

# Hunting patterns and geographic profiling of white shark predation

R. A. Martin<sup>1</sup>, D. K. Rossmo<sup>2</sup> & N. Hammerschlag<sup>3</sup>

<sup>1</sup> Fish Museum, Zoology Department, University of British Columbia, Vancouver, BC, Canada

<sup>2</sup> Center for Geospatial Intelligence and Investigation, Department of Criminal Justice, Texas State University-San Marcos, San Marcos, TX, USA

<sup>3</sup> Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, USA

## Keywords

predator–prey interactions; predation risk; optimal foraging; geographic profiling; sharks; seals.

## Correspondence

Neil Hammerschlag, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA.  
Email: nhammerschlag@rsmas.miami.edu

Editor: Nigel Bennett

Received 30 October 2008; revised 19 March 2009; accepted 30 March 2009

doi:10.1111/j.1469-7998.2009.00586.x

## Abstract

Predators can play important roles in structuring their communities through top-down effects on the distribution and abundance of their prey. Sharks are top predators in many marine communities, yet few studies have quantified those factors influencing their distribution and hunting behaviour. Here, we use location data from 340 predatory interactions between white sharks *Carcharodon carcharias* (Linnaeus), and Cape fur seals *Arctocephalus pusillus pusillus* (Schreber), data on associated environmental factors, and spatial analysis, including a novel application of geographic profiling – a tool originally developed to analyse serial crime – to investigate spatial patterns of shark attack and search behaviour at Seal Island in False Bay, South Africa. We found that spatial patterns of shark predation at this site are nonrandom. Sharks appear to possess a well-defined search base or anchor point, located 100 m seaward of the seal's primary island entry–exit point. This location is not where chances of intercepting seals are greatest and we propose it may represent a balance among prey detection, capture rates, and competition. Smaller sharks exhibit more dispersed prey search patterns and have lower predatory success rates than larger conspecifics, suggesting possible refinement of hunting strategy with experience or competitive exclusion of smaller sharks from the most profitable hunting locations. As many of the features of this system will be common to other instances of foraging, our conclusions and approach employed may have implications and applications for understanding how large predators hunt and for studying other predator–prey systems.

## Introduction

Top predators can play important roles in structuring communities through top-down density- and risk-driven effects on the distribution and abundance of their prey (Creel & Christianson, 2008; Heithaus *et al.*, 2008). Sharks are top predators in many marine communities, yet few studies have quantified or determined those factors influencing their distribution and hunting behaviour (Heithaus, 2004). Although previous studies, using telemetry to study underwater shark movements, have suggested that sharks concentrate their movements to maximize encounter rates with prey [e.g. tiger sharks *Galeocerdo cuvier* (Péron & Lesueur), Heithaus *et al.*, 2002; Heithaus & Dill, 2006; white sharks *Carcharodon carcharias* (Linnaeus), Klimley *et al.*, 1992, 2001a,b; Goldman & Anderson, 1999], sample sizes were small, documented predation events were rare, and/or predator–prey causal relationships were generally inferred without the benefit of direct observation of their interactions. Further studies of large shark foraging behaviour, therefore, are important for understanding the ecology of

these species and are particularly important at this time in light of steep declines in their populations (e.g. Baum *et al.*, 2003; Dulvy *et al.*, 2008) and the recent realization that they may have important structuring roles in marine communities (e.g. Myers *et al.*, 2007; Heithaus *et al.*, 2008).

The waters surrounding Seal Island in False Bay, South Africa, provide a unique opportunity to study predator–prey interactions involving large sharks. Here, white sharks attack Cape fur seals *Arctocephalus pusillus pusillus* (Schreber) at the water's surface with steep vertical attacks that are highly visible. Attacks can easily be documented with high frequency in a confined area within 2 km of shore during the winter (May–August) (Martin *et al.*, 2005). Predatory behaviour of white sharks at Seal Island was studied over an 8-year period by Martin *et al.* (2005) and Hammerschlag, Martin & Fallows (2006). Based on observations made between sunrise and sunset, they found that frequency and success rate of shark predations are highest during low light levels, sharks selectively target lone, young of the year seals (<1 year old), and intraspecific competition among sharks may be great. Large white sharks (>3.5 m) exhibit higher

seal capture success rates than smaller individuals. Predatory success rate decreases with proximity to the island, which may be the result of sharks launching suboptimal strikes to prevent kleptoparasitism by conspecifics. What remains unknown at this site is whether sharks search for prey in the waters surrounding Seal Island in a random fashion, limit their searches to pinniped entry–exit points, or focus their hunting in specific areas along the seal’s travel path from land to open water. At Seal Island, the ability to document a large proportion of natural predation events that occur frequently in a restricted area facilitates investigation of spatial aspects of white shark predation, including both attack and search patterns.

