BEHAVIOURAL ECOLOGY OF WHITE SHARKS *CARCHARODON CARCHARIAS* IN FALSE BAY, SOUTH AFRICA:

Towards improved management and conservation of a threatened apex predator

By

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DECLARATION

I, Alison Ann Kock, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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ETHICS STATEMENT

Data were collected according to protocols approved by the University of Cape Town and South African Department of Environmental Affairs: Oceans and Coasts, and adhered to the legal requirements of South Africa. All research methods were approved and conducted under the South African Department of Environmental Affairs: Oceans and Coasts permitting authority. Permit # V1/1/5/1, V1/8/5/1.

Alison Ann Kock

STATEMENT OF CONTRIBUTION BY OTHERS

Chapter 1
The introduction was my own work. My supervisors, Prof. Justin O'Riain and Prof. Charles Griffiths proof-read and commented on earlier versions of the chapter.

Chapter 2
The general methods chapter was my own work. My supervisors, Prof. Justin O'Riain and Prof. Charles Griffiths proof-read and commented on earlier versions of the chapter.

Chapter 3
This chapter was published in PLOS ONE in 2013. I am primary author and Prof. Justin O'Riain, Katya Mauff, Michael Meyer, Deon Kotze and Prof. Charles Griffiths are co-authors. I was responsible for conception of the project, field work, data analysis, interpretation of results and writing the manuscript. Assoc. Prof. Justin O'Riain assisted with interpretation; Katya Mauff provided statistical assistance and assisted with interpretation, Michael Meyer and Deon Kotze assisted in the field with deployment of acoustic receivers and shark tagging. Prof. Charles Griffiths provided editorial comments. All authors, except Deon Kotze, helped in the revision of the manuscript. Two anonymous reviewers from PLOS ONE improved upon earlier versions of the manuscript.

Chapter 4
Michael Meyer and Deon Kotze assisted in the field with deployment of acoustic receivers and shark tagging. Katya Mauff provided statistical assistance and assisted with interpretation of results. Prof. Justin O'Riain proofread earlier versions of the chapter. Karl Laroche assisted with data collection on predatory events and field work. Ryan Johnson assisted with the statistical analysis. Prof. Justin O'Riain and Prof. Charles Griffiths proof-read and provided editorial comments on earlier versions of the chapter.

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Behavioural ecology of white sharks *Carcharodon carcharias* in False Bay, South Africa: Towards improved management and conservation of a threatened apex predator

ALISON A. KOCK, January 2014

ABSTRACT

The coastal waters off South Africa support a significant proportion of the global white shark population, with at least four well-established coastal aggregation sites. How critical these sites are to the southern African and hence global white shark population depends to a large extent, on their levels of residency and site fidelity, in relation to potential threats. Here, I attempt to provide such data by studying the annual and seasonal presence of white sharks in False Bay. From 1 April 2004 - 31 December 2007, a total of 68 (46 female, 22 male) sharks, ranging in length from 1.7 to 5 m, were tagged with acoustic transmitters and monitored on an array of 30 receivers, distributed along the Inshore region of False Bay and at Seal Island, for a maximum of 1349 days. I used generalized linear mixed effects models to investigate the effects of season, habitat type, sex, size and time of day on shark presence. Most tagged sharks were immature animals, some of which were detected in the Bay in all months and across all years. In autumn and winter, males and females aggregated around Seal Island, where they fed predominantly on young-of-the-year seals. Sharks, regardless of sex or size, over-dispersed on the South side of the Island at sunrise, where the probability of encountering predator-naïve seals was highest. Shark presence at Seal Island mirrored the spatial distribution of predation around the Island, which was highest on the South side within 400 m of the Island, and at sunrise. In spring and summer, there was marked sexual segregation in presence, with females frequenting the Inshore areas and males seldom being detected in the Bay. Within the Inshore region, female white sharks showed a preference for beach, compared to rocky, mixed and harbour habitats. The preference for beach habitat likely reflects a combination of high prey availability, in addition to an open habitat suitable for detecting and securing prey. Overall, the results confirm False Bay as a critical area for white shark conservation as both sexes, across a range of sizes, show high levels of fidelity to the Bay.

Keywords: *Carcharodon carcharias*, white shark, residency, spatial ecology, sexual segregation

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CHAPTER 1

INTRODUCTION

Our understanding of white shark behaviour is slowly revealing a much more complex creature than any of us originally anticipated.

Photo credit Morne Hardenberg

1.1. Decline and vulnerability of shark populations

The depletion of top marine predators, particularly sharks, is of great concern, because their loss carries risks of ecosystem degradation (Bascompte *et al*. 2005, Heithaus *et al*. 2008). Significant declines in shark populations have been documented in areas where they were once common (Rose 1996, Baum *et al*. 2003, Baum & Myers 2004, Dulvy *et al*. 2008, Worm *et al.* 2013). Currently, over 21% of the species assessed by the Shark Specialist Group (SSG) of the International Union for the Conservation of Nature (IUCN) are listed as threatened (ranging from Vulnerable to Critically Endangered) (Dulvy *et al*. 2008). Globally, three-quarters (16 of 21) of pelagic sharks and rays have further elevated risk of extinction due to overfishing (Dulvy *et al*. 2008). Conserving sharks is thus a global conservation priority (Stevens *et al.* 2000) and devising successful conservation and management strategies is largely limited by our scientific knowledge of their biology and the identification of past, current and future threats to their survival.

Sharks are highly susceptible to a range of anthropogenic influences (Baum *et al*. 2003, Myers and Worm 2003, Ward-Paige *et al*. 2010) due to their life-history characteristics, including low fecundity, slow growth and late age of sexual maturity (Musick *et al*. 2000, Heithaus 2004, Garcia *et al*. 2008). Other factors, such as low global abundance, as well as complex migration patterns, spatial segregation of sexes (Sims 2005) and site fidelity (Heupel and Simpfendorfer 2005) can further increase the vulnerability of elasmobranchs to overfishing. Sharks that frequent coastal regions are particularly vulnerable, as they are threatened by diverse anthropogenic activities, including intensive shore-based fishing, pollution and the transformation or disturbance of natural habitat (Knip *et al*. 2010, Speed *et al*. 2010, Simpfendorfer *et al*. 2011). While limited in geographical extent, coastal perturbations may have a disproportionate effect on some shark populations, as many species utilize inshore, shallow water environments as birthing, nursery and/or feeding grounds (Speed *et al*. 2010, Simpfendorfer *et al*. 2011). The conservation of these species therefore requires the mitigation and regulation of these various threats in high priority conservation areas (Knip *et al*. 2010).

1.2. Conservation and management issues related to wide-ranging sharks

Wide-ranging sharks are often large, mobile animals capable of long-distance migrations, and their effective protection thus necessitates a coordinated, global conservation effort, including all areas that are critical for their different life history stages (Simpfendorfer and Milward 1993, Ward-Paige *et al*. 2010, Simpfendorfer *et al*. 2011). Protecting sharks which range across multiple oceanic ecosystems, is exacerbated by the difficulty associated with both detecting illegal human activities that impact adversely on sharks, or pursuing legal action in waters that are outside the Exclusive Economic Zones (EEZ) of countries, and thus beyond the responsibility and immediate concerns of national jurisdictions (Dulvy *et al*. 2008). In light of these challenges, there has been a recent emphasis on managing and protecting aggregation areas (Bizzarro *et al*. 2007, Speed *et al*. 2010, Field *et al*. 2011, de la Parra Venegas *et al*. 2011, Jewell *et al*. 2012), especially those that include high levels of philopatry and site fidelity associated with key life history stages, such as feeding and reproduction (Simpfendorfer *et al.* 2011, Bruce and Bradford 2012a) of a given species.

1.3. Importance of behavioural ecology studies in conservation

Our current lack of knowledge on the behaviour and ecology of most shark species is arguably one of the major obstacles to the development of sustainable local and global conservation and management plans. Behavioural ecology aims to understand the way in which behaviour contributes to the survival and reproduction of individual animals under different ecological conditions (Krebs and Davies 1993). Thus, behavioral ecology studies collect information on the behaviour, habitat use, movement patterns, and ecological interactions of individuals (Sundström *et al*. 2001, Parra 2005). In combination, these factors contribute to an individual's survival and reproductive success and are vital for the conservation and management of any target species. Therefore, the study of an organisms' behavioral ecology can contribute greatly to its conservation and management (Caro and Sherman 2011).

1.4. Importance of temporal and spatial patterns of site-fidelity and residency for the development of management plans

Research that identifies essential activities (e.g. mating), critical periods (e.g. pupping seasons) and habitats (e.g. nursery areas, or feeding grounds) that are adversely impacted by anthropogenic change offers the best short-term contribution to the development of relevant management approaches (Simpfendorfer *et al*. 2011). Such research requires fine-scale movement data (Simpfendorfer *et al*. 2011, Speed *et al*. 2010) to identify distinct home ranges (Holland *et al*. 1993, Morrissey and Gruber 1993, Holland *et al*. 1999, Hueter *et al*. 2005) and site fidelity (Speed *et al*. 2010, Knip *et al*. 2012), even for species that exhibit long distance migratory behaviour. Site-fidelity is the tendency for individuals to frequent, or return to, a site or region, and may include areas such as nursery grounds, mating or pupping grounds, and specific cleaning and feeding sites (Hueter *et al*. 2005, Speed *et al*. 2010). Many shark species show site fidelity at different temporal scales, including daily, annual and over the course of a lifetime (Speed *et al*. 2010, Knip *et al*. 2012). The degree of site fidelity is predicted to have a strong influence on a species susceptibility to human-induced disturbances e.g. fisheries, pollution, habitat destruction and shark control programs that target large sharks (Bruce and Bradford 2012a, Dulvy *et al*. 2014).

1.5. Conserving a species in conflict with humans

The white shark’s seasonal distribution along some popular recreational coastlines, natural opportunistic predatory tactics and large size, increase the potential for human-shark conflict (Curtis *et al*. 2012). White sharks have been implicated in a total of 346 unprovoked attacks on humans worldwide since 1839, including 102 (29.5%) fatalities (Curtis *et al*. 2012). Over the last century, the global frequency of white shark attacks has increased gradually (Burgess and Callahan 1996). In South Africa, a similar trend is apparent, with less than five attacks recorded during the period 1900 to 1909, 20 attacks from 1950 to 1959 and 60 attacks between 1990 and 1999 (Curtis *et al*. 2012). This increase is largely attributed to increasing human use of the ocean for recreation, as well as improved reporting of attacks (Klimley and Curtis 2006, Burgess *et al*. 2010).

Conservation goals can be difficult to achieve when the species in question poses a threat to human safety (Nyhus *et al*. 2003, Madden 2004). Although relatively rare, shark bites that result in human injury or death threaten existing shark protection measures through negatively influencing the public's perception of sharks and the further funding of their conservation (Kock *et al*. 2012). Furthermore, shark bites can negatively impact local business and tourism, and hence the perceived amenity value of the coast by the broader public. Together, these negative public perceptions and associated economic impacts may compel stakeholders to urge local authorities to initiate a variety of measures to mitigate human-shark conflict levels, many of which may be in contradiction to conservation objectives (Neff 2012). Currently white sharks are listed in Appendix II of the Convention on International Trade in Endangered Species and classified as "Vulnerable" by the World Conservation Union (Fergusson *et al*. 2009). Despite this, lethal control programmes, targeted at white sharks, have been implemented at many coastal recreational areas (Dudley 1997). These control measures, which include the use of large-mesh gill nets and/or baited "drum lines, aim to reduce the probability of a shark bite by reducing shark numbers (Dudley 1997). However, such methods are environmentally costly because they both decrease this threatened species and unselectively kill many other species (Cliff and Dudley 2011). Thus, alternative strategies are needed to mitigate conflict between water users and conservationists so that conservation of marine ecosystems and white sharks are not jeopardized. Understanding how and when large carnivores use areas that are frequented by humans (typically for recreational purposes) and reducing the amount of time that they overlap in space and in time, can help to mitigate negative interactions with people in a non-lethal way (Bruce and Bradford 2012a) and thus aid conservation efforts.

