by 50 m, its maximum elevation is 7 m above the high tide line, and is centred at approximately 34°8'6"S 18°34'00"E. The underwater topography of Seal Island features a relatively sharp drop-off along most of the western side of the islet and a broad, gently sloping shallow shelf along the north-east side. The waters surrounding Seal Island were divided into six sectors, based on natural topographic features. Seal Island is inhabited by some 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 island at irregular intervals (authors, unpublished data). The primary pinniped entry/exit point, termed the 'Launch Pad', is a small craggy outcrop located off the south terminus of the island, near the juncture of Sectors 3 and 4 (Figure 1C). Birth of Cape fur seals occurs in November–December and pups are weaned in May–June. Cape fur seals leave the island in coordinated groups of 5–20, returning as solitary individuals or in groups of 2–3 (authors, unpublished data).

Observations were made at Seal Island during every month, weather permitting, by teams of two to eight from a single 8-m outboard boat from 1997 to 2000, and by teams of four to 16 from two such boats from 2001 to 2003. At least part of the research team averaged some 200 days per year on the water. Arrival at Seal Island was before sunrise at ± 0730 h, sea conditions permitting. By

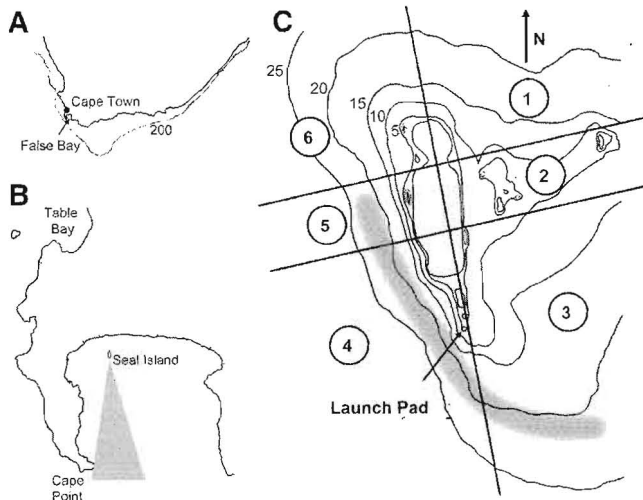


Figure 1. Study site: (A) location of False Bay, South Africa, with the 200 m depth contour indicated; (B) location of Seal Island within False Bay, showing the main path of pinniped movement leaving and returning to the island (grey triangle); and (C) depth contours (m) and sectors (circled numbers) of area around Seal Island, showing a typical decoy tow-path (grey) along the drop-off on the south-west side of the island.

stationing at a terminus of Seal Island, a single vessel could survey some 270° uninterrupted to a distance of ≥ 3.5 km. With two vessels at opposite terminals, nearly all the water surrounding Seal Island could be surveyed to a comparable distance.

Seal group size was estimated as solitary, 2–4, 5–10, or 11+, and their direction of travel relative to the island categorized as either outgoing from or incoming. Cape fur seals were divided into four classes that combine their length, maturity state, and sex (when determinable under field conditions): Class 1: neonates (black pelt, <70 cm); Class 2: young of the year (YOY, 70–100 cm); Class 3: adult females and sub-adult males (lack of sagittal crest, 1.1–1.5 m); and Class 4: adult males (pronounced sagittal crest, >2 m).

Surface predatory events were detected by one or more of the following: (1) white shark breach, with or without a seal in its mouth; (2) a sudden change in the travel behaviour of seals, switching from directional porpoising to either zigzag evasive manoeuvres or head-stand subsurface scanning, with indications of a shark in pursuit (large surface boils and/or direct observation of the shark); (3) a large splash accompanied by a blood stain, oil slick, and a distinctive odour, sometimes accompanied by secondary indicators such as a floating seal head, excised heart and/or lungs, and entrails either floating on the surface or trailing from the gill openings of a white shark in the immediate vicinity; (4) highly localized circling and/or plunge-diving black-backed kelp gulls (*Larus dominicanus vetula*) and other seabirds, with kills often accompanied by active competition for seal entrails by seabirds. Sequences of predatory events were scored and documented using standard techniques. Circumstantial evidence of ± 10 subsurface strikes by white sharks on Cape fur seals were recorded during the study period, but could not be scored due to limited visibility.

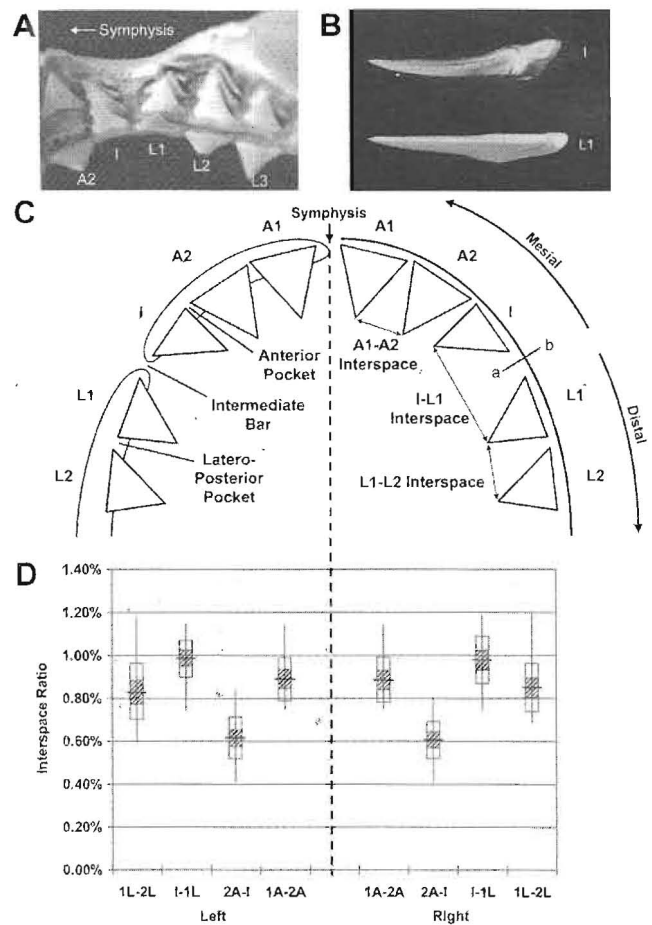


Figure 2. White shark dentition and terminology: (A) labial (inner) view of anterior part of a representative upper jaw, showing location of the intermediate bar between the intermediate (I) and first lateral (L1) teeth; (B) distal view of I and mesial view of L1, showing curved cutting edge of the former; (C) jaw terminology, tooth identification and measurements, with position of the intermediate bar indicated by chord a–b; and (D) Dice diagram of interspace ratio between successive pairs of upper teeth, where vertical bar=range, horizontal bar=mean, white box=standard deviation, and hashed box=95% confidence limits. In both (C) and (D), the vertical dashed line indicates head axis through the jaw symphysis.

Every effort was made to minimize observer effects on predatory events. Predatory events were classified as either successful, in which the seal was consumed, or unsuccessful, in which the seal escaped. Duration of predatory events was timed from initial strike to either consumption of the prey or continuation of seal travel on an identifiable course for ≥ 30 s; in those few cases in which a seal was killed but not consumed (N=10), end of the predation event was considered the time after which the floating carcass was unattended by a shark for ≥ 120 s. Distance of predatory events from the island was estimated to the nearest 10 m with the aid of an on-board Global Positioning System. Shark length was estimated to the nearest 0.1 m by comparison against known dimensions of the attending observation vessel. Shark sex was based on the presence or absence of claspers, verified whenever possible by polecamera images of the cloaca from below.