Geographic profiling (GP) was originally developed as a criminal investigative tool to analyse patterns of serial crime (Rossmo, 1997, 2000). It uses the locations of a series of crimes linked to a common offender to determine the most probable area for that offender’s origin of search behaviour (referred to as the search base or anchor point). GP is the most sophisticated and accurate method available for investigating the possible location of an anchor point from a spatial pattern of connected incidents (Rossmo, 2000; Rich & Shively, 2004). In addition to applications in a wide range of human geographic behaviour (Kucera, 2005; Rossmo, Hammerschlag & Martin, 2007), GP has also been used to study the foraging behaviour of pipistrelle bats *Pipistrellus pipistrellus* (Schreber) and *Pipistrellus pygmaeus* (Leach) (Le Comber *et al.*, 2006) and bumblebees *Bombus terrestris* (Linnaeus) (Raine, Rossmo & Le Comber, 2009). However, in those studies, GP was used to test the technique in describing and distinguishing between different foraging patterns. In contrast, we apply GP here for the first time to the marine environment to determine whether or not shark search behaviour is influenced by an anchor point. Establishing the existence, including location, size and shape of an anchor point – the ‘centre of gravity’ for a search pattern – provides insight into the hunting behaviour (search, attack and kill retention) and optimal foraging of sharks at Seal Island. GP is further described in the ‘Materials and Methods’.

The objective of this study is to determine whether there are any identifiable and predictable patterns of white shark predatory attacks on Cape fur seals at Seal Island using spatial analysis and GP. We analysed the locations of 340 predatory events and associated environmental data to determine whether: (1) there is a relationship between shark attack locations and distance from the island; (2) the point pattern of shark attack locations at this site are random, clustered or dispersed; (3) white sharks possess a search base or anchor point, and if so, where is it located and what is its size and shape.

## Materials and methods

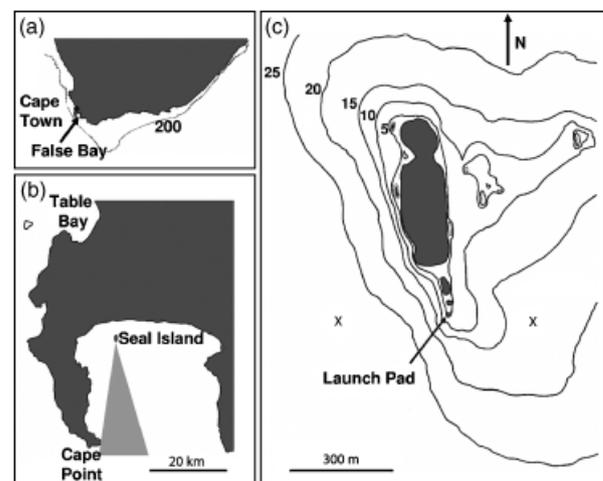
### Study site

Seal Island is a rocky islet located at the north end of False Bay, South Africa, centred at latitude 34.1374°S, longitude

18.5825°E (Fig. 1). Its underwater topography features a sharp drop-off along most of the western side where 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 from shore. Some 64 000 Cape fur seals (David, 1991; Kirkman, Oosthuizen & Meyer, 2006) occupy the island and forage within the bay and offshore, primarily leaving and returning in groups from a single point: a variably submerged rocky outcrop called the Launch Pad (LP), located just south of the island’s south point (Fig. 1c). Predatory attacks by sharks occur at the surface and are concentrated close to shore (within <2 km) on the southern side of the island, primarily when seals are travelling to and from LP (Martin *et al.*, 2005). In the winter, mean daily (between sunrise and sunset) attack frequency is 6.7 with up to 43 predatory events recorded on a single day (Hammerschlag *et al.*, 2006).

### Data collection

By stationing at a terminus off Seal Island, a single vessel can survey the waters around the island some 270°, uninterrupted to a distance of 3.0 km. With two vessels at opposite terminals, nearly all the water surrounding Seal Island can be surveyed to a comparable distance (Fig. 1c). During the winter of 2004, environmental and GPS-referenced data were recorded from 340 natural predatory interactions between white sharks and seals within 2000 m of Seal Island. Methods of predation event detection and approach follow Martin *et al.* (2005) and Hammerschlag *et al.* (2006). When a predatory event was detected, at least



**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); (c) depth contours (m) with location of the Launch Pad marked. While waiting for predation events, boats were stationed (indicated with an ‘x’) on opposite ends of the south side of the island. This allows nearly all the water surrounding Seal Island to be surveyed by two boats, but is closest to where the majority of predation events occur.

two observers from the research team were dedicated to guiding the vessel to the location of the initial strike where GPS coordinates were recorded, accurate to within 5 m. Ocean depth here was measured using an on-board depth sounder. Predatory attacks were categorized as successful (seal eaten) or unsuccessful (seal not eaten). During or immediately following many predatory events, sharks were close enough (<3 m) for sufficient time to permit estimation of shark size. Estimations were made independently by two trained observers. Shark lengths were estimated to the nearest 0.5 m against known dimensions of the boat and placed into one of three size categories: small (<3 m); medium (3–3.5 m); or large (>3.5 m). Shark length was only recorded when it could be estimated with confidence by both trained observers (85 out of 340 total predations).