1.6. Predator-prey interactions and the ecological role of top order predators

Top order predators in both terrestrial and aquatic environments play a key role in ecosystem structure, functioning and resilience (Stevens *et al*. 2000, Estes *et al*. 2011, Heithaus *et al*. 2008, Baum and Worm 2009, Ferretti *et al*. 2010, Estes *et al*. 2011, Ruppert *et al*. 2013). Predators can shape the ecosystems in which they live in a direct (lethal) way by reducing prey densities, which in turn may affect populations at lower trophic levels (Abrahams 1995, Mann and Watson-Capps 2005, Luttbeg and Kerbey 2005, Ruppert *et al*. 2013, Heupel *et al*. 2014). Alternatively, predators can affect prey populations in an indirect way (non-lethal) manner, as anti-predator behaviour may manifest as changes in prey resource use, ultimately shaping community composition and dynamics (Lima 1998, Brown *et al*. 2001, Peacor and Werner 2001, Heithaus and Dill 2002, Schmitz *et al*. 2004, Owen-Smith and Mills 2006, Cresswell 2008, Wirsing *et al*. 2008).

It is recognized that removal of top predators in terrestrial and marine ecosystems has a 'top-down' effect on organisms at lower trophic levels (Estes and Duggins 1995, Estes *et al*. 1998, Ruppert *et al*. 2013, Heupel *et al*. 2014). Empirical studies have identified causal relationships between the loss of large, predatory sharks, and changes in abundance of populations lower down on the food web (Ruppert *et al*. 2013). For example, Ruppert *et al*. 2013 showed a significant change in the abundance of carnivores and herbivores between coral reefs with high shark density (non-fished reefs) compared to reefs with low shark densities (fished reefs). Their results offer empirical support that the loss of sharks contributes to mesopredator release, which in turn can possibly alter the numbers of primary consumers (Ruppert *et al*. 2013). Similarly ECOSIM models of the Venezuelan shelf, the Alaska Gyre and the French Frigate shoals in Hawaii suggest the removal of sharks will result in changes in the abundance of some prey species (Stevens *et al*. 2000). Predation attempts do not have to occur frequently, or always be successful, to have a major influence on the behaviour, group composition, group size, and habitat use of prey species (Bertram 1978, Lima 1998, Lima and Dill 1990). Thus the risk alone of predation can strongly influence population dynamics, energy flow, and ecosystem function (Boonstra *et al*. 1998, Creel *et al*. 2007). The loss of large sharks can therefore alter ecosystems in significant and unpredictable ways and emphasizes the need to conserve top predators.

1.7. Habitat use, selection and preference

Accurately describing and understanding the distribution of organisms is a fundamental problem in ecology (Goetz *et al*. 2007). Characterization of spatiotemporal habitat use within a specific environment is crucial for effective management, as threats need to be identified (Krausman 1999, Morris 2003, Goetz *et al*. 2007). Terrestrial and aquatic habitats are generally composed of a mosaic of patches that differ from each other physically and biologically (Ballance 1992) and thus offer different levels of protection from the elements and predation, while also offering different concentrations of food (Ballance 1992). Because of such heterogeneity, one expects to see specific patterns in the way animals are distributed and in the way they use patches within a given habitat (Ballance 1992).

Habitat selection is an active behavioral process by an animal, and each species searches for features within an environment that are directly or indirectly associated with the resources that an animal would need to reproduce, survive, and persist (Krausman 1999). Habitat preference is the consequence of habitat selection, resulting in the disproportional use of some resources over others (Krausman 1999, Franklin *et al*. 2000) and to survive, predators must persistently track spatial and temporal distributions of prey patterns at varying scales (Benoit-Bird and Au 2003). Foraging theory predicts that animals will select habitats that provide the greatest return in some form of currency, such as prey encounter rate (Stephens and Krebs 1986). However, for many animals, it is difficult to distinguish habitat selection for foraging purposes from those associated with mating or predator avoidance (Papastamatiou *et al*. 2009).

Technological advances, such as the rapid miniaturization and increasing sophistication of tags and tracking arrays that permit both localized (e.g. Heupel *et al*. 2006, Barnett *et al*. 2012) and global (Domeier and Nasby-Lucas 2012) detection of individual shark movement patterns (Simpfendorfer *et al.* 2011) have enabled the advancement of the study of spatial ecology in elasmobranchs. Understanding how individuals use an area over the course of a day, month or a year, is vital to understanding their habitat requirements at different temporal scales and, furthermore, the risks faced by endangered species throughout their life histories (Speed *et al*. 2010, Simpfendorfer *et al*. 2011).

Furthermore, effective management of shark populations requires a detailed understanding of essential habitats and of how these are utilized by sharks (Yates *et al*. 2012). Inshore environments typically support high biodiversity and productivity, and therefore provide important habitat for many shark species (Branstetter 1990, Simpfendorfer and Milward 1993, White and Potter 2004, Knip *et al*. 2010). However, differences in biotic and abiotic characteristics may require sharks to adopt different strategies in different areas (see Knip *et al*. 2010 and Speed *et al*. 2010 for reviews). This suggests that habitat plays a crucial role in driving how sharks use space and that populations will alter their habitat use patterns as required (Knip *et al*. 2010, Yates *et al*. 2012).

1.8. Study species

White sharks *Carcharodon carcharias* are vulnerable to human impacts, as they share all of the life history traits that threaten other shark species, in addition to being apex predators with low abundance and circum-global ranging patterns (Fergusson *et al*. 2009, Bruce 2008). Worldwide, they are protected by CITES Appendix II, which restricts exploitation, and they are listed as Vulnerable by the IUCN (Fergusson *et al*. 2009). They are protected in seven countries, including South Africa, but despite enacting protective legislation, there is limited knowledge available on how best to make such protection effective. Key to this objective is the identification of critical areas that function as nursery, breeding and feeding grounds and how the use of such areas varies in time and with the age and sex of individuals.

Whilst white sharks are known to engage in broad-scale coastal (Bonfil *et al*. 2005, Jorgensen *et al*. 2010, Bruce and Bradford 2012a) and oceanic migrations (Boustany *et al*. 2002, Bonfil *et al*. 2005, Bruce *et al*. 2006, Weng *et al*. 2007a, Domeier and Nasby-Lucas 2008, Bonfil *et al*. 2010), they typically aggregate in select coastal areas associated with pinnipeds (Goldman and Anderson 1999, Malcolm *et al*. 2001, Bruce *et al*. 2005, Domeier and Nasby-Lucas 2007, Laroche *et al*. 2008, Bruce and Bradford 2012a). In South Africa, white sharks are most often associated with coastal Cape fur seal (*Arctocephalus pusillus pusillus*) colonies in the southern and western Cape, but they have also been shown to frequent the inshore regions of False Bay (Kock *et al*. 2012), Mossel Bay (Johnson *et al*. 2009) and KwaZulu-Natal (Dudley 2012) when not feeding on seals. Limited information is available on the extent and reason(s) for white sharks aggregating in these inshore areas. It is also not known whether there are differences in the sex and/or age classes of sharks frequenting inshore or island aggregation sites and whether these patterns vary seasonally.

Sex-specific and size differences in migratory and aggregation patterns have been identified for white sharks, including differences in migration between the sexes for adult sharks off the coast of California (Anderson and Pyle 2003, Jorgensen *et al*. 2010), Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2007), Neptune Islands, Australia (Robbins 2007) and in the offshore area in the North Pacific (Jorgensen *et al*. 2010, Domeier and Nasby-Lucas 2012). These studies report differences in the arrival and departure times of male and female sharks at aggregation sites, with females typically arriving and leaving earlier than males at the Neptune Islands, Australia, while males arrive and leave earlier than females in the Pacific. Furthermore, previous research has suggested a clear size-based preference for different prey species, with white sharks ≤3 m feeding predominantly on teleosts and elasmobranchs, while white sharks >3 m supplement their diet with marine mammals, such as seals (Cliff *et al*. 1989, Weng *et al*. 2007b, Hussey *et al*. 2012). There are limited data on the fine-scale habitat use and movement patterns of white sharks at aggregation sites in South Africa.

1.8.1. Taxonomy

White sharks belong to the Class Chondricthyes (sharks, skates, rays and chimeras), of which there are an estimated 1200 species (Fowler *et al*. 2005) and Family Lamnidae, also called mackerel sharks, of which there are five extant species. Lamnids are characterized by having large, spindle-shaped bodies, large teeth, conical heads, long gill openings and crescent-shaped caudal fins with strong caudal keels (Compagno *et al*.

2005). All members of the Family are endothermic, with the ability to maintain a body temperature up to 15°C above ambient, distinguishing them further from over *ca* 500 other species of elasmobranchs (Carey *et al*. 1982, Goldman *et al*. 1996, Compagno *et al*. 2005). Lamnids are large upper trophic-level predators in their respective habitats, ranging in maximum size from 3 m total length (TL) for salmon sharks (*Lamna ditropis*) and porbeagle sharks (*Lamna nasus*), >4 m for short-fin mako (*Isurus oxyrinchus*) and longfin mako (*Isurus paucus*) to the maximum size of >6 m TL for white sharks, which are the largest of all the predatory sharks (Compagno *et al*. 2005).

The genus *Carcharodon* is characterized by diversification and an increase in abundance during the rise of marine mammals in the Oligocene period (Purdy 1996). Furthermore, more recent evolutionary change in tooth structure, such as increased serration and tooth size (larger) suggests *Carcharodon* species were initially piscivorous, before adapting to include marine mammals in their diet (Applegate and Espinosa-Arrubarrena 1996). These changes, in addition to adaptations, such as large body size and endothermy (Carey *et al*. 1982, Tricas and McCosker 1984, Block and Carey 1985, McCosker 1987, and Goldman *et al*. 1996), appear to be specific functional adaptations to enable white sharks to successfully exploit temperate-occurring marine mammals, in areas where other large sharks, such as bull (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) rarely occur.

1.8.2 Distribution by size and life history stage

White sharks have a circumglobal distribution with primary concentrations in South Africa (Pardini *et al*. 2001, Bonfil *et al*. 2005), Australia (Pardini *et al*. 2001, Bruce *et al*. 2006), New Zealand (Bruce *et al*. 2006, Duffy *et al*. 2012) and the northeastern Pacific (Boustany *et al*. 2002, Weng *et al*. 2007a, Domeier and Nasby-Lucas 2008) (Fig. 1.1.). As recently as 2001, white sharks were considered primarily to be inhabitants of continental, coastal waters (Compagno 2001). However, satellite technology has allowed migration behaviour to be documented and white sharks tagged in California, South Africa, Mexico and Australia have been shown to be capable of long-distance migrations to oceanic habitats, in addition to long-distance coastal migrations (Boustany *et al*. 2002, Bonfil *et al*. 2005, Bruce *et al*. 2006, Weng *et al*. 2007a, 2007b, Domeier and Nasby-Lucas 2008, and Duffy *et al*. 2012). Recent studies have further defined transoceanic migrations, diel and temporal movements in relation to physical parameters, tropical excursions, and seasonal migrations to specific pelagic and coastal areas (Boustany *et al*. 2002, Bonfil *et al*. 2005, 2010, Bruce *et al*. 2006, Weng *et. al*.2007a, 2007b, Domeier and Nasby-Lucas 2008, Jorgensen *et al*. 2010, Bruce and Bradford 2012a, Duffy *et al*. 2012). In South Africa, white sharks have been recorded all along the coast, from Namibia to Mozambique, but their regional centre of abundance encompasses the Western Cape, Eastern Cape and KwaZulu-Natal (Bass *et al*. 1975, Compagno 2001, Zuffa *et al*. 2002, Dudley 2012). While white sharks of various sizes have been documented for areas in South Africa, preliminary information suggests that the waters of the Eastern Cape serve as a nursery area, while those of the Western Cape are frequented by juveniles and sub-adults (Cliff *et al*. 1996, Kock and Johnson 2006, Dicken 2008, Dicken and Booth 2013). Adults of both sexes are rarely encountered in South African waters (Ferreira and Ferreira 1996, Dudley and Simpfendorfer 2006, Kock and Johnson 2006, Dudley 2012).