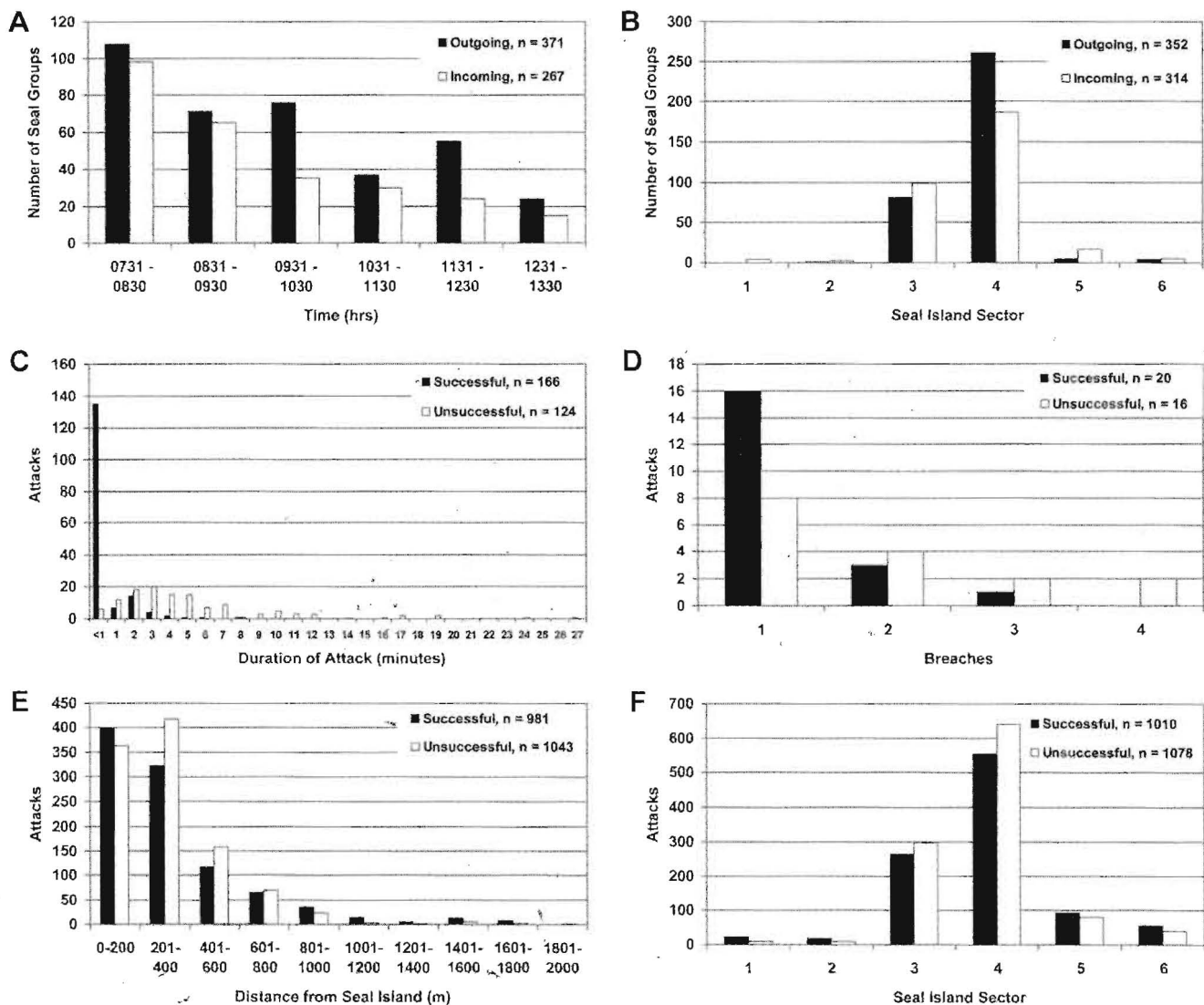


Figure 3. Cape fur seal movements and white shark attack patterns at Seal Island, South Africa: (A) number of seal groups versus time; (B) number of seal groups versus Island Sector; (C) number of attacks versus duration of attack; (D) number of attacks versus number of breaches; (E) number of attacks versus distance from Seal Island; and (F) number of attacks versus Island Sector.

Individual white sharks were identified at predatory events whenever possible. From 1997 to 2000, 73 colour-coded streamer tags and 20 pinger tags were attached to white sharks at Seal Island. Tagging of white sharks in western and southern Cape waters was banned by Marine and Coastal Management in 2000, resulting in initiation in 2001 of a non-invasive identification technique based on cataloguing and coding individual white sharks by natural pigmentation patterns and other persistent marks; this technique will be described in detail elsewhere. Identification of individual white sharks relied on field records of shark length and sex (if known), tag placement, type, and (where relevant) colour code, plus natural pigmentation pattern.

Data on white shark attack frequency and success with respect to seal group size, direction of travel, and age-class, time of day, distance from shore and by Island Sector were compared via one and two-way analysis of variance (ANOVA) and Tukey-Kramer tests (Type I error=0.05) with replication. Shark length and Cape fur seal size-class were easier to identify in successful attacks,

thus one-way ANOVA was employed in these cases to minimize the effects of bias in the data. Frequency and event sequence analyses of behavioural units of our predatory ethogram follow the methods of Klimley et al. (1996a).

After frequency of predatory activity attenuated each day, some 2–2.5 h after sunrise, a seal-shaped decoy was towed behind our research vessel to elicit strikes by white sharks. Decoys were carved from compressed closed-cell rubber camping mats that preserved individual tooth impressions and did not injure attacking sharks. The decoys were towed through Sectors 3, 4, and 5 of Seal Island over the 15–18-m depth contour some 8+ m behind the vessel at a constant speed of ± 2.5 km h^{-1} (Figure 1C). Strikes against decoys were limited to < 3 per day, afterward the island was circumnavigated slowly at a distance of 4 to 15 m, scanning for shark bitten Cape fur seals and documenting wound characteristics (location, relative severity, degree of healing).

Strikes on decoys were documented via videography and still photography. Jaw position of individual upper tooth impressions could readily be identified following

the terminology of Shimada (2002). Interspace measurements were made following Collier (1992, 2003) from 25 white shark jaws, uniformly prepared by G. Hubbell, representing individuals of both sexes and total lengths (TLs) ranging from 158 to 594 cm. To correct for size differences among sharks sampled, interspace measurements were converted to per cent TL, resulting in a new measurement here termed 'interspace ratio'. Interspace ratios of the first five upper anterior teeth on either side of each jaw were compared statistically. Tooth identification and representative interspace measurements are indicated in Figure 2A&C. For comparison, 44 cleaned and dried white shark jaws were examined from the reference collections of the Los Angeles County Museum of Natural History (LACM), British Museum of Natural History (BMNH), the Cape Town Museum (CTM), the Natal Sharks Board (NSB), and the private collection of G. Hubbell (Jaws International).

RESULTS

A total of 2088 natural predatory interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) was documented at the study site between 1997 and 2003. Most predatory activity occurred between late May and late August, with the greatest frequency occurring between mid-June and mid-August (winter). Up to 25 predatory interactions were observed in a single day, with a mean of 5.6 attacks per day. Mean predatory success rate was 47.3%. Movement of seal groups away from and toward Seal Island was significantly greater in the early morning between 0730 and 0930 h ($P < 0.0001$), but remained high until at least early afternoon (Figure 3A), with most movement centred on the Launch Pad at the junction of Sectors 3 and 4 and significantly more seals leaving from or returning to Sector 4 than Sector 3 ($P < 0.0001$) (Figure 3B). Group size of seals attacked ranged from 1 to at least 15, with frequency and success rate decreasing with increasing group size and significantly more attacks on solitary seals than any other group size category ($N = 973$; $P < 0.0001$). Both incoming and outgoing seals were attacked, but frequency ($N = 287$, $P < 0.0001$) and success rate ($N = 287$, $P < 0.05$) were significantly higher on incoming seals. Seals representing all size-classes except Class 1 were attacked, but predatory frequency decreased with increasing seal class and was significantly higher on Class 2 seals than any other size-class ($N = 1088$, $P < 0.0001$).

Predatory attacks took place between 0730 and 1830 h, but the greatest frequency occurred between 0730 and 0830 h; the next greatest frequency of attacks occurred between 0830 and 0930 h, followed by 0930 and 1030 h ($N = 1948$, $P < 0.0001$). Fewer than 13% of all attacks took place after 1030 h. Repeated attempts to bait-attract white sharks to our research vessel(s) within three hours of sunrise proved uniformly unsuccessful. Only after frequency of natural predations on Cape fur seals attenuated to almost nil did sharks show any interest in bait or boats. Predatory success and duration of attack were negatively correlated, with 73% of successful attacks lasting < 1 min (Figure 3C) and 80% of successful attacks consisting of a single breach (Figure 3D). Attacks occurred

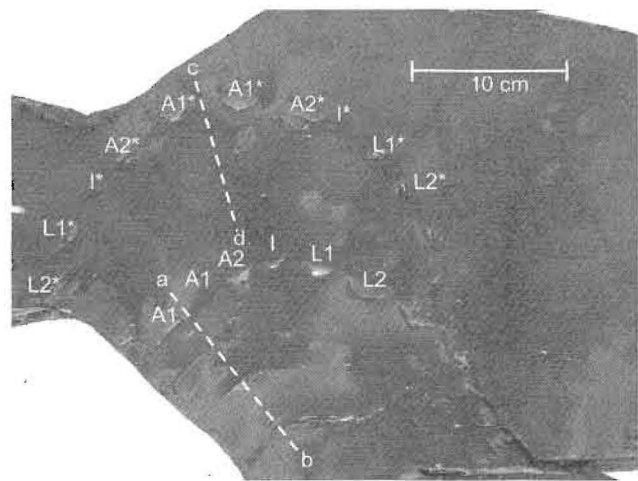


Figure 4. Identification of initial and secondary (repurchase) tooth impressions in a seal-shaped decoy. Tooth terminology follows Figure 2; tooth impressions A1 through L2 represent the shark's initial grasp on the decoy, while L2* through L2* represent its repurchase. Dotted lines indicate approximate longitudinal axis of the shark's head during initial strike (a-b) and repurchase (c-d).

between 0 and 2000 m from Seal Island, with significantly higher frequency of predatory events recorded between 0 and 400 m from the island ($N = 2024$; $P = 0.0002$), but higher predatory success was recorded at distances of 800–1800 m from the island (Figure 3E). Attacks took place in all Island Sectors, but the greatest frequency of attacks took place in Sectors 3 and 4, with significantly more in Sector 4 than any other sector ($N = 2088$, $P < 0.0001$). However, the highest mean success rate occurred in Sectors 1, 2, 5, and 6 (Figure 3F). Duration

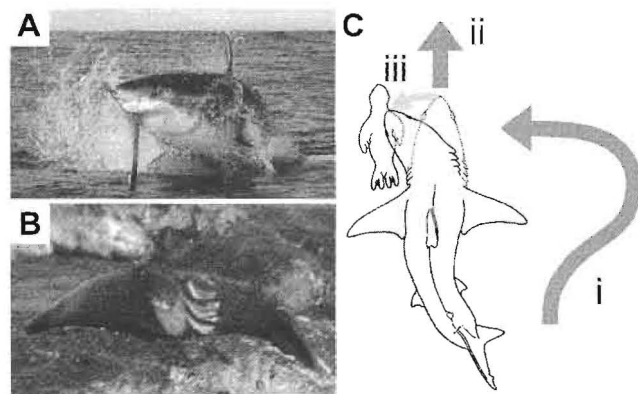


Figure 5 Initial bites by white sharks on seal-shaped decoys and Cape fur seals: (A) oblique bite on decoy in Figure 4—note that the decoy is grasped from the side via the anterolateral teeth; (B) wounds on an escaped Cape fur seal—note that tooth rakes are well spaced and parallel to seal's long axis, consistent with being grasped obliquely via the anterolateral teeth; and (C) hypothesized tactical advantage of lateral snap (SNL) behaviour to a pursuing white shark. If the shark broke from its pursuit to grasp the prey perpendicular to its axis of travel (i), it would cost speed and time. By maintaining a parallel course (ii) and grasping the prey via a sudden lateral snap of the jaws (iii), the shark can inflict a disabling bite without sacrificing its oriented pursuit.