### Spatial analysis and geographic profiling

To gain further insight into shark foraging at Seal Island, their attack locations were spatially analysed and geographically profiled. While we could not observe shark search patterns directly, attack locations could be recorded. These locations are a function of predator and prey intersections in time and space, so it is possible to make inferences about shark hunting behaviour from the point pattern of attacks. Telemetry tracking of tagged seals (Laroche *et al.*, 2008) as well as following individual groups (Martin *et al.*, 2005) indicate that seals travel from Seal Island to the Atlantic Ocean and back in a wedge-shaped path (Fig. 1b), the apex of which is LP – their primary entry and exit point (Fig. 1c). This movement means that prey density decreases linearly with distance from LP as the same number of seals are spread over an increasingly larger area as they swim from a single point (LP) outwards toward the ocean.

To study the spatial relationship between shark attack locations and distance from the Island, attacks were plotted against distance from LP, while a radar chart was used to examine the directional distribution of shark attacks relative to LP.

To determine whether shark attack locations in False Bay are random, clustered or dispersed, and to investigate the possibility of an anchor point for shark hunting behaviour, the locations of predation events were entered into a GP program called *Rigel* (developed by ECRI, <http://www.ecri.canada.com>, accessed 25 January 2008). *Rigel* generates a number of spatial statistics, and outputs a probability surface called a geoprofile, which shows the most likely anchor point area (referenced to the attack locations). A geoprofile consists of 40 000 pixels, each with its own likelihood value (*z*-score) displayed through a colour scale. For this study, we used only the peak 1% of the geoprofile (the 400 pixels with the highest *z*-scores, indicating the area that most probably contains the anchor point). If sharks engage in random or uniform search behaviour, then the geoprofile will not possess a clearly defined peak as no single location will have a high *z*-score (either most *z*-scores will be similar in value, or several random pixels will have moderate *z*-scores).

However, if shark search behaviour is influenced by an anchor point, then a peak profile area will be evident.

The GP algorithm incorporates two main concepts: distance decay; and a buffer zone (Rossmo, 1997, 2000; Equation 1). Distance decay is the tendency for spatial interactions to occur close to a predator's anchor point and then decrease with distance, a consequence of travel costs (e.g. energy and time), or selection of first encountered prey. The buffer zone is an area of reduced attack probability immediately surrounding the anchor point, resulting from the interaction of nonlinear distance decay and a linear increase in predatory opportunities with distance. In cross section, this function looks like a sloping calderic volcano (Fig. 2). To locate a predator's anchor point, the function is reversed and centred on the attack site. If there are multiple attack sites linked to the predator, multiple functions are used and combined to create a three-dimensional probability surface (for further illustration, see Le Comber *et al.*, 2006).

For each attack site (*i, j*) within the study area, the algorithm used in GP calculates the score function *p* as follows (Rossmo, 2000):

#### Equation 1 GP Algorithm

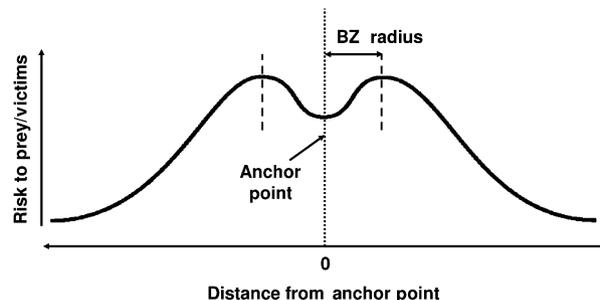
$$p_{ij} = k \sum_{n=1}^C \left[ \phi / (|x_i - x_n| + |y_j - y_n|)^f + (1 - \phi)(B^{g-f}) / (2B - |x_i - x_n| - |y_j - y_n|)^g \right] \quad (1)$$