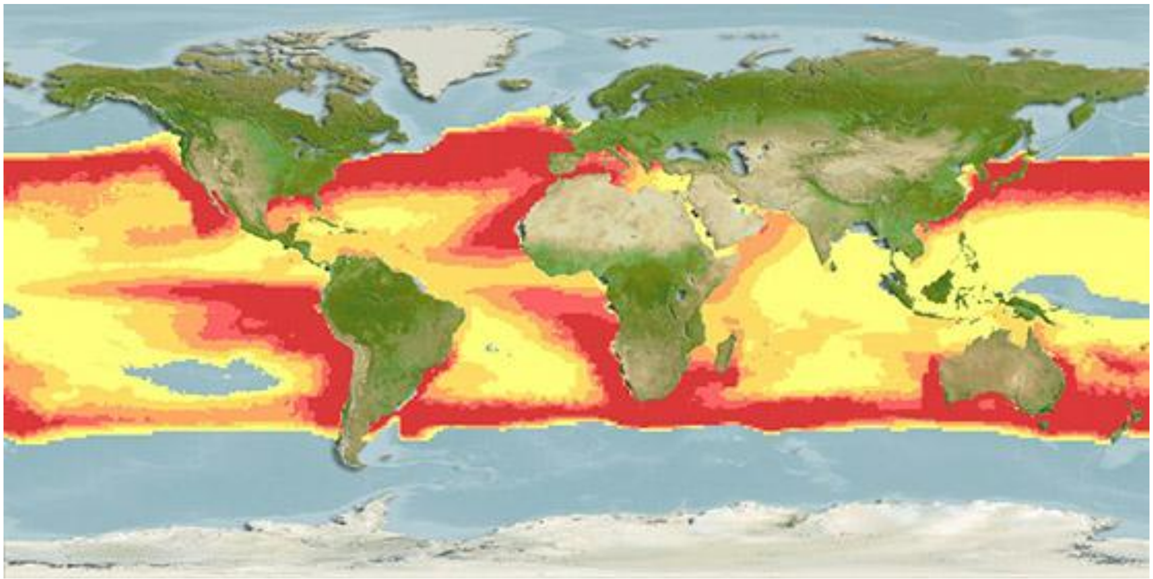

Figure 1.1. Global distribution of white sharks (Great White Sharks, *Carcharodon carcharias*, MarineBio.org). Red indicates areas of maximum abundance.

1.8.3 Distribution, movement patterns and site fidelity

While white sharks are widely distributed they are most often associated with coastal or island aggregation areas, like pinniped colonies (Goldman and Anderson 1999, Bonfil *et al*. 2005, Domeier and Nasby-Lucas 2007). This is probably as a result of a combination of pinnipeds being a preferred prey (Cliff *et al*. 1989, Hussey *et al*. 2012) and the accessibility to and conspicuous nature of their presence in these areas (Pyle *et al*. 1996, Laroche *et al*. 2008). Studies on white shark occurrence and movement patterns have been conducted primarily in California (Ainley *et al*. 1985, Klimley 1985, Anderson and Goldman 1996, Goldman *et al*. 1996, Klimley and Anderson 1996, Goldman and Anderson 1999, Klimley *et al*. 2001), Australia (Bruce 1992, Malcolm *et al*. 2001, Bruce and Bradford 2012a), Guadalupe, Mexico (Domeier and Nasby-Lucas 2007, 2008, Nasby-Lucas and Domeier 2012) and to a lesser extent in South Africa (Bonfil *et al*. 2005, Johnson *et al*. 2009, Dudley 2012).

White sharks show seasonal patterns of activity in all these areas, with their occurrence in some areas being positively correlated with the density of pinniped prey. At the South Farallon Islands, California, shark predatory activity corresponds to a peak in the number of juvenile northern elephant seals (*Mirounga angustirostris*) in the waters around the island (Klimley *et al.* 1992, Klimley and Anderson 1996, Klimley *et al*. 1996, Pyle *et al*. 1996). Similarly, white shark presence at seal colonies in South Africa peaks during the season when juvenile seals first take to open water around the rookeries (Martin *et al*. 2005, Kock and Johnson 2006, Laroche *et al*. 2008).

White shark behaviour appears to vary regionally, suggesting phenotypic plasticity in response to environmental differences (Domeier and Nasby-Lucas 2008). This highlights both the importance and limitation of site-specific studies to our understanding of the species across its distributional range. White sharks utilize a broad range of habitats, from rocky reefs and surf beaches in shallow coastal areas, to open ocean and oceanic islands (Boustany *et al*. 2002, Compagno *et al*. 2005, Bruce *et al*. 2006). However, characterization of preferred habitats are still lacking for this species. White shark coastal habitat use in the North East Pacific, Australia and South Africa comprises a network of high residence levels at focal points, with direct travel between them (Bonfil *et al*. 2005, Jorgenson *et al*. 2010, Bruce and Bradford 2012a). Telemetry data from these regions revealed a preference for select hotspots, with residence at these sites ranging from a few days to months. In central California residence was longest at the two main elephant seal rookeries, suggesting a close link between predator presence and prey availability (Jorgenson *et al*. 2010). Bruce and Bradford (2012a) demonstrated that juvenile white sharks in Australia exhibit broad-scale movement patterns, interspersed with seasonal patterns of temporary residency at specific beaches. Johnson *et al*. (2009) reported a similar pattern of residency at inshore beaches in Mossel Bay, South Africa, which they concluded were being used as sites for resting and socializing.

1.8.4 Connectivity of white shark populations

The global phylo-geography of white sharks is yet to be studied comprehensively (Gubili *et al*. 2012). Highly distinct mitochondrial haplotypes from populations either side of both the Indian and Pacific Oceans suggest female philopatry and long-term isolation (Pardini *et al*. 2001). However, the evolutionary history of remaining populations is poorly known (Gubili *et al.* 2012). Mitochondrial DNA analyses suggest that white sharks sampled in South Africa are a genetically distinct population to those in Australia/New Zealand, despite the identification of gene flow among the Indo-South Pacific Oceans following microsatellite analyses (Pardini *et al*. 2001). Overall, analyses suggest the existence of distinct mitochondrial haplotypes in South Africa, New Zealand/Australia, northeast Pacific, northwest Atlantic, and the Mediterranean (Pardini *et al*. 2001, Jorgensen *et al*. 2010, Gubili *et al*. 2012). This means that countries like South Africa, have crucial roles to play in the conservation of a possible genetically distinct populations of white sharks, as immigration from other areas is unlikely in the event of significant population declines.

1.8.5. Biology and life-history

White sharks exhibit common elasmobranch life-history characteristics, which include slow growth, late maturity, low fecundity and long life spans (Cailliet *et al*. 1985, Adams *et al*. 1994, Compagno *et al*. 1997, Wintner and Cliff 1999, Musick 2000, Castro 2012)

(Table 1.1). White sharks are the largest predatory shark species, reaching a maximum length of 6 m (Castro 2012). Pups are born at 120 – 169 cm, with males reaching sexual maturity at an earlier age (size) than females (Cailliet *et al.* 1985, Francis 1996, Wintner and Cliff 1999, Compagno 2001). White shark reproductive biology is poorly understood, but the reproductive mode is thought to be aplacental viviparity, with embryos nourished by unfertilized eggs (Compagno *et al.* 2005). Two to ten pups are born after a suspected 12-18 month gestation period, every 2-3 years (Francis 1996, Uchida *et al.* 1996, Cliff *et al.* 2000, Compagno 2001, Compagno *et al.* 2005, Domeier 2012). Thus, white sharks have a low intrinsic rebound potential and once populations suffer significant declines, they will struggle to recover (Smith *et al.* 1998, Dudley and Simpfendorfer 2006, Bruce 2008).

Table 1.1. Estimated life-history parameters of white sharks

Life-history parameter	**Data currently available (maximum, minimum or range)**
Maximum size (cm)	610 cm (Castro 2012)
Size at birth (cm)	120 – 169 cm (Francis 1996, Uchida *et al.* 1996, Wintner and Cliff 1999)
Size at maturity (cm)	450 – 500 (female) (~ 16 years old) (Francis 1996, Compagno 2001) 350 – 410 (male) (8 – 10 years old) (Cailliet *et al.* 1985, Wintner and Cliff 1999)
Longevity (years)	40 – 70 years (Francis 1996, Pratt 1996, Bruce 2008, Hamady *et al.* 2014)
Gestation period (months)	Uncertain (12 – 18 months) (Compagno 2005, Domeier 2012)
Reproductive periodicity (years)	Uncertain (2 or 3 years) (Compagno 2001)
Litter size (number)	2 – 10 pups / litter (Francis 1996, Uchida *et al.* 1996, Cliff *et al.* 2000)
Intrinsic annual rate of population increase (percentage)	0.04 – 0.119 (Smith *et al.* 1998, Dudley and Simpfendorfer 2006)

1.8.6 Feeding habits and trophic position

White sharks are apex predators, occupying the highest trophic levels in marine ecosystems (Cortes 1999) and, as such, can potentially exert significant control across multiple components of marine ecosystems (Hussey *et al.* 2011). They feed on a diverse array of prey, including teleosts, elasmobranchs, invertebrates and marine mammals (Compagno 1984). White sharks exhibit an ontogenetic shift in diet with age and consequently the predatory pressure they exert within ecosystems varies with different life-history stages (Hussey *et al.* 2011). Stomach content analysis and the use of stable isotopes from tissue biopsies suggest that sharks <3 m in length feed predominantly on teleosts and elasmobranchs (Tricas and McCosker 1984, Klimley 1985, Cliff *et al*. 1989, Hussey *et al*. 2012), but as they approach 3 m, so their dentition changes and gape size increases (Tricas and McCosker 1984, Hubbell 1996) and they begin to include larger prey, such as marine mammals, in their diet. Stable isotope and stomach content analysis has further revealed that white sharks forage on prey found in a diverse range of habitats, including reefs, demersal and oceanic habitats (Hussey *et al*. 2012, Smale and Cliff 2012). Therefore, at the population level, white sharks are considered generalist predators that forage opportunistically and have multiple feeding strategies. This foraging strategy likely contributes to them being considered one of the most successful predators on earth.

1.8.7 Abundance and population trends

To date, there are no estimates of global white shark abundance and only limited regional abundance estimates and trends from select study areas where they regularly occur. This is because white sharks are elusive, travel large distances and individuals are difficult to reliably identify (Chapple *et al.* 2011). Complex ontogenetic and sex-biased behavioural patterns further complicate attempts to produce robust population estimates (Chapple *et al.* 2011) with much debate around absolute numbers. However, regional abundance estimates have been calculated for Neptune Islands, Australia (191.7 individuals) (Strong *et al*. 1996), northeastern Pacific (219 individuals) (Chapple *et al*. 2011), south and east coasts, South Africa (1279 individuals) (Cliff *et al*. 1996), Gansbaai, South Africa (1000 individuals) (Towner *et al.* 2013) and Seal Island, False Bay (723 individuals) (Hewitt 2013). The most dramatic and rapid decline that has been reported comes from the NW Atlantic, where numbers were estimated to have decreased by up to 79% since 1986, with no catches reported in some areas since the 1990's (Baum *et al*. 2003). Australia has also experienced declines in white shark numbers over time, as evident by a decline in catch per unit effort (CPUE) by the shark control programs (Reid and Krough 1992) and by game fishing catch statistics in SE Australia (Pepperell 1992). Declines have also been reported for eastern USA (Casey and Pratt 1985) and California (Pyle *et al*. 1996). The most reliable long-term data on white shark abundance and temporal trends in South Africa come from sharks caught in the protective gillnets off the coast of KwaZulu-Natal (Cliff *et al*. 1989). Cliff and Dudley (1992) reported substantial declines in the CPUE of white sharks between the mid 1960's and mid 1970's, but the decline has not persisted and catches of white sharks in the nets have stabilized between 1978 and 2003 (Dudley and Simpfendorfer 2006). However, there has also been no evidence of an increase or recovery in the population since protective legislation was enacted in 1991 (Dudley and Simpfendorfer 2006, Kock and Johnson 2006).

1.8.8. Conservation status and threats

White sharks are afforded the highest protection of any elasmobranch (Dulvy *et al*. 2008). They are a listed threatened species in several regions of the world, including South Africa, Namibia, Australia, New Zealand, Malta and the United Stated, as well as being listed on Appendix II of the Convention for International Trade in Endangered Species (IUCN 2013) and under the Convention on Migratory Species (CMS, sharks 2010). Illegal trade in white shark products, primarily their fins, nevertheless persists (Shivji *et al*. 2005) and where white shark populations go unprotected, their iconic status and high value jaws and fins mean that they are subject to exploitation (Dulvy *et al*. 2008). Dulvy *et al*. (1998) also revealed the existence of a commercial market for white shark neonates. Recreational and trophy fisheries that use non-selective fishing methods continue to catch white sharks in South Africa, despite the threat of legal consequences (Cape Argus 2011). A further challenge to the protection of white sharks is the conflict that results when they bite and injure, or kill, humans. Such events result in public support for the deployment of beach nets or drumlines that are designed to kill large sharks frequenting inshore regions, with the explicit assumption that such deaths will reduce the frequency of encounters between recreational ocean users and white sharks (Reid and Krogh 1992, Cliff *et al*. 1989, Dudley and Simpfendorfer *et al*. 2006).