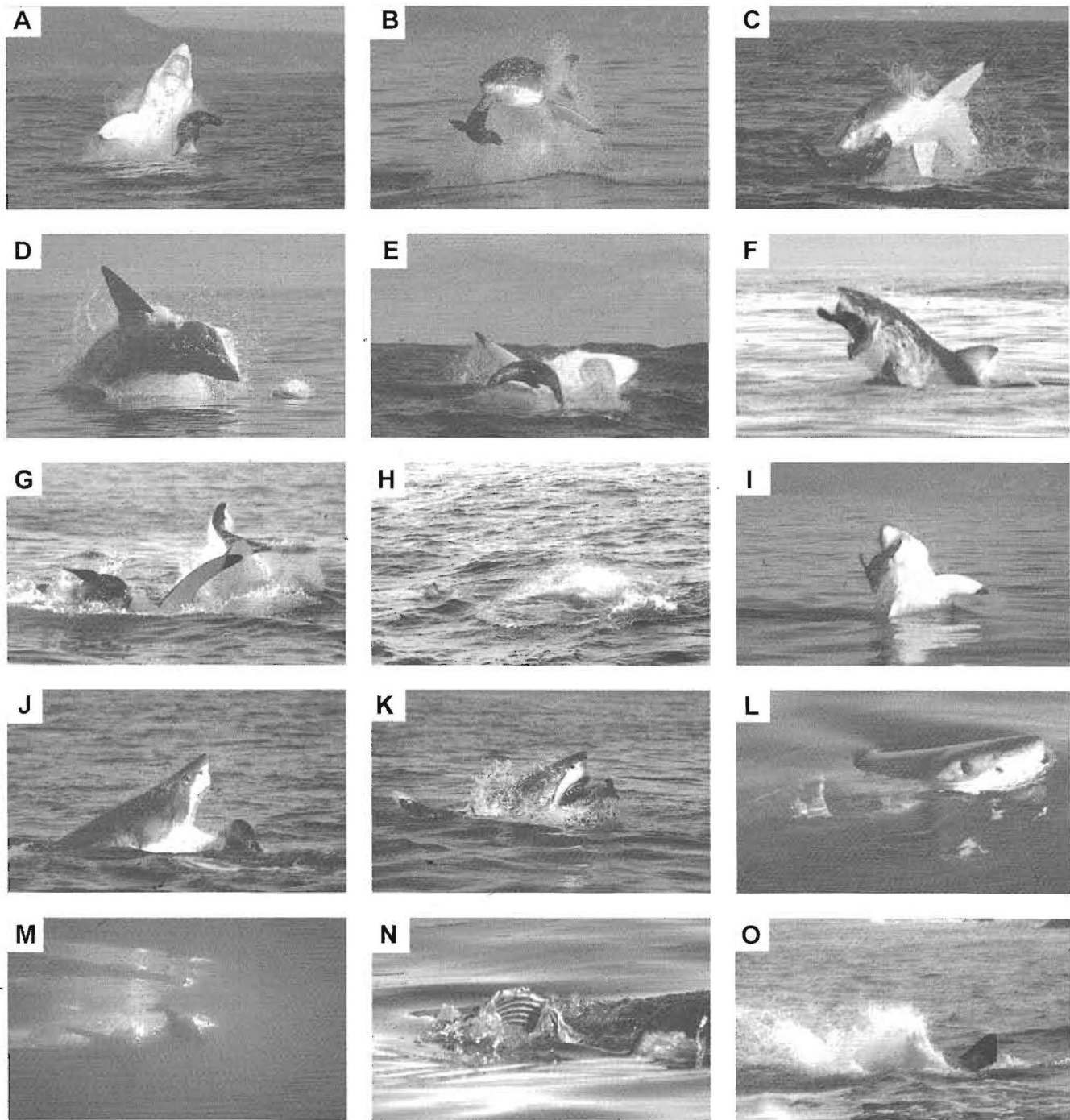


Figure 6. Predatory behaviours in white sharks at Seal Island, South Africa: (A) Polaris breach; (B) surface broach; (C) lateral broach; (D) inverted broach; (E) surface lunge; (F) surface intercept above water; (G) lateral roll; (H) surface arc; (I) lateral snap; (J) direct surface approach; (K) killing bite; (L) surface grasp horizontal approach; (M) subsurface carry; (N) surface feed; and (O) lateral head shake.

of attacks ranged from <1 min to 27 min, although nearly 2/3 lasted ≤ 2 min ($N=290$, mean=3.0, SD=3.73). There was an inverse relationship between attack duration and success rate as well as between number of breaches and success rate (Figure 3C,D). Mean duration of 166 successful attacks was 1.42 min with SD=2.18 min; if the 27-min outlier is discounted, mean duration of successful attacks was 1.27 min with a SD of only 0.88 min.

Upper teeth of all prepared white shark jaws examined featured a reversed intermediate tooth, located just anterior to the intermediate bar near the point of maximum curvature of the upper jaw (Figure 2A). The blade of this tooth, I, typically has a curved to slightly sinusoidal distal cutting edge, unlike the nearly straight mesial cutting edge of the 1st lateral tooth, L1 (Figure 2B). Interspace ratios of I–L1 of left and right sides of the

jaw were significantly larger than for any other tooth-pair on either side of the jaw (Figure 2D).

Over the study period, 121 strikes on towed seal-shaped decoys were documented. Identification of individual upper tooth punctures in compressed rubber decoys indicated that all strikes were asymmetrical and inconsistent with being grasped by the shark with the anterior teeth while oriented perpendicular to the longitudinal (travel) axis of the decoy (Figure 4). Videotape footage and still images revealed that decoys are typically grasped between the anterolateral or lateral teeth via a sudden, lateral snap of the jaws (Figure 5A). This is consistent with footage and still images of initial (capture) bites on Cape fur seals (Figure 6F&I) and wounds on escaped seals (Figure 5B).

Based on observations of natural predations and strikes on seal-shaped decoys, a predatory ethogram consisting of 20 behavioural units was constructed. These units are divided into four functional phases and, in approximate sequential order, defined as follows.

Phase 1: Initial strike

Polaris breach (POL): the shark leapt partially or completely out of the water in a vertical or nearly vertical head-up orientation, with or without a seal grasped in its jaws. In POL that launch a shark completely from the water, the shark may clear the surface by as much as 3 m and often rotates tail over head around the centre of gravity, located $\pm 1/3$ along its standard length, re-entering the sea head-first close to its original exit point. During POL in which the seal is not grasped by the shark and continues evasive manoeuvring, the shark often turns its head mid-flight as though visually tracking the seal's movements (Figure 6A).

Surface broach (BRS): the shark leapt partially or completely out of the water in an upright orientation with its body axis forming an angle with the horizon between 45 and 0 degrees, with or without a seal in its jaws. In BRS that launch a shark completely from the water, the shark usually clears the surface by ≤ 1 m, re-entering the sea in the direction of travel ± 0.5 to 1.5 body lengths (BLs) away from its original exit point and with its dorsum upward. During BRS in which the seal is not grasped by the shark and continues evasive manoeuvrings, the shark often turns its head mid-flight as though visually tracking the seal's movements (Figure 6B).

Lateral broach (BRL): the shark leapt partially or completely out of the water in a lateral orientation with its body axis forming an angle with the horizon between 45 and 0 degrees, with or without a seal in its jaws. In BRL that launch a shark completely from the water, the shark usually clears the surface by ≤ 1 m, re-entering the sea in the direction of travel ± 0.5 to 1.5 BLs away from its original exit point and with one flank upward (Figure 6C).

Inverted broach (BRI): the shark leapt partially or completely out of the water in an inverted orientation with its body axis forming an angle with the horizon between 45 and 0 degrees, with or without a seal in its jaws. In BRI that launch a shark completely from the water, the shark usually clears the surface by ≤ 1 m, re-entering the sea in the direction of travel ± 0.5 to 1.5 BLs away from its original exit point and with the belly upward (Figure 6D).

Table 1. Frequency and rank order of behavioural units scored from 210 white shark predatory attacks at Seal Island, South Africa.