where

$$|x_i - x_n| + |y_j - y_n| > B \supset \phi = 1 \quad (2)$$

$$|x_i - x_n| + |y_j - y_n| \leq B \supset \phi = 0 \quad (3)$$

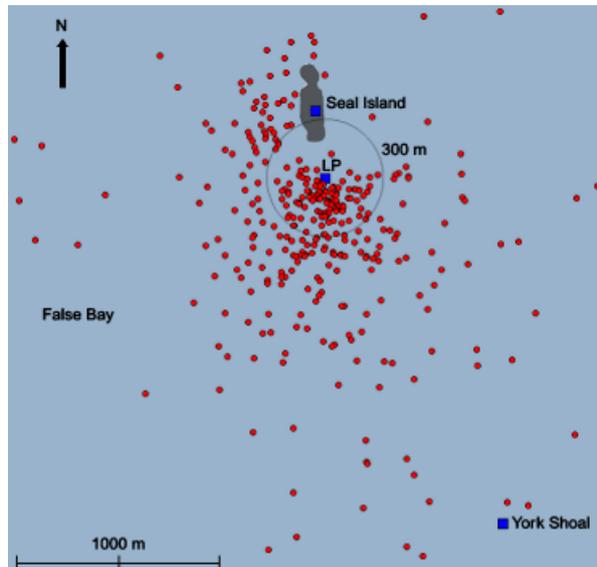
such that  $\phi$  functions as a weighting factor that is set to 0 for sites within the buffer zone, and 1 for sites outside the buffer zone, *k* is an empirically determined constant, *B* is the radius of the buffer zone, *C* is the number of foraging sites, *f* and *g* are empirically determined exponents, (*x<sub>i</sub>, y<sub>j</sub>*) are the coordinates of point (*i, j*) and (*x<sub>n</sub>, y<sub>n</sub>*) are the coordinates of the *n*th site. Thus, *p<sub>ij</sub>* describes the probability that the predator's



**Figure 2** Probability function used in the geographic profiling algorithm, showing the relationship between distance from a predator's anchor point and risk of victimization/predation (adopted from Rossmo, 2000). The buffer zone (BZ) is an area of reduced attack probability immediately surrounding the anchor point.

base or anchor point occurs at point  $(i, j)$ , given the location of the attack sites.

The following geospatial measures were calculated by *Rigel* from the point pattern of attack locations: (1) number of attack locations; (2) size of rectangular hunting area encompassing the attack locations; (3) whether the point pattern was random, clustered or dispersed; (4) LP hit score percentage; (5) distance from LP to the geoprofile peak; (6) direction from LP to the geoprofile peak; (7) depth at the



**Figure 3** Point pattern of 340 white shark *Carcharodon carcharias* attacks (red dots) on Cape fur seals *Arctocephalus pusillus pusillus* at Seal Island, False Bay, South Africa (June–July 2004), three reference points (blue squares) of known GPS coordinates [centre of Seal Island; Launch Pad (LP), seal entry–exit point; and York Shoal, a shallow reef almost 2 km south-east of LP], and 300 m radius circle centred on LP.

peak 1% of the geoprofile (equal to mean depth recorded for those attacks best defining that area). Hit score percentage (HS%) is a performance efficiency measure used in GP. The HS% for a given pixel is equal to the number of pixels with a higher  $z$ -score divided by the total number of pixels. The smaller the HS%, the more accurate the geoprofile; here, however, we use it here to evaluate LP's position on the geoprofile. The lower the HS% of the LP, the closer it is on the geoprofile to the peak area, and the more likely it serves as the search anchor point. HS% can therefore serve as a method of differentiating between anchor point locations for various shark groups.