Currently, the population size and hence vulnerability of white sharks off the South African coastline remains unknown, despite concerns regarding their status since protective legislation was introduced in 1991 (Compagno 1991, Kock and Johnson 2006). This legislation was motivated using the precautionary approach (due to biological vulnerability and large demand for products), rather than actual data on numbers and their rate of change (Dudley 2012). A number of studies have highlighted that effective management of white shark populations is limited by the general lack of knowledge on key aspects of their biology, including their distribution, levels of residency and site-fidelity and habitat preference (Adams *et al*. 1994, Wintner and Cliff 1999, Bruce *et al*. 2006, Weng *et al*. 2007a, Nasby-Lucas *et al*. 2009).

1.9. Aims and structure of thesis

The primary aim of this thesis is to provide data on white shark presence at different spatial and temporal scales within False Bay, the largest true bay in Southern Africa. These data will be used to explore levels of residency and site fidelity for white sharks of different sexes and sizes to firstly improve our understanding of their biology and secondly our ability to manage and conserve a marine apex predator by identifying its critical resources. In this study I used acoustic telemetry to test the null hypothesis that there are no sex-specific, size or seasonal differences in white shark residency and habitat use at a pinniped colony and the inshore region of False Bay, South Africa. Where possible, I include data on biotic and abiotic factors (e.g. prey availability, habitat type, season, time of day, and anthropogenic disturbance) to explain the variation in that influence both on white shark presence and relative abundance within False Bay. An improved understanding of white shark space use within this inshore region, which is characterized by high levels of commercial and recreational activities, may also assist the local authority (City of Cape Town) to mitigate conflict between white sharks and humans and assist the national government (Department of Environmental Affairs) to establish conservation priorities in what is suspected to be one of the largest aggregations of white sharks in the world (Hewitt 2013).

To avoid repetition, I have structured this thesis to consist of a single, cohesive *Introduction*, *Methods* and *Discussion* section, and three *Results* sections. Chapter 1 provides an introduction and detailed literature review. Chapter 2 provides the methods for the entire thesis. Chapters 3 to 5 provide the results. Chapter 3 describes the movement patterns of white sharks in two regions of False Bay, the area around Seal Island and the inshore area, and investigates the influence of season, sex and size, area tagged and year on habitat use. Chapter 4 describes the fine-scale habitat use at the seal colony over the peak period of autumn and winter, and investigates the influence of sex and size, time of day, area tagged, year and chumming. Chapter 4 also describes the patterns of predation on Cape fur seals. The fine-scale habitat use of the inshore sites during the peak period of spring and summer and the influence of habitat type, distance from shore, sex and size, range of the receiver and time of day are described in Chapter 5. Chapter 6 comprises a discussion for the entire thesis, with recommendations for future research and management.

CHAPTER 2

GENERAL METHODS

The research needed to take into consideration public interests, due to the sensitive and sometimes controversial nature of working with these large, potentially dangerous sharks in a multi-user environment.

Photo credit Chrysoula Gubili

2.1. Study site

This study was conducted in False Bay, on the southwestern tip of South Africa (34°04` - 34°23`S, 18°26` - 18°51`E) (Fig. 2.1). False Bay is the largest bay in southern Africa, and is almost rectangular in shape, with a total surface area of 1082 km². At its widest point the Bay is over 30 km across, but it is nowhere more than 100 m deep (Spargo 1991, Dufois and Rouault 2012). False Bay opens to the Atlantic Ocean, but is situated in an area of overlap between the cold Benguela Current to the west and the warmer Agulhas Current to the south and east.

False Bay falls within the warm-temperate marine bioregion (Griffiths *et al.* 2010) and experiences a Mediterranean climate with warm, dry and windy summers and cool, wet winters (Clark *et al.* 1996a). Water temperature in the Bay varies seasonally from an average summer temperature of 21.5°C to an average winter temperature of 13.2°C (Clark *et al.* 1996a). During winter the water column is isothermal through most of the Bay, whereas it is strongly stratified during summer, with an 8-9°C difference between the surface and a depth of approximately 50 m (Atkins 1970). The Bay also experiences localized, wind-induced upwelling during the spring and summer months, particularly off Cape Hangklip and to a lesser degree off Gordon's Bay. This results in the western and middle regions of the Bay having colder water than the northern and eastern regions (Grundlingh and Largier 1991, Dufois and Rouault 2012). The shallower waters of the northern region of the Bay are also influenced by sun-warming during spring and summer (Lamberth *et al*. 1995, Dufois and Rouault 2012). Currents in the Bay are wind and tide dominated, with the predominant current being a slow clockwise gyre (Atkins 1970). The tidal range in False Bay is modest, with a mean range of about 1.6 m (Spargo 1991).

False Bay is home to an abundance of marine life, including preferred white shark prey species (Cliff *et al*. 1996, Hussey *et al*. 2012) such as Cape fur seals, numerous species of migratory and shoaling fish, such as yellowtail (*Seriola lalandi*), white steenbras (*Lithognathus lithognathus*), kob (*Argyrosomus hololepidotus*) and snoek (*Thyrsites atun*) (Bennet 1993, Clark *et al*. 1996a, 1996b) and other elasmobranchs, such as soupfin sharks (*Galeorhinus galeus*), smoothhound sharks (*Mustelus mustelus*), sevengill cowsharks (*Notorynchus cepedianus*) and bronze whaler sharks (*Carcharhinus brachyurus*) (Lamberth 2006). The Bay is seasonally frequented by a variety of cetacean species, including common dolphins (*Delphinus capensis*), dusky dolphins (*Lagenorhynchus obscurus*), Brydes whales (*Balaenoptera edeni*) and humpback whales (*Megaptera novaeangliae*), as well as serving as a seasonal resting, mating and breeding area for large numbers of Southern right whales (*Eubalaena australis*) (Elwen *et al*. 2011).

False Bay is exploited by diverse user groups from both the commercial and recreational fishing sectors. Commercial fishing boats operate from False Bay and there are five licensed beach purse-seine net (treknet) fisheries that exploit the eastern and northern Inshore region during spring and summer (Lamberth 2006). False Bay is popular for both boat and land-based recreational fishing who, together with spear-fishermen, typically focus their efforts along the western and eastern shores.

False Bay forms part of the City of Cape Town metropole, home to approximately 3.8 million people, with a projected further population increase of 17% by the year 2020. The Bay is a highly valued recreational area, with the inshore region utilized throughout the year for swimming, diving, surfing, kayaking, stand-up paddling and kite-surfing (van Herwerden *et al*. 1989, Dotchim 2006). The abutting land mass to the west, the Cape Peninsula, is the second most important tourist attraction in South Africa (Macdonald and Cowling 1996), with 1.8 million international tourists visiting in 2007 alone. Servicing these diverse user groups are 11 affiliated life-saving clubs (www.lifesavingwp.co.za) and three National Sea Rescue Institute (NSRI) clubs (www.nsri.org.za) which operate in the area and use the waters for training purposes. Many small businesses also run their surf lessons or kayaking excursions in the Bay.

2.2 Study design using an acoustic array

To determine white shark presence in False Bay I deployed a total of 33 acoustic receivers (VR2, Vemco Ltd. Nova Scotia, Canada) along the inshore region (n = 31) and at Seal Island (n = 2) (Fig. 2.1). Underwater receivers are omni-directional, with a single channel (69 kHz) that listens continuously for the presence of coded-pulse acoustic transmitters (Voegeli *et al.* 2001).

In determining the design of the acoustic array I was limited by the total number of receivers I could deploy. I thus decided to use a non-random design which sampled two regions of the Bay, namely Seal Island and the inshore region (from Cape Hangklip to Cape Point), that are known areas of use by white sharks in False Bay. The inshore region (Inshore) is also the portion of False Bay most heavily utilized for recreational purposes, especially beaches, such as, Muizenberg and Fish Hoek, and hence the area with the highest levels of human-white shark conflict. Understanding how sharks use the Inshore, with its diverse habitat types (i.e., beaches, reefs, mixed and harbours), offers the greatest value for management authorities charged with reducing conflict and conserving ecological processes. It is clear from the design I employed that open water within the Bay was poorly sampled and this remains a caveat of the study design. It is hoped that SPOT tags will in the future address this gap in our knowledge of how white sharks use this habitat type within False Bay and other coastal waters off South Africa, but these data are not yet available.

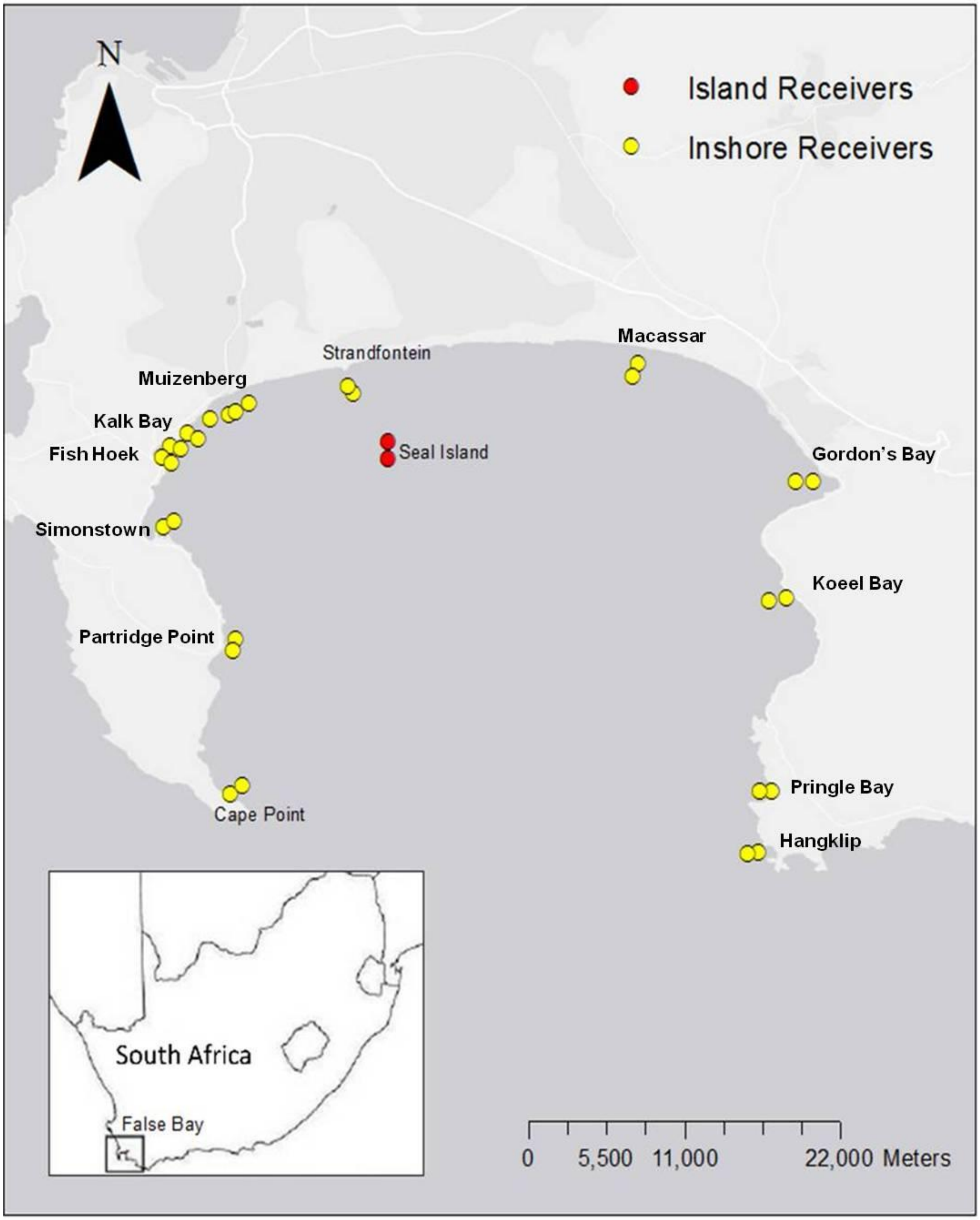

Figure 2.1. Locations of acoustic receivers in False Bay, South Africa. Receivers were grouped according to whether they were deployed in the Inshore and Island regions of False Bay. The insert shows the location of False Bay within the Western Cape region of South Africa.