Count	Behaviour unit	Code	N	%	
				Total	Rank
1	Surface lunge	LUN	153	17.5	1
2	Polaris breach	POL	122	13.9	2
3	Lateral snap	SNL	110	12.6	3
4	Surface broach	BRS	105	12.0	4
5	Subsurface carry	CAR	56	6.4	5
6	Subsurface feed	FDU	53	6.1	6
7	Lateral head shake	LHS	53	6.1	6
8	Killing bite	KIL	51	5.8	7
9	Food release	REL	49	5.6	8
10	Repurchase	REP	36	4.1	9
11	Lateral broach	BRL	20	2.3	10
12	Surface grasp, horizontal approach	GRH	14	1.6	11
13	Surface arc	ARC	12	1.4	12
14	Surface feed	FDS	11	1.3	13
15	Surface grasp, vertical approach	GRV	8	0.9	14
16	Direct surface approach	DIR	7	0.8	15
17	Lateral roll	ROL	6	0.7	16
18	Surface intercept, above water	INA	5	0.6	17
19	Inverted broach	BRI	2	0.2	18
20	Surface intercept, underwater	INU	2	0.2	18
Totals			875	100.0	

Phase 2: Secondary pursuit

Surface lunge (LUN): the shark, oriented dorsum up and with its back partially out of the water, accelerated quickly toward an injured or uninjured seal at the surface. During LUN, the shark accelerates from ± 0.5 BL s^{-1} to ≥ 1.5 BL s^{-1} for a period of not less than 2 s, with its jaws held open $\geq 35^\circ$ and with or without its upper jaw protruded, exposing the upper teeth. During LUN, the eye was not rolled tailward in its socket, exposing the whitish sclerotic coat (Figure 6E).

Surface intercept, above water (INA): the shark that had been chasing an injured or uninjured seal along the surface broke from oriented pursuit by leaping partially or completely out of the water on a non-parallel course, intercepting it on the surface ≤ 5 BLs away a few seconds later and grasping it between the jaws. In INA, the shark appeared to anticipate the flight path of the seal and changed its behaviour to intercept it (Figure 6F).

Surface intercept, under water (INU): the shark that had been chasing an injured or uninjured seal along the surface breaks from its oriented pursuit, diving below the surface and reappearing under the leaping seal, to intercept it on the surface ≤ 5 BLs away a few seconds later, grasping it between the jaws. In INU, the shark appeared to anticipate the flight path of the seal and changed its behaviour to intercept it.

Lateral roll (ROL): the shark rolled onto its left or right side with its belly toward the escaping seal, apparently changing the orientation of its eyes to keep it in

sight. The ROL occurred underwater or partially above the surface with a pectoral fin projecting into the air (Figure 6G).

Surface arc (ARC): the shark swam slowly to moderately quickly at or near the surface adopting a broad, semi-circular course around a surface-borne seal. During ARC, the diameter of the arc described is $\pm 2-3$ BLs, the shark swam between 0.5 and 2 BL s^{-1} , and its eyes rotated in their sockets, apparently to keep the stricken seal in sight (Figure 6H).

Phase 3: Prey capture

Lateral snap (SNL): the shark captured a rapidly fleeing pinniped via a sudden lateral snap of the jaws, protruding the upper jaw and grasping the prey with its anterolateral teeth. During SNL, the shark's head is flexed sideways some 10 to 15° toward the prey. The SNL is very rapid and usually lasts <0.5 s. Upon contact with the prey item, the eyes are rolled tailward in their sockets, exposing the whitish sclerotic coat, after which the head, with or without the seal grasped in the jaws, is swung medially until collinear with the body axis (Figure 6I). Often followed by REP.

Repurchase (REP): the shark shifted its peripheral grasp on a seal, leaving the lower dentition inserted while rapidly lifting the snout, thereby removing the upper dentition, then quickly protruding the upper jaw and bringing the upper teeth back into contact with the prey farther from the periphery than previously; often accompanied by a sudden lateral movement of the head.

Killing bite (KIL): the shark delivered a deliberate, powerful bite with the anterior teeth to the head and neck of a captured seal, apparently to kill it prior to feeding. During KIL, upon initial contact with the prey, the eyes are rolled tailward in their sockets, exposing the whitish sclerotic coat. Often followed by LHS (Figure 6K).

Direct surface approach (DIR): the shark performed a relatively slow, oriented approach along the surface to a surface-borne dead or severely injured but weakly swimming seal. During DIR, the shark's swimming speed was typically ≤ 1 BL s^{-1} (Figure 6J). Usually followed by FDS or FDU.

Surface grasp, horizontal approach (GRH): the shark slowly and deliberately approached a surface-borne dead or otherwise incapacitated (non-swimming) seal along the surface and grasped it with the anterior teeth. During GRH, the shark's swimming speed was usually <0.5 BL s^{-1} (Figure 6L). Usually the first reacquisition of a food item after REL.

Surface grasp, vertical approach (GRV): the shark slowly and deliberately approached a surface-borne dead or otherwise incapacitated seal from below at an angle of 45 to nearly 90° and grasped it with the anterior teeth. During GRV, the shark's swimming speed was usually <0.5 BL s^{-1} .

Phase 4: Feeding

Subsurface carry (CAR): the shark slowly carried a dead or otherwise incapacitated seal underwater for ≥ 3 s, transporting it >6 m before feeding. During CAR, the shark's swimming speed was reduced to ± 0.5 BL s^{-1} and amplitude of each caudal stroke was increased nearly 50% over that exhibited during normal swimming

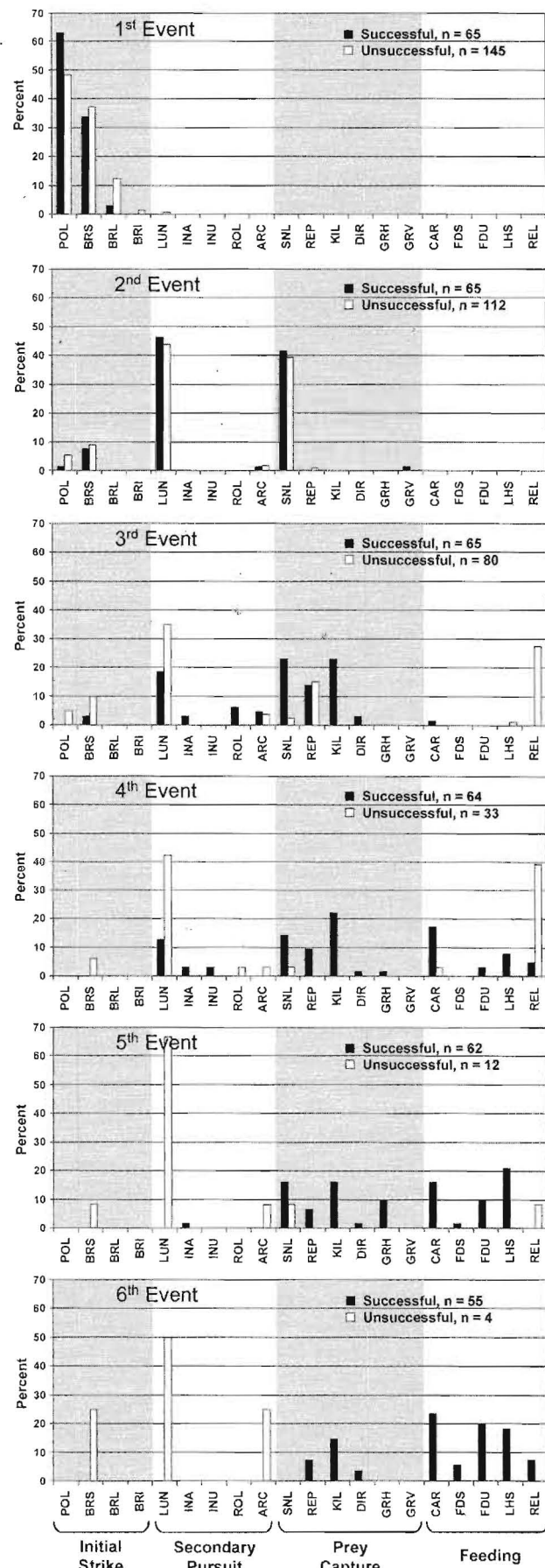


Figure 7. Per cent occurrence of white shark behavioural units scored during first six events in successful versus unsuccessful predatory attacks at Seal Island, South Africa (n total=210 attacks).

Table 2. Probabilities that each behaviour unit precedes or follows each other behaviour unit during predatory attacks on Cape fur seals at Seal Island, South Africa ($N=210$ attacks).

Preceding behaviour Code N		Subsequent behaviour																			
		Initial strike				Secondary pursuit				Prey capture				Feeding							
		POL	BRS	BRL	BRI	LUN	INA	INU	ROL	ARC	SNL	REP	KIL	DIR	GRH	GRV	CAR	LHS	FDS	FDU	REL
		11	29	0	0	152	5	2	6	12	110	36	51	7	14	8	56	53	11	53	49
POL	103	0.07	0.13			0.38				0.01	0.41					0.01					
BRS	88	0.05	0.10			0.56			0.01	0.03	0.25										
BRL	13					0.38					0.54	0.08									
BRI	1										1.00										
LUN	99		0.07			0.44	0.05	0.01	0.04	0.07	0.29				0.01						0.01
INA	5										0.80				0.20						
INU	2										0.50				0.50						
ROL	6					0.50		0.17			0.17				0.17						
ARC	10					0.50			0.10	0.10	0.20				0.10						
SNL	100					0.07						0.35	0.33	0.01			0.02	0.01			0.21
REP	36												0.47	0.08			0.06	0.03		0.03	0.33
KIL	51																0.63	0.12	0.04	0.08	0.08
DIR	7										0.14				0.06		0.29	0.14	0.14	0.14	0.14
GRH	14															0.07	0.50	0.07	0.14	0.21	
GRV	8																0.63	0.13	0.13	0.13	
CAR	54															0.02		0.78	0.02	0.13	0.06
LHS	52														0.04		0.10		0.06	0.69	0.12
FDS	0																				
FDU	3																0.33				0.33
REL	13																				0.33