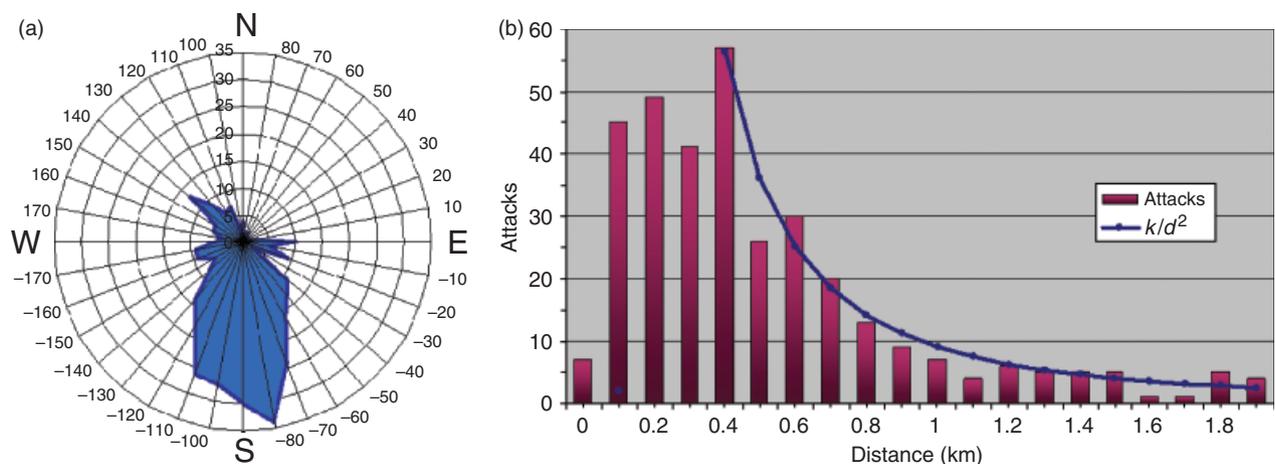
## Results

The shark attack locations create a point pattern on the ocean surface (Fig. 3). A radar plot of locations of shark predation on Cape fur seals displayed a strong directional bias south of LP (towards the opening of False Bay), where prey concentration is greatest (Fig. 4a).

All else being equal, attack frequency should be directly related to prey density. Because seals move outward from LP in a wedge-shaped pattern, spreading out over larger areas with distance, prey density in False Bay is inversely related to distance ( $A = k/d$ , where  $A$  represents attack frequency,  $k$  is a constant and  $d$  is the distance from LP).

But instead of an inverse relationship, we found that an inverse square distance curve ( $k/d^2$ ; where  $k$  is an empirically determined constant) provided the best fit to the attack frequency data in the 400–1900 m interval ( $n = 16$ ,  $r = 0.975$ ,  $P < 0.001$ ). This suggests that, at least within this range, predator density must also decrease with distance. At distances  $\leq 300$  m, where mean ocean depth abruptly decreases from  $> 25$  to  $< 10$  m, the pattern was decoupled (Fig. 4b).

Spatial analytic measures for the point patterns of all shark attack sites ( $n = 340$ ) and various subgroupings are



**Figure 4** Spatial patterns of 340 attacks by white sharks *Carcharodon carcharias* on Cape fur seals *Arctocephalus pusillus pusillus* at Seal Island, South Africa: (a) radar chart centred on Launch Pad (LP), showing strong southward bias of attack clustering; and (b) attack frequency versus distance from the LP (pinniped entry–exit point), overlain with a  $k/d^2$  curve (100 m categories) – note that the curve decouples at distances  $\leq 0.3$  km, where mean ocean depth changes attack probability.

**Table 1** Geospatial measures for 340 white shark *Carcharodon carcharias* attacks on Cape fur seals *Arctocephalus pusillus pusillus* at Seal Island, South Africa (data from June–July 2004, unless otherwise indicated)

Subgroup	Sites ( <i>n</i> )	Area (km <sup>2</sup> )	Pattern	LP hit score %	Distance (m)	Direction	Depth (m)
All attacks	340	7.9	CL	1	101	S	24
Successful attacks	150	7.9	CL	0	92	S	25
Failed attacks	190	7.5	CL	1	136	S	25
Incoming seals	73	6.5	CL	1	123	S	24
Small sharks <sup>a</sup>	20	2.9	<sup>b</sup>	1	71	SW	23
Medium sharks <sup>a</sup>	45	5.97	CL	3	179	SSW	24
Large sharks <sup>a</sup>	20	3.2	<sup>b</sup>	4	166	SSW	24

<sup>a</sup>2004–2005 data pooled.

<sup>b</sup>Insufficient data.

Area is the size of the rectangular hunting area encompassing the attack locations. Distance and direction are from LP to geoprofile peak. Depth is at the peak 1% of the geoprofile. A factor (subgroup listed) was recorded only when it could be clearly identified. The number of observations (*n*) vary because not all factors could be identified at every predatory event.

CL, clustered; LP, Launch Pad.

presented in Table 1. All subgroup point patterns were clustered. The peak geoprofile area for small shark attacks is located closer to LP in terms of both Euclidean distance and HS% than the peak geoprofile areas for large and medium-sized shark attacks.

The geographic profile of the shark attacks produced a clear and obvious peak area. This area, which corresponds with the most probable location of the anchor point, occurred 100 m south of the LP, the seal's primary dispersion point (Fig. 5a), where the average depth is 24 m. Geoprofiles showing the anchor points of small, medium and large white sharks are presented in Fig. 5b, c and d, respectively. The pattern of attacks by small sharks resulted in an unfocused anchor point, while that for larger sharks resulted in a more focused anchor point, located further from LP. The higher HS% for larger sharks also indicates their anchor point is further from LP than the anchor point of smaller sharks (Table 1).