2.2.1. Seal Island

Seal Island is located within the northern section of the Bay and is home to the second largest island-based breeding colony of Cape fur seals in South Africa (Department of Environmental Affairs, Oceans and Coasts Branch, unpublished data). The population of seals varies from approximately 36 000 to 80 000 in the non-breeding and breeding season, respectively, and overall numbers have been relatively stable over the last 50 years (Kirkman *et al.* 2006). The breeding season starts in November and lasts until January, with young of the year pups being weaned when they are about eight months old (Kirkman *et al.* 2006). The seals have to leave the Island to feed (Rand 1967) and appear to favour travelling to foraging grounds south of the island in the direction of the mouth of False Bay (de Vos 2010). The Island is also inhabited by a small colony of African penguins (*Speniscus demersus*), and is used as a roost for small numbers of Cape gannets (*Morus capensis*), Cape cormorants (*Phalacrocorax capensis*), Bank cormorants (*Phalacrocorax neglectus*) and Black-backed kelp gulls (*Larus dominicanus*).

Seal Island is one of four areas in South Africa where white shark cage diving and tourism is permitted and three permits have been allocated to this area (Kock and Johnson 2006, Laroche *et al*. 2008). Chumming and baiting activities are restricted to within 1 km of the Island. Daily activities include watching for predatory events between white sharks and Cape fur seals, towing seal decoys to elicit predatory behaviours, such as breaches (Martin *et al*. 2005), and attracting sharks to stationary boats by chumming to facilitate both cage diving and surface viewing of white sharks (Laroche *et al*. 2007).

At the beginning of this study, in 2004, the companies typically ran one trip per day, arriving at sunrise and leaving the Island by 14h00. In 2006 the companies started running two trips per day, a morning trip from sunrise to 12h00 and an afternoon trip from 14h00 - 17h00. The number of days on which trips were conducted was highest over the winter season (April - October), when white sharks aggregate in the area (Martin *et al*. 2005, Laroche *et al*. 2007). Commercial and recreational fishing boats also operated on the reefs around the Island, occasionally interacting with white sharks. An independent (to my study) research vessel operated over the winter months of 2007, and over the autumn and winter months small pleasure boats and yachts visit the Island, particularly over weekends. The Island, is thus an area frequently visited by a range of boats.

Initially, six acoustic receivers were placed at the Island in 2004 (see Laroche *et al*. 2007). However, due to the large spatial overlap of the effective acoustic range and the duplication of data, four of these were removed in 2005 (this study). Therefore, for the remainder of the study period only two receivers were deployed at the Island, one located on the south side (South) and the other on the north side (North) of the Island (Fig. 2.2). This design ensured optimal coverage of the Island without spatial overlap. The south side of Seal Island faces the mouth of False Bay and is the area seals typically depart from (Laroche *et al*. 2008, de Vos 2010). A steep drop-off to 30 m depth exists on the south side and the benthos is predominantly reef, which flattens out to sand. The north side of the Island is 6 km from the False Bay coastline and has less seal activity (Laroche *et al*. 2008, de Vos 2010). There is a gradual drop-off over a reef to about 20 m depth, after which it flattens out to a predominantly sand substrate heading in the direction of Strandfontein Beach.

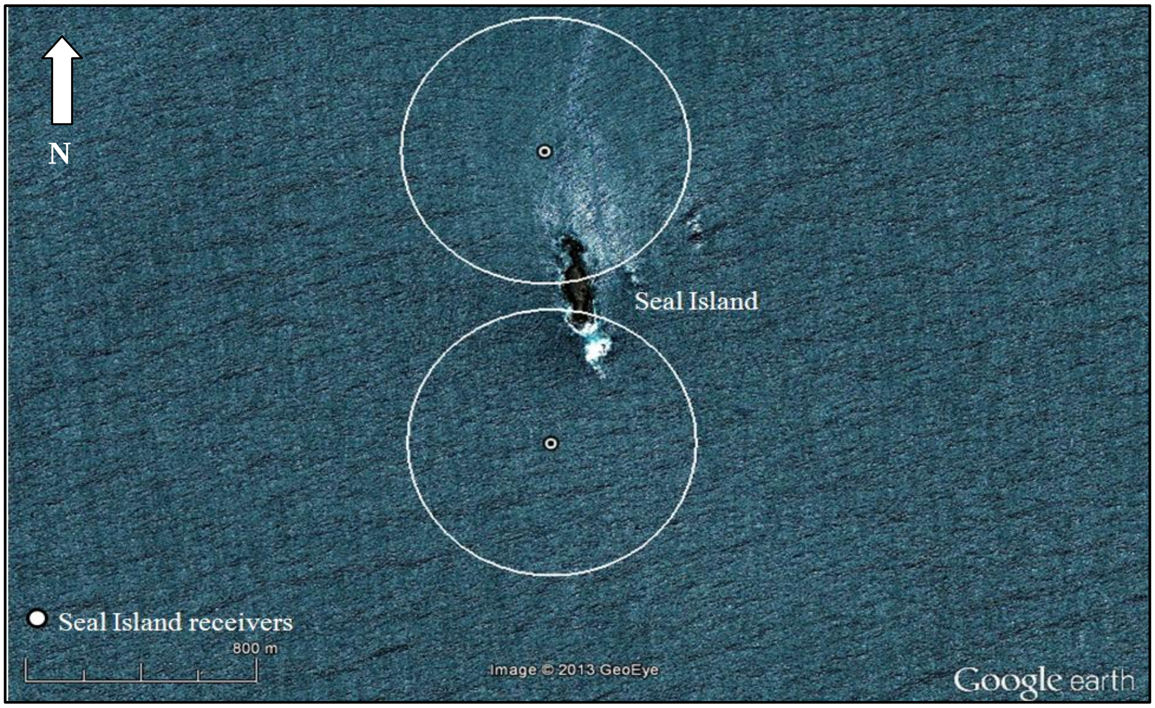

Figure 2.2. Location and the 500 m receptive range (white circle) of acoustic receivers at Seal Island.

2.2.2. Inshore

The Inshore region of the Bay is characterized by a broad range of habitats and supports a rich diversity of both teleosts and elasmobranchs (Lamberth *et al*. 1995, Clark *et al*. 1996a). The eastern (Strand to Cape Hangklip) and western (Muizenberg to Cape Point) shores of False Bay are characterized by steep rocky shores, with small intermittent bays e.g. Fish Hoek and Koeel Bay, while the northern shore (Muizenberg to the Strand) is characterized by gently sloping, long, dissipative sandy beaches (Spargo 1991). A small rocky shore is situated to the east of Strandfontein (Kaptein's Klip). Commonly occurring fish species in this northern region include mullet (*Liza richardsonii*), white steenbras (*Lithognathus lithognathus*), yellowtail (*Seriola lalandi*), bronze whalers (*Carcharhinus brachyurus*), smooth hound sharks (*Mustelus mustelus*) and soupfin sharks (*Galeorhinus galeus)* (Lamberth 2006).

Eleven catchments drain into False Bay, with peak river flow occurring over winter months. Most of these are situated on the western and eastern shores (Morant and

Grindley 1982, Morant 1991). There are two perennial rivers, the Eerste (near Macassar) and Zeekoe (near Muizenberg) situated along the northern shore (Morant and Grindley 1982, Morant 1991). Tidal pools have been constructed along the northern and western shores of the Bay. There are four harbours within False Bay, namely, Simonstown, Kalk Bay, Strand and Gordon’s Bay. Kalk Bay is the largest fishing harbour. The South African Navy has a substantial base in Simonstown harbour.

I deployed acoustic receivers at 12 Inshore sites between the two headlands of Cape Hangklip and Cape Point (Fig. 2.3). The selection of sites allowed me to investigate white shark presence and visitation patterns at fairly regular intervals along the Inshore region, in addition to subsampling four different habitat types that together comprise most of the Inshore region, namely 1) sandy beach (Beach = 7 acoustic receivers) 2) rocky shore (Rocky = 8 acoustic receivers) 3) mixed sandy beach and rocky shore (Mixed = 7 acoustic receivers) and 4) recreational and fishing harbours (Harbour = 6 acoustic receivers) (Fig. 2.3). All Inshore sites were equipped with at least two receivers (maximum of four), with the first an average of 660 m from the shore (range 230-1230 m) and the second an average of 1163 m meters (range 500-2260 m) from the shore, along a straight line perpendicular to the coast. Sites, such as, Muizenberg and Fish Hoek beach had four receivers each, in an effort to gain detailed information on shark presence at these large recreational nodes. Due to the large surf zone (~300 m) at Muizenberg I was not able to deploy receivers in the 500 m from shore range. This array design maximised the probability of shark detection in the Inshore region of the Bay.

Figure 2.3. Locations of inshore acoustic receivers in False Bay, South Africa. The major habitat types (Beach, Rocky, Mixed or Harbour) associated with each location, are indicated by the colour of the dot.

Table 2.1. Description, range and monitoring period of individual acoustic receivers deployed in False Bay, South Africa from 1 May 2004 - 31 December 2007.

Site	Site code	Habitat type	Range of VR2 (m)	Distance from shore (m)	Date receiver first deployed	Date receiver last deployed	End of study	Days monitored	Related Chapters
Cape Point	RKI	Rocky	≤500	≤1000	1-May-05	23-Jan-08	31-Dec-07	974	3, 5
	RKO	Rocky	≤500	>1000	1-May-05	18-Oct-08	31-Dec-07	974	3, 5
Fish Hoek	FHNI	Mixed	>500	≤1000	30-Apr-05	05-Feb-08	31-Dec-07	975	3, 5
	FHNO	Mixed	>500	≤1000	30-Apr-05	05-Feb-08	31-Dec-07	975	3, 5
	FHSI	Mixed	≤500	≤1000	28-Apr-05	19-Oct-08	31-Dec-07	977	3, 5
	FHSO	Mixed	>500	≤1000	28-Apr-05	19-Oct-08	31-Dec-07	977	3, 5
Gordon’s Bay	GBI	Harbour	>500	≤1000	29-Apr-05	02-Nov-07	02-Nov-07	917	3, 5
	GBO	Harbour	≤500	>1000	29-Apr-05	18-Oct-08	31-Dec-07	976	3, 5
Hangklip	HKI	Rocky	≤500	≤1000	27-Apr-06	02-Nov-07	02-Nov-07	554	3, 5
	HKO	Rocky	≤500	≤1000	27-Apr-06	20-Oct-08	31-Dec-07	613	3, 5
Kalk Bay	KLBI	Harbour	>500	≤1000	30-Apr-05	19-Oct-08	31-Dec-07	975	3, 5
	KLBO	Harbour	>500	>1000	30-Apr-05	05-Feb-08	31-Dec-07	975	3, 5
Koeel Bay	KBI	Mixed	≤500	≤1000	29-Apr-05	14-Feb-08	31-Dec-07	976	3, 5
	KBO	Mixed	≤500	>1000	29-Apr-05	18-Oct-08	31-Dec-07	976	3, 5
Macassar	MI	Beach	≤500	>1000	29-Apr-05	14-Mar-06	14-Mar-06	319	3, 5
	MO	Beach	>500	>1000	29-Apr-05	21-Oct-08	31-Dec-07	976	3, 5
Muizenberg	MBC	Mixed	>500	≤1000	28-Apr-05	23-Sep-06	23-Sep-06	513	3, 5
	MJB	Beach	>500	>1000	28-Apr-05	28-Jun-06	28-Jun-06	426	3, 5
	MSB	Beach	>500	>1000	28-Apr-05	23-Sep-06	23-Sep-06	513	3, 5
	MZV	Beach	>500	>1000	28-Apr-05	23-Jan-08	31-Dec-07	977	3, 5
Partridge Point	PPN	Rocky	≤500	≤1000	30-Apr-05	23-Jan-08	31-Dec-07	975	3, 5
	PPS	Rocky	≤500	≤1000	1-May-05	18-Oct-08	31-Dec-07	974	3, 5
Pringle Bay	PBI	Rocky	≤500	≤1000	27-Apr-06	02-Nov-07	02-Nov-07	554	3, 5
	PBO	Rocky	≤500	≤1000	27-Apr-06	21-Oct-08	31-Dec-07	613	3, 5
Seal Island	SIN	Rocky	>500	>1000	21-Apr-04	20-Oct-08	31-Dec-07	1349	3, 4
	SIS	Rocky	>500	>1000	21-Apr-04	20-Oct-08	31-Dec-07	1349	3, 4
Simonstown	STI	Harbour	≤500	≤1000	27-Apr-05	23-Jan-08	31-Dec-07	978	3, 5
	STO	Harbour	>500	≤1000	27-Apr-05	23-Jan-08	31-Dec-07	978	3, 5
Strandfontein	SF2	Beach	>500	>1000	28-Apr-05	14-Feb-08	31-Dec-07	977	-
	SF3	Beach	>500	>1000	28-Apr-05	04-Apr-07	04-Apr-07	706	3, 5
	SFI4	Beach	>500	>1000	28-Apr-05	04-Apr-07	04-Apr-07	706	3, 5
	SFO1	Beach	>500	<1000	28-Apr-05	19-Oct-08	31-Dec-07	977	-

2.3. Study period

In 2004 both acoustic monitoring and observation of predatory events were restricted to Seal Island, but from April 2005 I expanded the study to include the Inshore region of False Bay, by deploying an array of acoustic receivers at 12 additional sites along the False Bay coast (described above). Although some acoustic monitoring continued past 2007 (Table 2.1), the analyses presented here used acoustic data gathered from 1 April 2004 up to 31 December 2007. In Chapters 3 and 5 I use acoustic data from both the Inshore and Island from 1 May 2005 - 31 December 2007, and in Chapter 4 I use acoustic data from the Island for which I had a year's extra monitoring from 1 May 2004 – 1 May 2005.