(Figure 6M). Often, at least one other shark was visible in the immediate vicinity at the onset of CAR. **Lateral head shake (LHS):** the shark grasped a dead seal in its mouth and shook its head violently from side-to-side, the snout describing an arc of $\pm 90^\circ$, removing a piece from the carcass (the remains of which typically

floated to the surface). Period of each LHS was ± 2 s (Figure 6O). Usually followed by FDU. **Surface feed (FDS):** the shark consumed a dead seal at the surface, usually in one or two bites, circling slowly but tightly (turning radius ± 2 BL) between bites. During FDS, circling speed was < 1.5 BL s^{-1} (Figure 6N). The

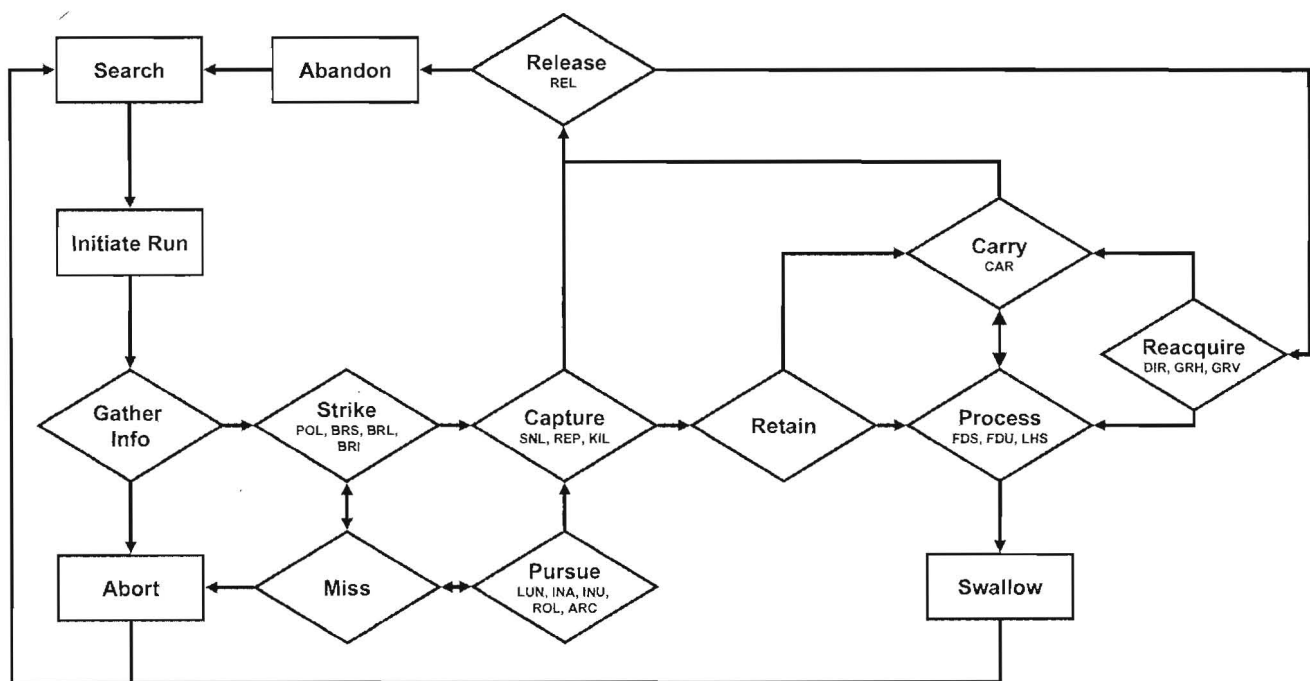


Figure 8. Hypothesized decision tree of predatory tactics employed by white sharks on surface-borne Cape fur seals at Seal Island, South Africa. Three-letter codes for individual behaviour units match those used in the ethogram (see text for details).

entrails are rarely consumed. Usually preceded by KIL, GRH, or GRV and accompanied by LHS.

Subsurface feed (FDU): the shark consumed a dead seal underwater, usually in one or two bites, circling slowly but tightly (turning radius ± 2 BL) between bites. During FDU, circling speed was < 1.5 BL s^{-1} . The entrails are rarely consumed. Usually preceded by KIL, GRH, or GRV and accompanied by LHS.

Food release (REL): the shark released a whole or partial seal carcass, which floated to the surface, and did not reclaim it for 10+ min. Often, at least one other shark was visible in the immediate vicinity. The seal carcass was usually consumed by either its original possessor or a conspecific; occasionally ($N=10$), the carcass simply drifted away from the kill site and out of visual range.

Frequency and event sequence of the preceding behavioural units were scored from video footage and field notes on 210 predatory attacks, of which 65 were successful and 145 were unsuccessful. Frequency and rank order of the resultant 875 behavioural units are presented in Table 1. Successful attacks consisted of 3–14 units (mean 7.5, SD 2.1), while unsuccessful attacks consisted of 1–9 units (mean 2.7, SD 1.4). For both successful and unsuccessful attacks, POL was the most frequently employed initial strike, while LUN was the most frequent second event, closely followed by SNL. In successful attacks, 63% of sharks captured prey as the 3rd event, 48% captured prey and 32% fed as 4th event, with 100% feeding or having fed by the 6th event. Conversely, in unsuccessful attacks, 55% of sharks were pursuing prey as the 3rd event and 23% were still pursuing prey as the 4th event. Some 23% of unsuccessful initial strikes were not followed by a 2nd event (Figure 7). Occurrence of a given behavioural unit was not a good predictor of the following behavioural unit, except INA was likely to be followed by SNL (probability 0.8) and CAR was likely to be followed by LHS (probability 0.78) (Table 2).

White sharks > 3.5 m TL had significantly higher success rate and launched attacks 800+ m offshore 2.5 times more often than smaller individuals and had a significantly higher success rate than sharks of the same length-class closer to Seal Island (67.5% vs 58.8%, $P < 0.001$). Seal kills were usually attended by a single white shark, but are sometimes attended by up to four sharks. In at least 28 predatory events documented during the study period, the shark that made a seal kill was not the same individual that consumed the carcass. For example, on 10 August 2002 at 0928 h, a 3.5-m white shark mortally wounded a Class 2 Cape fur seal but, before it could circle back to consume the moribund pinniped, it was followed at a distance of 2 BL and within one minute was displaced by a 3.7-m white shark, which consumed it; the 3.5-m shark that originally incapacitated the seal was not seen again. Within one month of this incident, three similar displacements were recorded.

DISCUSSION

Predatory strategy

White sharks (*Carcharodon carcharias*) at Seal Island appear to select Cape fur seal (*Arctocephalus pusillus pusillus*)

class, group size and travel direction, as well as hunting times and locations that maximize their probability for predatory success. During the season of peak predatory frequency (late June–early August), Class 2 (YOY) Cape fur seals are being weaned and many have just begun foraging away from the island (authors, unpublished data). They thus have a thick layer of insulating blubber but limited energy stores, swimming, and diving abilities. Class 2 seals may also be relatively naive and thus easier for stalking white sharks to ambush and capture. Lone seals are unable to share vigilance or defensive duties and thus may be more vulnerable to stalking white sharks than larger groups. Incoming seals are often solitary or in small groups and may be influenced by postprandial torpor and thus be more vulnerable and less attentive than outgoing seals.

A white shark's probability of predatory success is greatest if the targeted Cape fur seal is incapacitated in the initial strike. Capture success of many predatory fish depends upon speed and the element of surprise (Strong, 1996b). White sharks are clearly capable of impressive burst accelerations, as seen during Polaris Breaches (Figure 6A), but it is unknown how long they can sustain top swimming speed. Between 94 and 97% of a white shark's muscle mass is composed of white muscle (Bernal et al., 2001), which is capable of rapid contraction but has low stamina (Bone, 1988). Cape fur seals departing Seal Island are capable of maintaining rapid porpoising for ≥ 20 min. When pursued by a white shark, Cape fur seals exhibit remarkable agility, focus and control, consistently employing zig-zag evasive manoeuvres when a shark is below them and leaping toward the shark's back (away from its jaws) when the shark is at the surface (authors, personal observations). The longer a predation bout continues or the more numerous capture attempts a white shark makes, the lower its chances of making a successful kill (Figure 3C,D). This suggests that once a shark has launched its initial strike and the seal realizes its whereabouts and intentions, the odds greatly favour the seal. Thus, like other predatory fish, white sharks preying upon pinnipeds at Seal Island are ambush predators that rely heavily on the element of surprise.

Most white shark predations on Cape fur seals at Seal Island occur within two hours of sunrise, when ambient light levels are low. The large quantity of seal excreta released continually by the resident colony undoubtedly contributes to the murkiness of the waters around Seal Island, which average ± 7 m of horizontal visibility; when the sun is low on the horizon, light penetration in the water column is minimal (authors, unpublished data). These factors probably compromise a seal's ability to visually discern the darkly pigmented dorsum of a white shark stalking below. In addition, a pinniped may be particularly vulnerable to underwater attack while breathing, when its eyes are above the surface. The white shark retina possesses regional specializations for operating under low-light conditions (Gruber & Cohen, 1985). Strong (1996b) suggested that, for a white shark searching from below, prey at the surface would be highly visible silhouetted in Snell's window and has limited escape options. A shark stalking a porpoising seal from along the bottom can position itself directly below it before

launching a sudden vertical attack. This strategy would minimize strike distance and duration, thereby maximizing a shark's likelihood of successfully ambushing a surface-borne seal. Thus, under low-light conditions, white sharks hunting near the bottom at Seal Island may have a visual and tactical advantage over Cape fur seals at the surface.