## Discussion

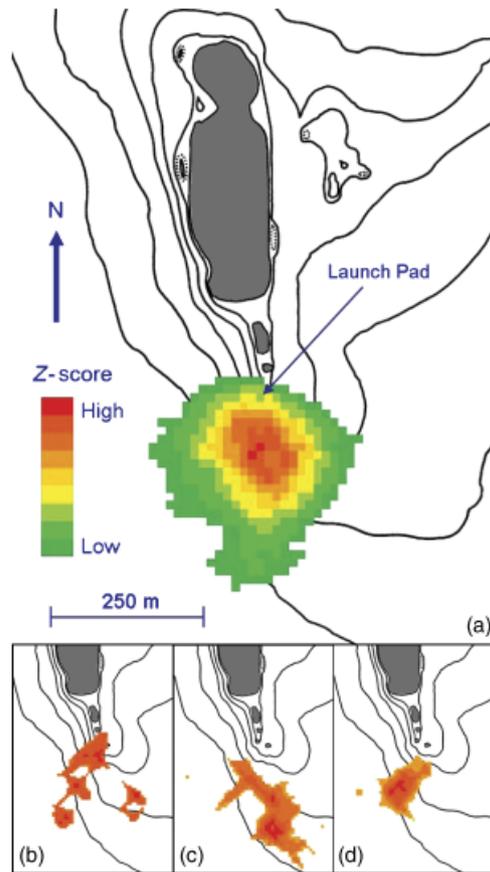
Only a few studies have quantified or determined those factors influencing the spatial distribution and hunting behaviour of large sharks (Heithaus, 2004). At Seal Island, it is unknown if sharks search for prey in a random fashion or focus their hunting in specific areas along the seal's travel path. Strong directional bias of shark attack sites south of LP (the seals' primary dispersion point) provides a reasonable two-dimensional approximation of the spatial distribution of predator and prey interactions relative to the latter's refuge/haul-out site (Fig. 4a), but it does not predict where individual shark predation will be greatest. Plotting attack frequency against distance from LP provides insight to this question. If sharks search in a random or uniform manner, then frequency of attacks – which require a spatial intersection between predator and prey – should be inversely related to distance from LP because of decreasing seal density. Instead, an inverse *square* distance curve ( $k/d^2$ ) provided the best fit to the attack frequency data in the 400–1900 m interval, suggesting predator search density also decreased

linearly with distance from LP (Fig. 4b). Such a pattern may reflect an optimal spatial arrangement, within which predators balance prey density against competition.

Seals are primarily detected by white sharks stalking from below via vision (Strong, 1996). At Seal Island, shark vision is limited by ocean visibility (ranging from 7 to 15 m, vertically), which increases with distance seaward from LP because of ocean depth and the trigonometry of Snell's Law. Light reflection within the cone defined by Snell's Law restricts the horizontal range of vision (*r*) to roughly the depth at which a shark is swimming; more precisely,  $r = D \tan 48.5^\circ$  ( $\sim 1.13D$ ), where *D* is the swimming depth of the shark. Therefore, at some point as a shark approaches LP, decreasing ocean depth and water clarity begin to restrict its ability to detect prey.

As expected, the decoupling of the  $k/d^2$  pattern at distances  $\leq 300$  m from LP is correlated with abrupt changes in bottom topography near Seal Island, in particular, decrease in mean depth (Fig. 1c). A decrease in depth (1) increases probability of visual detection of sharks by seals by reducing the amount of water between predator and prey; (2) reduces shark vertical strike distance, thereby reducing the impact energy and incapacitation probability of the initial strike (Hammerschlag *et al.*, 2006). This decoupling of the pattern also reflects the reduced ocean visibility near the island due to the continual release of seal excreta by the resident colony as well as the seals' behaviour of negotiating the last 60 m or so of their return to LP along the ocean bottom, thereby eliminating their vulnerability to attack from below.

GP was used to outline the nature of spatial patterning in shark predation in False Bay. However, the application of GP to shark attacks raises two issues. First, unlike predators with a den, burrow or nest, sharks are constantly mobile and do not have a fixed anchor point. But this does not necessarily mean their search behaviour is unconstrained. An anchor point represents a 'centre of gravity' around which a predator's efforts to locate prey are based, characterized by an optimal balance between prey density, competition and environment. Presence of prey and



**Figure 5** (a) Peak 1% geoprofile of 340 white shark *Carcharodon carcharias* attacks on Cape fur seals *Arctocephalus pusillus pusillus* at Seal Island, South Africa, over primary seal travel path from and returning to the island (a triangle originating at Launch Pad and widening to the south; see Fig. 1b); the geoprofile shows a strong, well-defined anchor point (the ranges for the z-score – the likelihood value of the anchor point for a given pixel in a geoprofile – are depicted with different colours, outlined in the legend). Peak 1% geoprofiles of white shark *C. carcharias* attacks at Seal Island by total length, showing increasing focus of anchor point with increasing size (i.e. experience): (b) small sharks (<3 m); (c) medium sharks (3–3.5 m); (d) large sharks (>3.5 m).

competitors are dynamic, so the optimality of an anchor point will flux over time, necessitating predator searches of nearby areas between return visits to the anchor point.