2.4. Tagging of sharks

White sharks were tagged at both Seal Island and the Inshore region closest (6 km) to the Island off Strandfontein beach (Fig. 2.1). At Seal Island, white sharks were attracted to the research vessel for tagging purposes using a standardized chumming and baiting method (Laroche *et al*. 2007). By contrast, in the Inshore region, tagging was achieved by actively searching for sharks at or near the water surface and then approaching them cautiously with the research vessel. I used a dense foam seal decoy, or a tuna head tied to a rope, to lure sharks to the research vessel. The size of the tagged shark was estimated to the nearest 0.5 m using the width of the research vessel (2.6 m) as a reference. The sex of the shark was determined by visual inspection for presence or absence of claspers, and only tagged once this was confirmed.

Acoustic transmitters were deployed into the base of the first dorsal fin using a modified spear gun (Fig. 2.4). Sharks were tagged with acoustic transmitters (Vemco Ltd. V16, Nova Scotia, Canada) programmed with two different delay periods. In 2004 I used V16-5H-R04K (code intervals: 20-69 s, 17 x 95 mm, battery life approx. 12 months) and from 2005 V16-5H-R04K (code intervals: 150-300 s, 17 x 95 mm, battery life approx. 36 months). Transmitters were encased in the manufacturer's 'shark case' for added protection against physical damage. Cases were painted with two layers of anti-fouling paint, since bio-fouling can reduce signal transmission, create more drag, or result in physical damage to sharks as a result of abrasions on the sharks' skin (Heupel *et al.* 2008). The transmitters periodically emit a pulse train of closely-spaced 69 kHz pings, which serve to uniquely identify each shark. Each successfully decoded pulse train is recorded as a single detection by a VR2 receiver and stored in the receiver memory as the unique transmitter number, with date and time of detection (Lacroix and Voegli 2000).

2.5. Acoustic mooring design and range testing

Acoustic receivers were attached via a metal pole attached to concrete moorings deployed on the seafloor. Each mooring was constructed from a truck tyre halved along the midline of the tyre tread (creating two equal sized circles). The circular half-tyre was then filled with concrete, with a galvanized steel pole mounted vertically in the centre (Fig. 2.5). The receiver was attached to its own galvanized pole, which was mounted to the mooring's pole using stainless steel bolts and nuts. The receiver thus stood approximately 1.75 m off the seafloor. As with the transmitters, all moorings and receivers were painted with anti-fouling paint to prevent the accumulation of marine organisms, which could lead to poor signal detection over time (Heupel *et al.* 2008). Receivers were retrieved every 6-12 months for maintenance and to download the data. Replacement receivers were prepared beforehand and deployed immediately to ensure continuous monitoring.

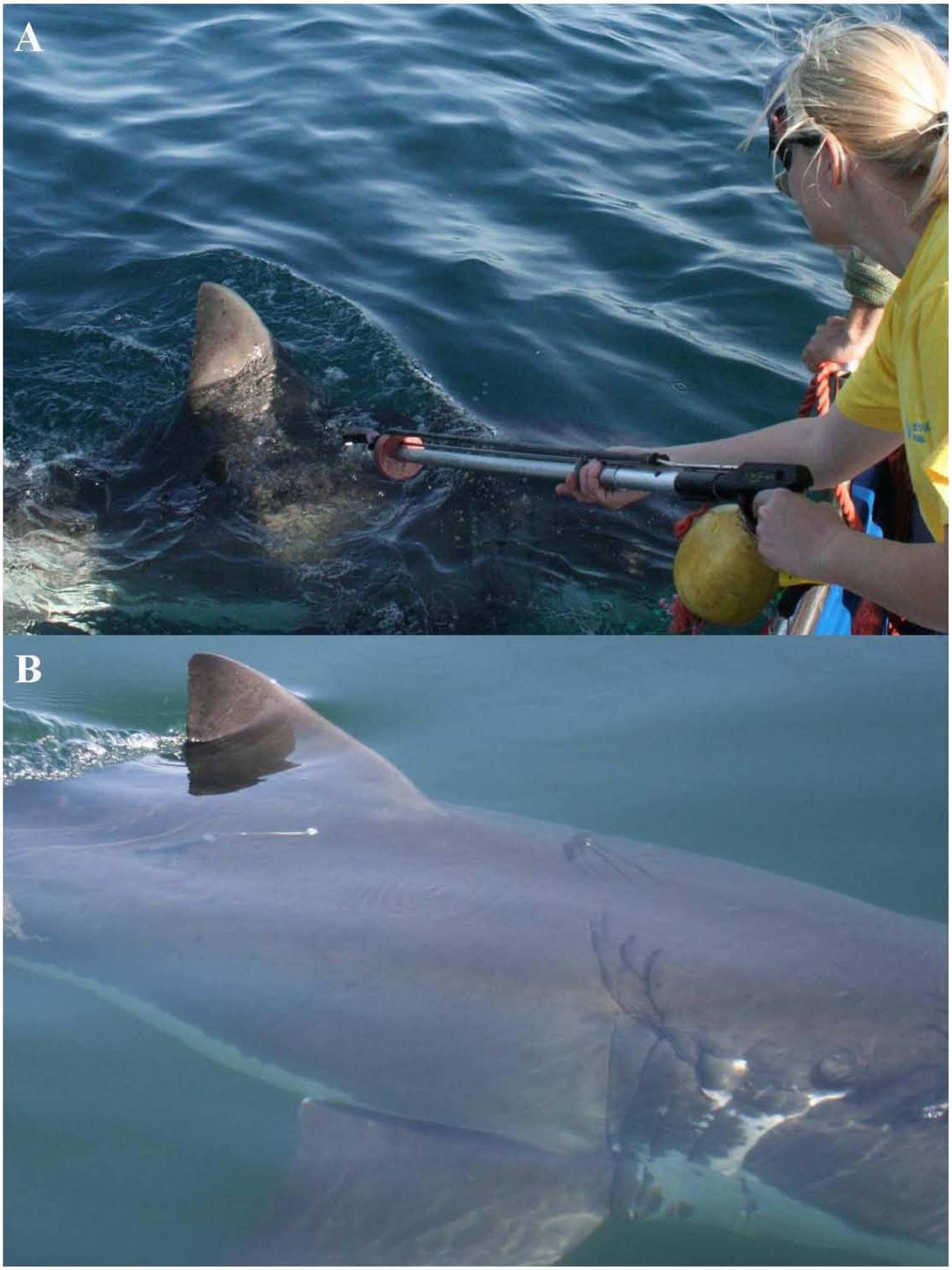

Figure 2.4 (A) Modified speargun used to tag white sharks attracted to the research vessel. (B) Tag deployed near the base of the first dorsal fin.

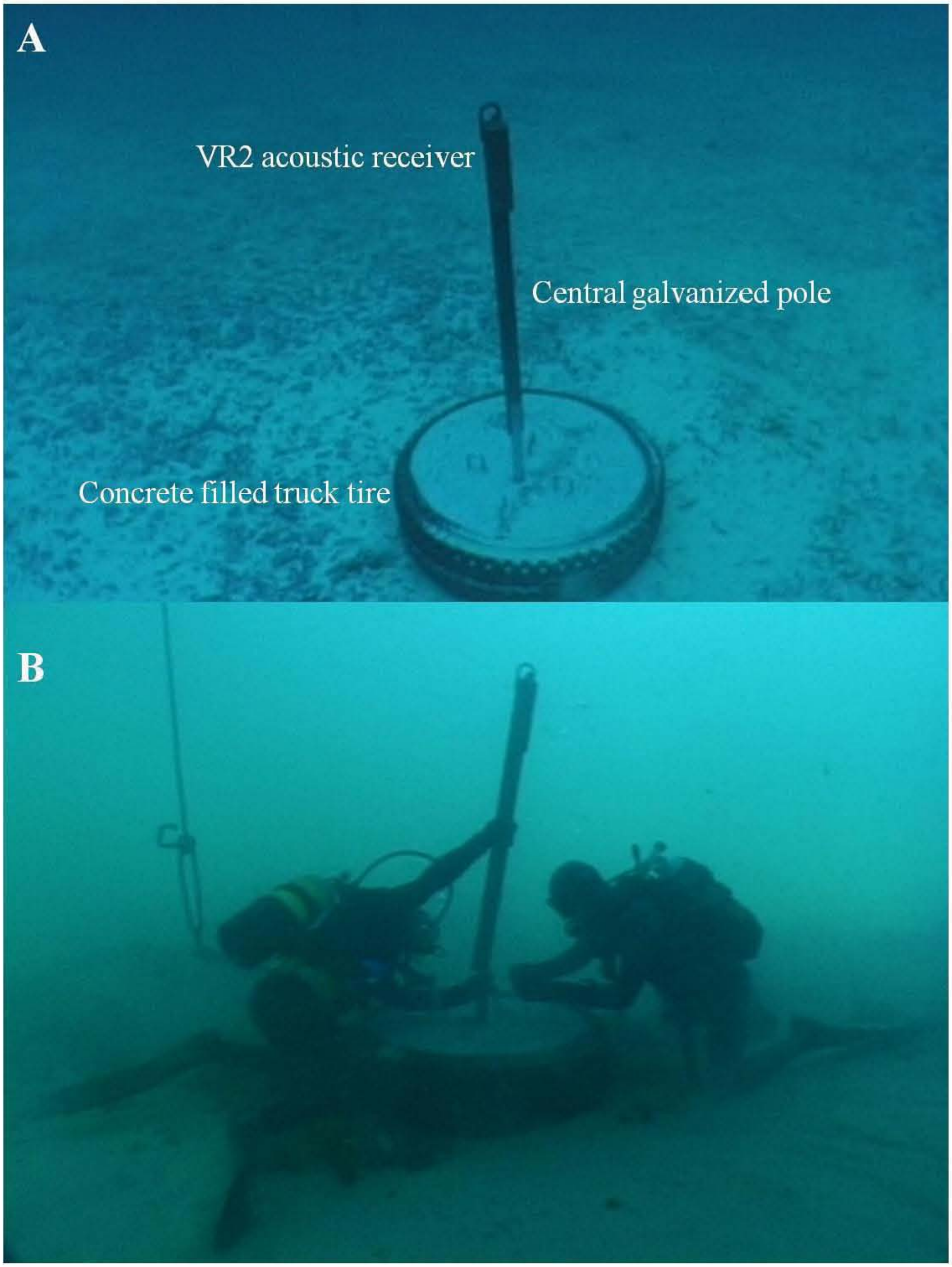

Figure 2.5. (A) Mooring system and VR2 placement and (B) divers attaching the galvanized steel pole and acoustic receiver to the galvanized steel pole embedded in the concrete mooring block on the seafloor.