It is significant that white sharks at Seal Island appear to limit active predation to within a few hours of sunrise. Basking sharks (*Cetorhinus maximus*) in the English Channel selectively forage at high densities of calanoid copepods concentrated at thermal fronts but swim out of these areas on straight courses when zooplankton concentration fell below $\pm 1 \text{ gm}^{-3}$ (Sims & Merrett, 1997; Sims & Quayle, 1998). Similarly, our data show that white sharks at Seal Island cease active predation on Cape fur seals when success rate drops to $\pm 40\%$. This is the first evidence of cessation of foraging at unproductive times by any predatory fish.

Although white sharks are present in False Bay year-round, sightings and attacks on Cape fur seals are rare at Seal Island after mid-August. A small number of white sharks appear resident in False Bay but seem to move away from Seal Island and closer to shore, where they pursue summer fish such as yellowtails (*Seriola lalandi*), bronze whaler sharks (*Carcharhinus brachyurus*), and bull rays (*Pteromylaeus bovinus*) (authors, unpublished data). It seems feasible that, by spring, those Class 2 Cape fur seals that remain at Seal Island are too few or too experienced to constitute energetically worthwhile prey, favouring a dietary shift in False Bay resident white sharks to fish prey, which may be more abundant or easier to capture. This idea is intriguing and consistent with OFT, but remains to be tested.

Mechanics of predation

Applegate (1965) introduced lamnoid tooth terminology based on the sandtiger shark (*Carcharias taurus*), differentiating the upper dentition into anterior, intermediate, lateral, posterior, and symphyseal teeth. This terminology has been extended to the white shark, with the exception of symphyseal teeth, which this species lacks (Hubbell, 1996; Long & Waggoner, 1996). Siverson (1999) pointed out that intermediate teeth *sensu* Applegate (1965) are reduced teeth restricted to the intermediate bar which separates the anterior and lateroposterior tooth pockets. In this sense, only the lamniform genera *Carcharias* and *Odontaspis* possess true intermediate teeth and the so-called 'intermediate' teeth of *Carcharodon* are reduced third anterior teeth, with reversed cusps. However, in his review of dental homologies in lamniform sharks, Shimada (2002) retains use of the term intermediate for these teeth in white sharks and other lamnoids, based on their consistent geometry relative to the dental bulla. This terminology is adopted provisionally here.

The upper dentition of all modern white sharks features reversed intermediate teeth. If these teeth have a function, they cannot be considered in isolation but in conjunction with the teeth that flank it. The teeth of adolescent and adult white sharks are unique among lamnoids in having coarsely serrated crowns and in having lateral teeth that are proportionately broader than those of any other lamnoid (Bass et al., 1975). The first and second anterior

teeth (A1 and A2) of white sharks are erect and nearly symmetrical, while the lateral teeth (L1–L5) become progressively slanted toward the jaw corner (Bass et al., 1975). The reversed intermediate tooth (I) of white sharks creates a significantly larger interspace measurement between it and the first lateral tooth (L1) than between any other two teeth of the upper jaw. As a consequence, the longest cutting edges of these teeth face one another. Such an arrangement, combined with the curved cutting edge of I, would produce the largest puncture wounds at this site on either side of the jaw. The large space between I and L1 is buttressed by the intermediate bar and occurs at the point of maximum curvature of the upper jaw, which may make this region the strongest part of the upper jaw. If the importance of incapacitating pinniped prey in the initial strike is as vital to the predatory success of white sharks as the results presented here suggest, and the lateral snap (LS) behaviour is a typical mode of prey capture employed by white sharks, then the functional significance of the reversed intermediate teeth is clear.

Head shape and musculature facilitate rapid lateral head movements in white sharks. Like that of other sharks, the head of the white shark is flattened dorsoventrally while the body is flattened laterally, creating a hydrodynamically optimal reversal of planes (Budker, 1971; Weihs, 1981). The W-shaped anterior muscle blocks of all sharks are arranged segmentally on either side of the vertebral column, so that muscular contraction on one side of the body causes it to bend toward that side (Bone & Marshall, 1982; Leim & Summers, 1999). Thus, head shape and musculature that evolved under constraints of efficient swimming are conducive to performing the LS behaviour. The LS affords delivery of a devastating oblique bite with the anterolateral teeth that is probably faster than a perpendicular bite with the anterior teeth, because it allows a pursuing shark to maintain a parallel course to fleeing prey without sacrificing speed (Figure 5C).

Ethology of predation

Klimley et al. (1996a) presented a white shark predatory ethogram based on their studies of white-shark pinniped interactions at the South Farallon Islands (SFI), California. Their ethogram includes 24 behavioural units, some of which broadly overlap ours. The white shark predatory ethogram presented here is unusual in that most of the proposed behavioural units are described in considerable detail and supported by photographs. This is probably an artefact of the frequency and intensity of natural white shark predatory activity at Seal Island combined with the exceptional (seven-year) length of the present study. Selected behavioural units of the predatory ethogram warrant discussion of their likely functional significance and in the context of methodological limitations of this study.

Surface intercepts, whether occurring above (INA) or under water (INU), denote anticipation by a pursuing white shark. This may strike some readers as giving white sharks too much credit. But we have seen this behaviour often enough to be reasonably confident that at least some individuals are capable of anticipating where a fleeing prey animal will be a few seconds in the future. For example, on 29 July 2003, nicknamed Rasta, a 3.9-m

female white shark that has been recorded frequently at Seal Island since 21 July 1997, initiated a surface attack on a Class 2 Cape fur seal 300 m offshore in Sector 3. The attack began with a Lateral Broach (BRL) at 0813 h, followed 6 s later by a Surface Broach (BRS), followed 7 s later by a Surface Lunge (LUN); the seal dived and disappeared from view for 15 s, performing a high leap (possibly to locate the island visually) and, just as it began to fall back into the sea, Rasta rose directly underneath the seal and captured it between its jaws (INU). This entire sequence has been captured on videotape and is available, unedited, as supplementary material to this paper (http://www.mba.ac.uk/education/education_outreach.php?JMBA). Rasta employs an idiosyncratic predatory strategy featuring relatively low-energy but sustained pursuit in three spatial dimensions and enjoys a success rate of nearly 80%.

Repurchase (REP) seems to function to increase security of a white shark's grasp on a prey item. From Figure 4, it is clear that REP not only brought more of the decoy within grasp of the jaws, but also brought the longitudinal axis of the shark's head closer to perpendicular to the long axis of the decoy. Such a shift in grasp was probably accomplished via a sudden lateral movement of the head while the lower dentition remained largely inserted into the decoy. The lower dentition of white sharks is less flattened and blade-like in cross-section than that of the upper dentition (authors, personal observations). Anterior lower tooth impressions on the ventral surface of the decoy are less distinct than the upper impressions and with shredded margins, consistent with the lower teeth having rotated in place. The REP can be regarded as prey handling behaviour, which Helfman et al. (1997) define as a postcapture manipulation that facilitates subjugation and consumption of prey.

Subsurface carry (CAR) may reduce risk of injury to a white shark by drowning the seal or it may simply assert ownership over a kill and/or prevent another white shark usurping it. As many as 26 individual white sharks have been catalogued at Seal Island at once and as many as four observed attending a kill. Thus, competition among white sharks for a disabled seal at Seal Island is likely intense and CAR may help prevent kleptoparasitism by another white shark. Like Klimley et al. (1996a), this study found no evidence to support the 'bite, spit, and wait' hypothesis. The brief duration of successful white shark predatory events at Seal Island (Figure 3C) may reflect the relatively small mean size of pinniped prey and/or the intensity of competition among white sharks at Seal Island.

Lateral head shake (LHS) likely maximizes the cutting efficiency of a white shark's coarsely serrated teeth clamped on a food item. Performed underwater, LHS is often accompanied by depression, rotation and curling under of both pectoral fins. Such action probably braces the body in the water column and further increases the sawing efficiency of LHS (Eibbl-Eibesfeldt, 1964). The LHS and pectoral fin depression are action patterns common to the feeding of many predaceous sharks and, as Barlow (1974) suggested for the grey reef shark (*Carcharhinus amblyrhynchus*), in white sharks may be ritualized to serve in agonistic contexts as a social signal. Such an agonistic display was observed on 25 August 2000 at 1325 h, when—in a baited context and

at a distance of about 4 m—a 4-m male white shark displayed for ± 3 s toward a 3.5-m white shark of indeterminate sex, which accelerated rapidly away and did not return.

Food release (REL) may represent food rejection due to unpalatability or regurgitation under social threat. On 31 July 2002 750 m offshore in Sector 4 at 0735 h, a 3.2-m white shark performed a GRH on a partially digested Class 2 Cape fur seal (Figure 6L). Based on other observations of regurgitated seal parts, this incident may represent kleptoparasitism of a seal carcass vomited-up by another white shark, possibly in response to a threat by yet another white shark, unseen several metres below. Seal intestines were often neatly excised and floated to the surface at sites of successful predation events, but were not consumed by white sharks attending a kill. Occasionally, a seal's lungs (sometimes with heart attached) or head floated near a kill site and were not consumed by white sharks. Whether non-consumption of these body parts by white sharks represents rejection due to low quality as food and/or unpleasant gustatory or tactile qualities is unknown.