Second, even if shark predation is spatially focused by an anchor point, different sharks in the same environment may not share the same anchor point. This could be problematic for GP, which is normally used to analyse serial crimes linked to a single offender. However, because predation is relatively inflexible (Martin *et al.*, 2005), the hunting behaviour of a single predator species on a single prey species at a given site converges on a narrow subset of possibilities. The geographic characteristics in a given environment should produce a limited number of optimal search bases.

The geoprofile resulting from our data provides a way of testing this hypothesis (see Kucera, 2005, for an example of

how this was done with group insurgent activity in Baghdad). The hunting behaviour of sharks could be constrained in one of three ways: (1) influenced by a single anchor point – this would result in a single peak area on the geoprofile; (2) influenced by multiple anchor points – this would result in multiple peak areas on the geoprofile; (3) uninfluenced by any anchor point (random or uniform search behaviour) – this would result in no obvious peak areas on the geoprofile, only a roughly uniform probability surface or perhaps several chance small peaks. Our data resulted in a clear and well-defined single peak on the geoprofile, suggesting not only that shark movement around Seal Island is nonrandom, but also that sharks follow search patterns around an optimal common anchor point.

The geoprofile peak, corresponding with the most probable location of the anchor point or search base, is not at LP, the seals' primary entry and exit point from the island; rather, it occurs 100 m south, in an area with an average depth of about 24 m (Fig. 5a). This anchor point location is not where a shark's chances of encountering and intercepting seals are greatest (which is at LP). We propose this location may be where individual white sharks optimize their predatory success rate as a function of proximity to LP and ocean depth under conditions of: (1) probability of prey encounter; (2) capture rate; (3) intraspecific competition. Acoustic tracking of both sharks and seals at this site could be used to further test these hypotheses. Supporting this interpretation, Klimley *et al.* (1992, 2001b) suggest that white sharks position themselves around shore-based seal rookeries off the coast of California to maximize their chance of intercepting and capturing pinnipeds at entry and departure points.

A range of animals exhibit size or ontogenetic differences in foraging behaviour and success rate [e.g. common marmosets, *Callithrix jacchus* (Linnaeus), in Brazil, Souto *et al.*, 2007; and lions, *Panthera leo* (Meyer), in the Serengeti, Schaller, 1972]. Our results suggest size-based differences in shark hunting behaviour at Seal Island, comparable to white sharks at other locations.

The anchor point of large sharks at Seal Island is considerably more focused than the anchor point of small sharks, while the anchor point of intermediate-length sharks falls somewhere in between (see Fig. 5b, c and d). Similarly, at South-east Farallon Island, California, Goldman & Anderson (1999) found white sharks <4 m long utilized significantly larger activity spaces (larger spatial range) than individuals >4.5 m. Size dominance is one possible explanation for this pattern as larger sharks may competitively exclude smaller sharks from the most profitable hunting areas. Smaller sharks could also choose to range further because of a higher probability of kill loss to larger and stronger competitors in optimal areas. Therefore, smaller sharks may only search in the most profitable hunting locations when larger sharks are not present.

Alternatively, experience and spatial learning could play a role in hunting site selection by white sharks. Goldman & Anderson (1999) concluded larger, presumably more experienced white sharks restricted their movements to smaller

areas where they had made successful kills in previous years, while younger, less experienced sharks moved over a wider area because they had not yet learned the best hunting sites. This pattern is also consistent with our geoprofiling results and the higher predatory success rate of larger sharks at Seal Island reported by Martin *et al.* (2005). Lions in the Serengeti limit their hunting activities to areas they have learned contain worthwhile concentrations of suitable prey (Schaller, 1972). White sharks, like other predators, may refine their search patterns with experience and learn to concentrate hunting efforts in those locations with the highest probability of successful prey capture.

GP provides a useful means of analysing large sets of spatial foraging data, modelling predator hunting methods, and graphically summarizing point patterns. Le Comber *et al.* (2006) used techniques of GP to study the foraging patterns in two sympatric colonies of pipistrelle bats and found that model variables can be used as numerical descriptors of foraging patterns that differentiate interspecies foraging patterns. In an experimental study of bumblebee foraging, Raine *et al.* (2009) applied GP to reduce complex patterns of spatial data to a small number of parameters, and discriminate between foraging patterns resulting from different hypothetical foraging algorithms and flower densities. In the present study, we used it to reveal that white shark hunting patterns at Seal Island are nonrandom and appear to be based around a common anchor point. Smaller sharks exhibit more dispersed prey search patterns and have lower predatory success rates than larger conspecifics. Our study system is likely to share features in common with other systems where predator hunting patterns are not well understood and difficult to study; our approach and conclusions may therefore be applicable to the study of other predator–prey systems.