The performance of acoustic receivers in marine environments can be variable and affect detection rates (Heupel *et al*. 2008). Therefore, *in situ* range tests were performed on each individual receiver in the array to determine its receptive range. I deployed a V16 transmitter, identical to the transmitters used in the study, over the side of the research vessel at a depth of 2 m. The boat was then moved in 50 m increments away from the receiver, using the on-board GPS system, to a maximum distance of 1200 m. At each stop, the motors were switched off and the boat was allowed to drift for five minutes, with the tag overboard. The timing of the detections were matched to the distance of the transmitter from the receiver to generate a detection profile for each receiver. Range testing was conducted on relatively calm days, < 3 m swell and 20 km / h wind and only completed once for all receivers.

White sharks tagged in this study were also detected by acoustic receivers outside of False Bay by other researchers at three coastal regions off South Africa, namely Gansbaai, Mossel Bay and Algoa Bay. These receivers were important in determining the number of active tags each month, and in confirming that periods of no detection in False Bay were not necessarily a result of tag failure, but of shark movement outside of the Bay.

2.6. Behavioural observations

2.6.1. Temporal and spatial variables

All predatory events by white sharks on Cape fur seals were recorded within 2 km of Seal Island from June - September 2003 and June - October 2004. *Ad libitum* behavioural observations were conducted from the deck (1 m above sea level) of a 26-foot vessel. I divided the daylight hours into four, equal 2.5-hour observation periods, between 07h30 (sunrise) and 17h30 (sunset) (times were extended slightly towards the end of the study periods due to increased daylight hours associated with spring). Each behavioural observation session was then randomly assigned to one of six spatially continuous quadrants around the Island (viz., northeast, southeast, southwest and northwest) and one of the observation periods

2.6.2. Detection, duration and classification of predation events

During an observation period, a minimum of two and a maximum of eight people were used to detect predatory events from the vessel within a given quadrant. Following the detection of a predatory event, the vessel was maneuvered close enough (>20 m) to allow for detailed information on the interactions and the outcome of the event, whilst minimizing disturbance to the shark and seal. The following data were then recorded.

Predation events were typically identified by any one of four visual cues: (1) a white shark breaching or lunging out of the water in pursuit of a seal, (2) the splash caused by a shark following a breach or lunge attack on a seal, (3) kelp gulls (*Larus dominicanus*) flying in a group to an area above the water surface (to scavenge seal remains following a successful attack), and (4) blood and/or oil slick staining the water surface, indicative of a kill (Fig. 2.6). The duration of each predatory event was recorded from the first time a shark appeared at the surface in pursuit of a seal, to when either the shark or the seal was no longer present, either due to the seal having been consumed, or having escaped from the shark. Predatory events lasting <1 min where rounded up to 1 min to calculate an average duration per predatory event category. Each predation event was categorized into one of five categories, as described in Table 2.2. During unsuccessful predations there was usually increased opportunity to categorize the seals into their respective size categories, as the seal was often seen leaving the attack area, unlike with successful predations, where the seal was often consumed before it was possible to observe it and thus determine its size.

Table 2.2. Classification and description of predatory events between white sharks and Cape fur seals at Seal Island.

Predation event	Description
Successful predation (SP)	Seal consumed by shark
Unsuccessful predation (UP)	Seal escaped an attack (with or without injury)
Unconfirmed predation (UC)	Neither the shark nor seal were seen again following an attempted predation, and there was no blood/oil or entrails in the water
Aborted predation (AB)	Seal was attacked and killed, or mortally wounded and vulnerable, but the shark did not consume the seal.
Scavenging (SC)	Shark feeding on an already dead seal

Figure 2.6. (A) Predation events were identified by one of four visual cues: a white shark breaching or lunging out of the water in pursuit of a seal, (B) a splash caused by a shark following a breach or lunge attack on a seal, (C) kelp gulls (*Larus dominicanus*) flying in a group to an area above the water surface to scavenge seal remains following a successful attack, (D) or blood/oil slick staining the water surface, in the area of an attack, conspicuous even when no shark present on the surface.

2.6.3. Phenotypic traits of the seal in each predation event

Seals that were observed were categorized into one of three exclusive age classes based on their relative size and pelt colouration: (1) young of the year with olive-brown coats, (2) sub adults or adults and (3) bull seals (Rand 1956).

2.7. Shark-human interactions in Cape Town

A record of all white shark-human interactions was kept for Cape Town over the study period. Interactions ranged from fisheries-related incidents to interactions with recreational ocean users. Opportunistic records of white shark captures in fisheries were kept and confirmed through photographs or interviews. With regard to unprovoked incidents between white sharks and recreational water users, detailed information on the incident was collected through interviews with the persons involved, or eyewitness accounts obtained by phone or in person.

2.8. Data analyses

For the purposes of this thesis, acoustic data were analyzed from 30 of the 33 receivers deployed for the period 1 May 2004 - 31 December 2007 (Fig. 2.1). Three receivers, two located between Strandfontein and Seal Island, and one at Whittle Rock, were dropped from the analysis, as they were deployed more than 2 km from shore and thus did not fit into the defined Inshore or Island regions. Data from the VR2 receivers were downloaded with the VUE software provided by Vemco Ltd. Files were adjusted to account for time drift on the internal clocks and data were archived in a Microsoft Access database.

For all analyses sharks were categorized as either male or female and into one of two size categories, ≤3 or >3 m. The size categories were selected based on previous findings (Cliff *et al*. 1989, Hussey *et al*. 2012) that white sharks ≤3 m feed predominantly on teleosts and elasmobranchs, while those >3 m supplement their diet with marine mammals, like seals. I thus predicted differences in habitat use between these two size categories. Descriptive statistics were performed using Statistica (Statsoft) and generalized linear mixed models (GLMMs) were generated using Stata software (version 11; StataCorp).

2.8.1. Residency

The number of days that individual tagged sharks were monitored over the study period (date from first tagged to date of last acoustic detection) was defined as the ‘monitoring period’. Residency of all tagged sharks was assessed on a daily basis, with individuals considered present in the study area if more than one detection was recorded on any receiver in the array on a given day, *sensu* Carlson *et al.* (2008). Residency was assessed at different spatial scales in the thesis. The number of days that each individual was present at any receiver in False Bay over the study period was plotted on a timeline and categorized as ‘days detected’. I evaluated whether sex or size influenced white shark residency in False Bay using *t*-tests to compare the 1) detection period (in days from date of tagging in False Bay to date last detected on any receiver along the South African coast), and 2) the number of days detected in False Bay for male and female sharks and sharks ≤ 3 and > 3 m, respectively (Chapter 3). To assess residency at the two receivers at Seal Island, I determined the number of days that each individual was present at the Island ('days detected'). I evaluated whether sex or size influenced white shark residency at the Island using *t*-tests to compare the 1) detection period (in days from date of tagging in False Bay to date last detected on receivers at the Island), and 2) the number of days detected at Seal Island for male and female and then for sharks ≤ 3 and >3 m, respectively (Chapter 4). The number of consecutive days individuals were present in each location was calculated each time they entered the study site (Heupel *et al.* 2010) (Chapter 4 and 5).

2.8.2. Effect of season, sex and size on habitat use in False Bay (Chapter 3)

GLMMs were used in all three data chapters to investigate the effects of a combination of variables on the presence and visitation patterns of white sharks at different spatial scales, including all acoustic receivers within False Bay (Chapter 3), only acoustic receivers at Seal Island (Chapter 4) and only acoustic receivers in the Inshore region (Chapter 5).

The non-random design of the acoustic array essentially restricts all analyses to a comparison of how white sharks use Seal Island and/or the Inshore region of False Bay. However, I analysed data for these two regions at different spatial scales, starting with patterns of visitation to either habitat type (Chapter 3) and then looking at each region in more detail to see how sharks use the different habitats at either the Island (Chapter 4) or the Inshore. All shark presence analyses were based on the number of visits of each shark to the two regions of False Bay (Inshore vs. Island). A single visit to either the Island or Inshore was defined as a recording of a tag at any single receiver within that region, followed by a period of at least 30 minutes during which that tag was not detected by any other receiver within that region. The number of visits was averaged per month to explore the seasonal visitation patterns for males and females, for both size categories (≤ 3 and >3 m), across years and for sharks tagged at Island versus Inshore. To investigate the effects of season, shark sex and size on habitat use, I used a GLMM (McCullagh and Nelder 1989, Johnson and Omland 2004, Zuur *et al*. 2009) with a binary response defined by sharks present on the Inshore (0) or sharks present at the Island (1). Generalized linear models accommodate different (non-normal) response types, by allowing for the generalization of ordinary regression techniques. In this instance, since the response was binary, a logistic model was used. The model included shark-specific random effects, which accounted for the variation in movement patterns by individual sharks.

The model was defined as follows:

$$logit\,(p) = \log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 X_1 + \ldots + \beta_k X_k + e_{ij} + b_{0i}$$

Where $p = P(Y=1)$, Y is the response variable, $X_1 \cdots X_k$ are the k explanatory variables, and $\beta_1 \cdots \beta_k$, the k corresponding coefficients, b_{0i} is the shark-specific random intercept effect, where $i = 1 \ldots M$ sharks, and $j = 1 \ldots n_i$ observations on each shark.

The recordings were categorized into four seasons of three months each (where summer represented December - February, autumn: March - May, winter: June - August and spring: September - November) (variable SEASON). Sex of the sharks (variable SEX) and size of the shark (variable SIZE) were also indicated. The year of study (variable YEAR) and whether the shark was tagged at the Island or Inshore (variable AREA TAGGED) were also considered for inclusion in the model. Descriptions of the independent variables used in the GLMM analysis are provided in Table 2.3. The impacts of the various explanatory variables were assessed by interpreting the odds ratios, which were obtained by exponentiating the relevant beta coefficients.

Table 2.3. Summary of the independent variables used in the generalized linear mixed models. The response term indicated the presence of a shark at either the Inshore vs. Island.

Independent variable	**Type**	**Description**	**Values**
SEASON	Categorical	Four seasons of three months each	Summer (*Dec* - *Feb*); Autumn (*Mar* - *May*); Winter (*Jun* - *Aug*); Spring (*Sep* - *Nov*)
SEX	Categorical	Sex of the shark	Female; Male
SIZE	Categorical	Size of the shark	≤3 m; >3 m
AREA TAGGED	Categorical	Region where shark was tagged	Inshore; Island
YEAR	Categorical	The year in which the tag was recorded	2005; 2006; 2007

2.8.3. Effect of sex, size and time of day on habitat use at Seal Island (Chapter 4)

These analyses were based on the number of visits of each shark to the two sites at the Island (South vs. North) during both autumn and winter months (March - August). A single visit to either the South or North during this period was defined as a recording of a tag at the single receiver within that site, followed by a period of at least 30 minutes during which that tag was not detected by that receiver. The number of visits was averaged per month to explore the seasonal visitation patterns for males and females, for both size categories (≤3 and >3 m), across years and for sharks tagged at Island vs. Inshore. To investigate the effects of time of day (TOD), sex and shark size on habitat use I used a GLMM (McCullagh and Nelder 1989, Johnson and Omland 2004, Zuur *et al.* 2009) with a binary response defined by sharks present at the South (0) or sharks present at the North (1). Since the response was binary, a logistic model was used. The model included shark-specific random effects, which accounted for the variation in movement patterns by individual sharks (see model parameters in section 2.7.2). Sharks that had <5 visits throughout the study period were excluded from the model.

The recordings were categorized into time of day (where sunrise represented 04h01-09h00, day: 09h01-16h00, sunset: 16h01-21h00 and night: 21h01-04h00) (variable TOD). Sex of the shark (variable SEX) and size of the shark (variable SIZE) were also included. The year of study (variable YEAR), and whether the shark was tagged at the Island or Inshore (variable AREA TAGGED) were also considered for inclusion in the model. Finally, the presence of chumming was considered for inclusion in the model as a control variable (variable CHUMMING). I recorded the time of arrival and departure of each commercial operator during observation sessions. Additionally, each operator is required to complete a logbook with daily activities submitted to the regulatory body, the Department of Environmental Affairs (DEA), Oceans and Coasts Branch and I used this to supplement my own dataset, as I was not present each day the operators were. Descriptions of the independent variables used in the GLMM analysis are provided in Table 2.4. The impacts of the various explanatory variables were assessed by interpreting the odds ratios, which were obtained by exponentiating the relevant beta coefficients.