Surface-based observations and the concentration of predatory activity near the Launch Pad afforded advantages and limitations. Thousands of white shark predatory attacks on Cape fur seals were observed, some launched <4 m from the observation vessel, allowing description of four variations of initial strikes of differing verticality and body orientation (POL, BRS, BRL, and BRI). But observations limited to behaviours visible from the surface restricts the present study to the last three stages of the predatory cycle (approach, subjugation, and consumption). As Barlow (1977) noted, choice of appropriate behaviour units to be measured is one of the most important and difficult decisions to be made. Aspects of the predatory ethogram and event sequence of behavioural units are superficially similar to those reported by Klimley et al. (1996a) based on white shark predation on sea lions and other otariids at SFI, however, they did not compare successful versus unsuccessful attacks. Degree of verticality and orientation of the initial strike of an attacking white shark may be opportunistic rather than reflect optimality under a set of tactical conditions. Similarly, surface grasps employing a vertical (GRV) approach rather than horizontal (GRH) may reflect individual preference, logistical expedience, observer proximity, or presence of a competitor. Further observations are needed to address these matters. Due to the briefness of successful predatory events (Figure 3C) and the large area over which they occurred (Figure 3E), data on white shark predatory behaviour units presented here are strongly biased toward longer-duration events, accounting for the disproportionate representation of unsuccessful attacks in the subsample of predatory attacks thus scored. However, frequency and event sequence analyses of predatory units scored during predatory attacks on Cape fur seals at Seal Island suggest that white shark predatory behaviour is relatively inflexible at the earliest stages of attack and highly complex and variable at later stages.

The predatory ethogram of white sharks attacking Cape fur seals at the surface presented here can be diagrammed as a decision tree (Figure 8). That decisions can be acted upon via up to five behavioural units suggests that, at least

at Seal Island, predation by white sharks on Cape fur seals at the surface is not a simple stimulus-response reflex, but a highly complex tactical situation that has resulted in the development of highly plastic predatory responses. That at least 11 post-initial strike behavioural units have not been previously reported by Klimley et al. (1996a) from SFI suggests that predatory behaviour of white sharks is dependent upon prey characteristics and local conditions.

Development of idiosyncratic predatory tactics in known individuals that enjoy differential success rates suggests some degree of trial and error learning. Goldman & Anderson (1999) reported that white sharks <4 m TL at SFI utilized significantly larger activity spaces than >4.5-m-TL individuals. They conclude that competitive displacement of smaller white sharks by larger individuals is unlikely, suggesting that smaller (younger) sharks at SFI may search for prey over relatively large areas because they are unfamiliar with the area and have not yet learned locations of the best hunting sites, while larger (more experienced) sharks restrict their movements to relatively discrete hunting sites where they had successfully located, attacked, and consumed prey in previous years. The different spatial distribution of smaller (≤ 3.5 m TL) versus larger (>3.5 m TL) white sharks and elevated success rate of larger sharks at Seal Island also suggests learning through accumulated experience, although competitive displacement of smaller sharks by larger cannot be ruled out.

Social facilitation and competition

Although frequency of attacks on Cape fur seals was greatest <400 m from Seal Island, success rate was greater at distances >400 m (Figure 3E). This spatial pattern may simply reflect unavailability of seal haul-out opportunities away from the island and thus prolonged secondary pursuit opportunity for hunting white sharks. But it may also reflect increased intensity of competition among white sharks near Seal Island compared with further away. Frequency of attacks on seals increases with proximity to Seal Island, especially in Sectors 3 and 4 (Figure 3E,F), which contain the Launch Pad and where seal concentration is highest (Figure 3B). It stands to reason that intensity of exploitation competition and possibly interference competition (*sensu* Krebs & Davies, 1987) among white sharks would likewise increase with proximity to Seal Island. Thus, white sharks near the Launch Pad may not have the luxury of waiting for optimal parameters before launching a strike on a seal.

Further evidence supporting this interpretation comes from relative predatory success rate in various island sectors. The number of unsuccessful attacks is greater than the number of successful attacks in Sectors 3 and 4 and, conversely, the number of successful attacks exceeds the number of unsuccessful attacks in Sectors 1, 2, 3, and 4 (Figure 3F). Thus, at Seal Island, white shark predatory success rate is greatest in those sectors where frequency is lowest. White sharks hunting near Seal Island in Sectors 3 and 4 may often launch suboptimal strikes on Cape fur seals due to increased competition from other white sharks and experience a concomitant reduced predatory success rate, while those hunting further from the island

and in other sectors may be able to optimize their predatory strikes due to reduced intraspecific competition and thus enjoy increased predatory success. This constitutes the first evidence of social facilitation of predatory success in any elasmobranch.

The white shark is the largest extant predatory fish, combining many unusual features including large size, regional endothermy (restricted to swimming muscles, viscera, and brain), and coarsely serrated dentition (Compagno, 2001). Yet many aspects of its predatory strategies are common to other predatory fish. Collectively, spatiotemporal patterns of white shark predation on Cape fur seals at Seal Island appear to maximize likelihood of encountering and remaining cryptic from prey. Like many ambush predators among bony fish, the white shark relies on fast-start performance to overtake prey and rapid jaw protrusion to increase reach and help generate suction to facilitate prey capture (Helfman et al., 1997). However, contrary to Krause et al.'s (1998) finding with rock bass (*Ambloplites rupestris*) ambushing creek chubs (*Semotilus atromaculatus*), white sharks ambushing Cape fur seals at Seal Island enjoyed a significantly greater predatory success rate with smaller groups of prey.

According to the absolute kinesis model (Benhamou & Bovet, 1989), animals can optimize their utilization of patchy resources by concentrating searches where perceived resource quality is greatest. White sharks at Seal Island appear to hunt most intensely where their preferred prey aggregates at its primary entry-exit site, much as Klimley et al. (1992, 1996a) demonstrated for this species at SFI. Sims & Quayle (1998) described similar area-restricted searching behaviour by filter-feeding basking sharks and Fouts & Nelson (1999) suggested that Pacific angel sharks (*Squatina californica*) may select ambush sites enabling them to better detect and remain cryptic from prey. Similar ambush site selection criteria have been demonstrated in terrestrial snakes (Reinart et al., 1984; Slip & Shine, 1988), suggesting that remaining cryptic near environmental features associated with concentrations of prey may be a convergent strategy of many ambush predators.

Many aspects of predatory behaviour in white sharks at Seal Island resemble those of other predatory fish. This suggests that—despite this species' great size, regional endothermy, and specialized dentition—general principles of fish foraging behaviour apply to it. As a consequence, aspects of the predatory ethogram presented here may be applicable to other fish taxa.

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REFERENCES

- Ainley, D.G., Henderson, R.P., Huber, H.R., Boekelheide, R.J., Allen, S.G. & McElroy, T.L., 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *Memoirs of the Southern California Academy of Sciences*, **9**, 109–122.
- Ainley, D.G., Strong, C.S., Huber, H.R., Lewis, T.J. & Morrell, S.J., 1981. Predation by sharks on pinnipeds at the Farallon Islands. *Fisheries Bulletin*, **78**, 941–945.
- Ames, J.A., Geibel, J.J., Wendell, F.E. & Pattison, C.A., 1996. White shark-inflicted wounds of sea otters in California, 1968–1992. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 309–319. San Diego: Academic Press.
- Ames, J.A. & Morejohn, G.V., 1980. Evidence of white shark, *Carcharodon carcharias*, attacks on sea otters, *Enhydra lutris*. *California Fish and Game*, **66**, 196–209.
- Applegate, S.P., 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. *Los Angeles County Museum Contributions in Science*, **86**, 1–18.
- Barlow, G.W., 1974. Derivation of threat display in the gray reef shark. *Marine Behaviour and Physiology*, **3**, 71–81.
- Barlow, G.W., 1977. Modal action patterns. In *How animals communicate* (ed. T.A. Seboek), pp. 94–125. Bloomington: University of Indiana Press.
- Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N., 1975. Sharks of the east coast of southern Africa. V. The families Odontaspidae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhinodontidae. *Oceanographic Research Institute Investigatory Reports*, **39**, 22–26.
- Benhamou, S. & Bovet, P., 1989. How animals use their environment: a new look at kinesis. *Animal Behaviour*, **38**, 375–383.
- Bennett, A.F., 1986. Measuring behavioural energetics. In *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates* (ed. M.E. Feder and G.V. Lauder), pp. 69–81. Chicago: University of Chicago Press.
- Bernal, D., Dickson, K.A., Shadwick, R.E. & Graham, J.B., 2001. Review: analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comparative Biochemistry and Physiology: Molecular and Integrative Physiology*, **129A**, 695–726.
- Bone, Q., 1988. Muscles and locomotion. In *Physiology of elasmobranch fishes* (ed. T.J. Shuttleworth), pp. 99–141. Berlin: Springer-Verlag.
- Bone, Q. & Marshall, N.B., 1982. *Biology of fishes*. Glasgow: Blackie & Son Ltd.
- Bonham, K., 1942. Records of three sharks on the Washington coast. *Copeia*, **1942**, 264–266.
- Bres, M., 1993. The behaviour of sharks. *Reviews in Fish Biology and Fishes*, **3**, 133–159.
- Brodie, P. & Beck, B., 1983. Predation by sharks on the grey seal (*Halichoerus grypus*) in eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 267–271.
- Budker, P., 1971. *The life of sharks*. London: Weidenfeld & Nicolson.
- Cockcroft, V.G., Cliff, G. & Ross, G.J.B., 1989. Shark predation on Indian Ocean bottlenose dolphins, *Tursiops truncatus*, off Natal, South Africa. *South African Journal of Zoology*, **24**, 305–310.
- Collier, R.S., 1992. Recurring attacks by white sharks on divers at two Pacific sites off Mexico and California. *Environmental Biology of Fishes*, **33**, 319–325.
- Collier, R.S., 2003. Suggested protocol for the scientific investigation of shark attacks. In *Field guide to the great white shark* (ed. R.A. Martin), pp. 152–159. Vancouver: ReefQuest Centre for Shark Research.
- Compagno, L.J.V., 2001. *Sharks of the world: an annotated and illustrated catalogue of shark species known to date*. Vol. 2. Bullhead, mackerel, and carpet sharks (heterodontiformes, lamniformes and orectolobiformes). FAO Species Catalogue for Fishery Purposes, no. 1, vol. 2. Rome: FAO.
- Corkeron, P.J., Morris, R.J. & Bryden, M.M., 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquatic Mammals*, **13.3**, 109–113.
- Dill, L.M., 1983. Adaptive flexibility in the foraging behaviour of fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 398–408.
- Eibbl-Eibesfeldt, I., 1964. *Land of a thousand atolls*. Cleveland: World Publishing Company.
- Ellis, D.V., 1986. *Animal behaviour and its applications*. Chelsea: Lewis Publishers, Inc.
- Endler, J.A., 1986. Defense against predators. In *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates* (ed. M.E. Feder and G.V. Lauder), pp. 109–134. Chicago: University of Chicago Press.
- Fitch, J.E., 1949. The great white shark *Carcharodon carcharias* Linnaeus in California waters during 1948. *California Fish and Game*, **35**, 135–138.
- Fouts, W.R. & Nelson, D.R., 1999. Prey capture by the Pacific angel shark, *Squatina californica*: visually mediated strikes and ambush-site characteristics. *Copeia*, **1999**, 304–312.
- Frazetta, T.H., 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology*, **108**, 93–107.
- Gerking, S.D., 1994. *Feeding ecology of fish*. San Diego: Academic Press.
- Goldman, K.J. & Anderson, S.D., 1999. Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environmental Biology of Fishes*, **56**, 351–364.
- Gruber, S.H. & Cohen, J.L., 1985. Visual system of the white shark, *Carcharodon carcharias*, with emphasis on retinal structure. *Memoirs of the Southern California Academy of Sciences*, **9**, 61–72.
- Hellman, G.S., Collette, B.B. & Facey, D.E., 1997. *The diversity of fishes*. London: Blackwell Science.
- Hubbell, G., 1996. Using tooth structure to determine the evolutionary history of the white shark. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 9–18. San Diego: Academic Press.
- Klimley, A.P., Anderson, S.D., Pyle, P. & Henderson, R.P., 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia*, **1992**, 680–690.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S. & Kelly, J.T., 2001. The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology*, **138**, 617–636.
- Klimley, A.P., Pyle, P. & Anderson, S.D., 1996a. The behavior of white sharks and their pinniped prey during predatory attacks. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 175–191. San Diego: Academic Press.