## Acknowledgements

We thank C. Fallows, M. Fallows, R. Lawrence and M. Bright for invaluable support, and our research assistants for their work and dedication. Thanks to ReefQuest Center for Shark Research and the Herbert W. Hoover Foundation for funding. We thank H. Oosthuizen and MCM for permitting us to work at Seal Island. A special thanks to C. Peyer and A.E. Martin for support. Thanks to T. Kellison, A.P. Klimley, S. Le Comber, M.R. Heithaus and the anonymous reviewers for helping us strengthen this paper.

## References

- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**, 389–392.
- Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**, 194–201.
- David, J.H.M. (1991). History and current status of the seal population in False Bay. *Trans. Roy. Soc. S. Afr.* **47**, 641–647.
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M., Gibson, C., Martinez, J., Musick, J.A., Soldo, A., Stevens, J.D. & Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conserv.: Mar. Freshw. Ecosyst* **18**, 459–482.
- Goldman, K.J. & Anderson, S.D. (1999). Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environ. Biol. Fish* **56**, 351–364.
- Hammerschlag, N., Martin, R.A. & Fallows, C. (2006). Effects of environmental conditions on predator–prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environ. Biol. Fish* **76**, 341–350.
- Heithaus, M.R. (2004). Predator–prey interactions. In *Biology of sharks and their relatives*: 487–522. Carrier, J.C., Musick, J.A. & Heithaus, M.R. (Eds). Boca Raton, FL: CRC Press.
- Heithaus, M.R. & Dill, L.M. (2006). Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* **114**, 257–226.
- Heithaus, M.R., Dill, L.M., Marshall, G.J. & Buhleier, B. (2002). Habitat use and foraging behaviour of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Mar. Biol.* **140**, 237–248.
- Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* **23**, 202–210.
- Kirkman, S.P., Oosthuizen, W.H. & Meyer, M.A. (2006). The seal population of Seal Island, False Bay. In *Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa. Proceedings of a Specialist Workshop. WWF South Africa Report Series – 2006/Marine/001*: 83–94. Nell, D.C. & Peschak, T.P. (Eds). Cape town: WWF South Africa.
- 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* **3**, 680–690.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F. & Van Sommeran, S. (2001a). Radio-acoustic positioning as a tool for studying site-specific behaviour of the white shark and large marine species. *Mar. Biol.* **138**, 429–446.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S. & Kelly, J.T. (2001b). The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar. Biol.* **138**, 617–636.
- Kucera, H. (2005). Hunting insurgents: geographic profiling adds a new weapon. *GeoWorld* 30–32.

- Laroche, R.K., Kock, A.K., Dill, L.M. & Oosthuizen, W.H. (2008). Running the gauntlet: a predator–prey game between sharks and two age classes of seals. *Anim. Behav.* **76**, 1901–1917.
- Le Comber, S.C., Nicholls, B., Rossmo, D.K. & Racey, P.A. (2006). Geographic profiling and animal foraging. *J. Theoret. Biol.* **240**, 233–240.
- Martin, R.A., Hammerschlag, N., Collier, R.S. & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. UK* **85**, 1121–1135.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. & Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846–1850.
- Raine, N.E., Rossmo, D.K. & Le Comber, S.C. (2009). Geographic profiling applied to testing models of bumblebee foraging. *J. Roy. Soc. Interface* **6**, 307–319.
- Rich, T. & Shively, M. (2004). *A methodology for evaluating geographic profiling software*. Cambridge, MA: Abt Associates.
- Rossmo, D.K. (1997). Geographic profiling. In *Offender profiling: theory, research and practice*: 159–175. Jackson, J.L. & Bekerian, D.A. (Eds). Chichester: John Wiley & Sons.
- Rossmo, D.K. (2000). *Geographic profiling*. Boca Raton, FL: CRC Press.
- Rossmo, D.K., Hammerschlag, N. & Martin, R.A. (2007). *Environmental criminology and optimal foraging models: Spatial analysis and geographic profiling of white shark predation*. London, UK: Environmental Criminology and Crime Analysis.
- Schaller, G.B. (1972). *The Serengeti lion: a study of predator–prey relations*. Chicago: University of Chicago Press.
- Souto, A., Bezerra, B.M., Schiel, N. & Huber, L. (2007). Saltatory search in free-living *Callithrix jacchus*: environmental and age influences. *Int. J. Primatol.* **28**, 881–893.
- Strong, W.R. (1996). Shape discrimination and visual predatory tactics in white sharks. In *Great white sharks: the biology of Carcharodon carcharias*: 229–240. Klimley, A.P. & Ainley, D.G. (Eds). San Diego: Academic Press.