- Klimley, A.P., Pyle, P. & Anderson, S.D., 1996b. Tail slap and breach: agonistic displays among white sharks? In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 241–255. San Diego: Academic Press.
- Krause, J., Ruxton, G.D. & Rubenstein, D., 1998. Is there always an influence on shoal size on predator hunting success? *Journal of Fish Biology*, **52**, 494–501.
- Krebs, J.R. & Davies, N.B., 1987. *An introduction to behavioural ecology*, 2nd edn. Oxford: Blackwell Scientific Publications.
- Le Boeuf, B.J., Riedman, M. & Keyes, R.S., 1982. White shark predation on pinnipeds in California coastal waters. *Fisheries Bulletin*, **80**, 891–895.
- Leim, K.F. & Summers, A.P., 1999. Muscular system gross anatomy and functional morphology of muscles. In *Sharks, skates and rays: the biology of elasmobranch fishes* (ed. W.C. Hamlett), pp. 93–114. Baltimore: Johns Hopkins University Press.
- Long, D.J., 1996. Records of white shark-bitten leatherback sea turtles along the central California Coast. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 317–319. San Diego: Academic Press.
- Long, D.J., Hanni, K.D., Pyle, P., Roletto, J., Jones, R.E. & Bandar, R., 1996. White shark predation on four pinniped species in central California waters: geographic and temporal patterns inferred from wounded carcasses. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 263–274. San Diego: Academic Press.
- Long, D.J. & Jones, R.E., 1996. White shark predation and scavenging on cetaceans in the eastern North Pacific Ocean. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 293–307. San Diego: Academic Press.
- Long, D.J. & Waggoner, B.M., 1996. Evolutionary relationships of the white shark: a phylogeny of lamniform sharks based on dental morphology. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 37–47. San Diego: Academic Press.
- Martin, R.A., 2003. *Field guide to the great white shark*. Vancouver: ReefQuest Centre for Shark Research.
- McCosker, J.E., 1985. White shark attack behavior: observations of and speculations about predator and prey strategies. *Memoirs of the Southern California Academy of Sciences*, **9**, 123–135.
- Moss, S.A., 1972. The feeding mechanism of sharks of the family Carcharhinidae. *Journal of Zoology*, **167**, 423–436.
- Moss, S.A., 1977. Feeding mechanisms in sharks. *American Zoologist*, **17**, 355–364.
- Motta, P.J., Hueter, R.E. & Tricas, T.C., 1991. An electromyographic analysis of the biting mechanism of the lemon shark, *Negaprion brevirostris*: functional and evolutionary implications. *Journal of Morphology*, **210**, 55–69.
- Motta, P.J., Hueter, R.E., Tricas, T.C. & Summers, A.P., 1997. Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *Journal of Experimental Biology*, **200**, 2765–2780.
- Motta, P.J., Hueter, R.E., Tricas, T.C. & Summers, A.P., 2002. Kinematic analysis of suction feeding in the nurse shark, *Ginglymostoma cirratum* (Orectolabiformes, Ginglymostomatidae). *Copeia*, **2002**, 24–38.
- Myrberg, A.A. Jr, 1987. Understanding shark behavior. In *Sharks: an inquiry into biology, behavior, fisheries, and use* (ed. S. Cook), pp. 41–83. Portland: Oregon State University Extension Service, Portland.
- Northcutt, R.G., ed., 1977. Recent advances in the biology of sharks. *American Zoologist*, **17**, 287–515.
- Northcutt, R.G., 1978. Brain organization in the cartilaginous fishes. In *Sensory biology of sharks, skates, and rays* (ed. E.S. Hodgson and R.F. Mathewson), pp. 117–193. Arlington: Office of Naval Research.
- Orr, R.T., 1959. Sharks as enemies of sea otters. *Journal of Mammalogy*, **40**, 617.
- Powlik, J.J., 1990. *Feeding structures of the white shark, Carcharodon carcharias (Linnaeus), with notes on other species*. MSc thesis, University of British Columbia, Vancouver, Canada.
- Powlik, J.J., 1995. On the geometry and mechanics of tooth position in the white shark, *Carcharodon carcharias*. *Journal of Morphology*, **226**, 277–288.
- Pratt, H.L. Jr, Casey, J.G. & Conklin, R.B., 1982. Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York. *Fisheries Bulletin*, **80**, 153–156.
- Preuschoft, H., Reif, W.-E. & Müller, W.H., 1974. Funktionsanpassungen in form und struktur an haifischzähnen. *Zeitschrift für Anatomie und Entwicklungsgeschichte*, **143**, 315–344.
- Reinart, H.K., Cundall, D. & Bushar, L.M., 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia*, **1984**, 976–981.
- Scholl, J.P., 1983. Skull fragments of the California sea lion (*Zalophus californianus*) in stomach of a white shark (*Carcharodon carcharias*). *Journal of Mammalogy*, **64**, 332.
- Shimada, K., 2002. Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). *Journal of Morphology*, **251**, 38–72.
- Sims, D.W. & Merritt, D.A., 1997. Determination of zooplankton characteristics in the presence of surface feeding basking sharks, *Cetorhinus maximus*. *Marine Ecology Progress Series*, **158**, 297–302.
- Sims, D.W. & Quayle, V.A., 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature, London*, **394**, 460–464.
- Siverson, M., 1999. A new large lamniform shark from the uppermost Giarle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh Earth Sciences*, **90**, 49–66.
- Slip, D.J. & Shine, R., 1988. Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology*, **22**, 323–330.
- Stewart, B.S. & Yochem, P.K., 1985. Radio-tagged harbor seal, *Phoca vitulina richardsi*, eaten by white shark, *Carcharodon carcharias*, in the Southern California Bight. *California Fish and Game*, **71**, 113–115.
- Strong, W.R. Jr, 1996a. Repetitive aerial gaping: a thwart-induced behavior in white sharks. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 207–215. San Diego: Academic Press.
- Strong, W.R. Jr, 1996b. Shape discrimination and visual predatory tactics in white sharks. In *Great white sharks: the biology of Carcharodon carcharias* (ed. A.P. Klimley and D.G. Ainley), pp. 229–240. San Diego: Academic Press.
- Tricas, T.C., 1985. Feeding ethology of the white shark, *Carcharodon carcharias*. *Memoirs of the Southern California Academy of Sciences*, **9**, 81–91.
- Tricas, T.C. & McCosker, J.E., 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proceedings of the California Academy of Sciences*, **43**(14), 221–238.
- Weih, D., 1981. Body section variations in sharks—an adaptation for efficient swimming. *Copeia*, **1981**, 217–219.

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