Table 2.4. Summary of the independent variables used in the generalized linear mixed models. The response term indicated the presence of a shark at either the South vs. North of the Island.

Independent variable	Type	Description	Values
TIME OF DAY	Categorical	The 24 hour day divided into four duration periods	Sunrise (04h01-09h00); Day (09h01-16h00); Sunset (16h01-21h00); Night (21h01-04h00)
SEX	Categorical	Sex of the shark	Female; Male
SIZE	Categorical	Size of the shark	≤3 m; >3 m
CHUMMING	Categorical	Presence or absence of chumming and baiting activities	Chumming; No chumming
AREA TAGGED	Categorical	Region where shark was tagged	Inshore; Island
YEAR	Categorical	Year in which tag was recorded	2005; 2006; 2007

2.8.4. Effect of habitat type, sex, size and time of day on habitat use along the Inshore (Chapter 5)

These analyses were based on the counts of the number of visits of each shark to the four habitat types along the Inshore locations of False Bay during both the spring and summer months (September - February), when white shark activity was shown to peak (see results of Chapter 3). A single visit to a site was defined as a recording of a tag at any receiver at that site, followed by a period of at least 30 minutes during which that tag was not detected by any other receiver within that region. Visits were placed in one of four time periods during each 24-hour cycle categorized as: sunrise (04h01-09h00), day (09h01-16h00), sunset (16h01-21h00) and night (21h01-04h00).

The numbers of visits were averaged per month to explore the visitation patterns for males and females to each habitat type (beach, mixed, harbour, rocky), for both size categories (≤3 and >3 m), during each time period, across years and for sharks tagged at both the Island or Inshore areas of the Bay. To investigate the effects of habitat type, sex, shark size and time of day on habitat use I used a GLMM (McCullagh and Nelder 1989, Johnson and Omland 2004, Zuur *et al*. 2009) with a Poisson distribution. The model included shark-specific random effects, which accounted for the variation in movement patterns by individual sharks. The model included an exposure variable, which accounted for the number of active tags (per year and per month) and the number of receivers in each habitat type classification.

The model was defined as follows:

For Y_i = the number of visits (observations) for a given exposure level, for each habitat, sex, time of day and range of receiver combination, the expected value of Y, $(E(Y_i) = \mu_i)$, is given by$\eta_i \times \theta_i$, where $\theta_i = \mathrm{e}^{x_i^T \times \beta}$, x_i refers to the covariates affecting θ, and η refers to the exposure.

Thus

$$\mu_i = \eta_i \times \mathrm{e}^{x_i^T \times \beta},$$

or equivalently,

$$\log(\mu_i) = \log(\eta_i) + x_i^T \times \beta.$$

In this,$\log(\eta_i)$ is known as the “offset” parameter and β is a vector of coefficients corresponding to the covariates in vector x_i^T.

For the mixed effects model:

$$\log(\mu_{ij}) = \log(\eta_{ij}) + x_{ij}^T \times \beta + u_i.$$

Where u_i is the shark-specific random intercept effect, and where $i = 1 \dots M$ sharks, and $j = 1 \dots n_i$ observations on each shark.

The recordings were categorized into habitat type (beach, rocky, mixed, harbour) (variable HABITAT). Sex of the sharks (variable SEX) and size of the shark (variable SIZE) were also indicated. The time of day (TOD), year of study (variable YEAR), whether the shark was tagged at the Island or Inshore (variable AREA TAGGED) and the distance of the receiver from shore (≤1000 or 1000 m) (variable DISTANCE) were considered for inclusion in the model.

The range tests determined that the average range of the Inshore receivers was 540.3 m (n = 28, range 200 – 1000 m). To account for the possibility that the results may be affected by the range of the receivers, I categorized receivers into those receivers with a range of ≤500 m and those with a range of >500 m and included this as a control variable (variable RANGE). A description of the independent variables used in the GLMM analysis are provided in Table 2.5. The impacts of the various explanatory variables were assessed by interpreting the incident rate ratios, which were obtained by exponentiating the relevant beta coefficients.

Table 2.5. Summary of the independent variables used in the generalized linear mixed models. The response term indicated was the frequency of visits (counts).

Independent variable	**Type**	**Description**	**Values**
HABITAT	Categorical	Broad scale habitat type along Inshore region	Beach (*Muizenberg, Strandfontein, Macassar*); Rocky (*Hangklip, Pringle Bay, Partridge Point, Cape Point*); Mixed (*Koeel Bay, Fish Hoek*); Harbour (*Gordon's Bay, Kalk Bay, Simonstown*)
RANGE	Categorical	Range of individual receiver	≤500 m;>500 m
DISTANCE	Categorical	Distance of receiver from coastline	≤1000 m; >1000 m
SEX	Categorical	Sex of the shark	Female; Male
SIZE	Categorical	Size of the shark	≤3 m; >3 m
TIME OF DAY	Categorical	Identifies the time of day	Sunrise (04h01-09h00); Day (09h01-16h00); Sunset (16h01-21h00); Night (21h01-04h00)
YEAR	Categorical	The year in which the tag was recorded	2005; 2006; 2007

In all three data chapters (Chapters 3 – 5), model building followed an all subsets procedure, but was led by specific hypotheses. I compared models and selected the best-fitting model by using standard selection criteria (AIC and BIC) to determine which variables best explained the variability in the data (Bozodogan 1987, Johnson and Omland 2004). Given a set of candidate models for the data, the preferred model is the one with the minimum AIC value. The BIC adjusts for the number of observations and variables in the model, and so will not decrease if the variable added to the model in the latest step does not sufficiently improve the fit, i.e. if its inclusion is not justified. Its use thus allowed me to penalize for non-parsimonious models. Likelihood ratio tests were also used to determine whether the inclusion of additional variables in the model significantly improved the amount of variability explained. In all instances I was looking for the best fitting predictive model i.e. the model that both fits the data and is the most parsimonious. Finally, I checked that the assumptions of the model were met by examining residual and random effects diagnostic plots.

The issue of pseudo-replication was managed by including Shark-ID as a random effect. The error structure of GLMM corrects for the non-independence of statistical units due to shared temporal structure, and permits the ‘random effects’ variance explained at different levels of clustering to be decomposed. The inclusion of individual shark as a random effect enabled us to account for lack of independence between observations within each identified shark.

2.8.5. Spatial and temporal patterns of predation

To test for differences in the frequency of predatory events across different spatial and temporal scales, I divided the number of predatory events (SP, UP, UC) by the number of observational hours for each time block and Island sector to account for differences in observational effort, expressed as the ‘predation rate’. Predatory success rate was calculated by dividing the total number of SP by the sum of SP and UP and expressing this as a percentage. The average rate of predatory events per day was used to extrapolate the total number of SP and UP during the autumn and winter months (multiplied by 184 days from 1 March - 31 August 2004) when white sharks are known to be present. These data were then summed to provide a total estimate of the minimum number of seals killed by white sharks at Seal Island over the study period.

In the spatial analyses I only used locations of predatory events for which a GPS position was recorded. This enabled the distance from the Island to be calculated and allowed me to accurately assign 62.2% (n = 310) of all predatory events to one of each of the 15 concentric 100 m zones and the 12 equal sized radial sectors around the Island (see Chapter 4, Fig. 4.4). Lastly I used published bathymetry maps to determine an approximate depth (0-10, 11-20, 21-30 m) for each predatory event with a GPS recording.

Chi-squared analyses (Zuur *et al*. 2007) were used to compare the observed versus expected rates of predation and predation success for the different sectors around the Island, distance from the Island, time of day and seal age class.

CHAPTER 3

RESULTS 1:

Residency, habitat use and sexual segregation within False Bay

It's fascinating that a shark capable of travelling thousands of kilometers across ocean basins can show such high fidelity to a few select areas.

Photo credit Jorge Torres

Summary

A total of 56 individual sharks were detected on Inshore and Island receivers over 975 days from 1 May 2005 – 31 December 2007 (Table 2.1, Fig. 2.1). Females were detected significantly more than males within the Bay and both sexes were detected more frequently during the winter months at both the Inshore and Seal Island. I used a generalized linear mixed effects model to explore the influence of season, year, area tagged, sex and size of tagged white sharks, on their detection frequency at Seal Island and along the inshore region of False Bay. The model revealed a significant effect of season and sex on detection probability, with females more likely to be detected along the Inshore region in spring and summer, compared to males.

3.1. Sex and size of tagged sharks

A total of 53 white sharks were tagged with acoustic transmitters in False Bay between 1 May 2005 and 31 December 2007 (2005, n = 23; 2006, n = 25; 2007, n = 5). Additionally, three sharks tagged in 2004 at Seal Island as part of a long-term study (see Chapter 4), returned in 2005 and were included in the analysis, bringing the total number of acoustically monitored sharks for the study period to 56 (Table 3.1). Most sharks were tagged at Seal Island (80%, 45 out of 56 individuals) with only 20% (11 out of 56) tagged in the Inshore region (Table 3.1). Inshore tagging was only conducted during the summer of 2006/2007 and only female sharks were encountered in the 11 tagging sessions. Sharks fell predominantly into the >3 m category (71%, 40 of 56) and were mostly female (69.1%, 39 of 56). Tagged animals in this study (based on their estimated size) were thus mostly juveniles and sub-adults, with possibly only eight (six males and two females) mature sharks.

Table 3.1. Summary of tagged white sharks monitored in False Bay between 1 May 2005 and 31 December 2007. Data include the Shark ID number, total length (TL) (estimated to nearest 0.5 m), size category (≤3 or >3 m), sex (male or female), area tagged (Island or Inshore), date of tagging, last date the tag was recorded in False Bay, detection period (days) and total number of days detected in False Bay. Sharks which are possibly mature are in bold.

Shark ID	TL (cm)	Size category	Sex	Area tagged	Date tagged	Date of last acoustic detection in False Bay	Detection period (days)	No. of days detected in False Bay
28	300	≤3	F	Island	09/03/04	08/31/05	363	22
520	**400**	**>3**	**M**	**Island**	**04/25/04**	**08/09/05**	**472**	**69**
521	370	>3	F	Island	04/25/04	06/13/05	415	103
533	340	>3	F	Island	04/06/06	06/15/06	71	44
534	330	>3	M	Island	04/06/06	08/06/06	123	88
545	280	≤3	F	Inshore	11/14/06	12/31/07	413	180
546	280	≤3	F	Island	04/28/06	12/27/06	244	210
547	350	>3	F	Island	06/30/06	07/27/07	393	282
548	320	>3	F	Island	04/28/06	11/04/07	556	164
549	300	≤3	F	Island	08/17/06	07/21/07	339	185
551	320	>3	F	Inshore	11/14/06	11/06/07	358	149
552	250	≤3	M	Island	06/30/06	07/13/06	14	10
553	340	>3	M	Island	06/30/06	08/01/07	398	110
554	340	>3	M	Island	07/03/06	08/18/06	47	33
556	380	>3	F	Island	08/09/06	10/30/06	83	76
557	280	≤3	M	Island	08/17/06	10/24/06	69	40
558	370	>3	F	Inshore	10/06/06	02/27/07	145	110
560	170	≤3	F	Inshore	11/13/06	04/17/07	156	129
562	340	>3	F	Inshore	11/14/06	05/23/07	191	181
601	**450**	**>3**	**F**	**Island**	**08/25/05**	**09/16/05**	**23**	**21**
603	380	>3	F	Island	05/20/05	01/03/06	229	169
604	**350**	**>3**	**M**	**Island**	**08/29/05**	**09/21/06**	**389**	**164**
605	320	>3	M	Island	08/24/05	11/07/06	441	67
606	350	>3	F	Island	06/04/05	06/10/05	7	4
608	360	>3	F	Island	06/04/05	10/03/05	122	84
609	**360**	**>3**	**M**	**Island**	**06/04/05**	**08/19/05**	**77**	**64**
610	420	>3	F	Island	06/04/06	06/23/06	20	7
611	250	≤3	F	Island	09/02/05	05/07/06	248	151
612	220	≤3	M	Island	05/19/06	06/15/07	393	74
613	320	>3	M	Island	06/28/05	09/16/06	446	71
614	360	>3	F	Island	06/06/05	07/23/05	48	28
615	320	>3	M	Island	08/30/05	06/18/06	293	22
616	**350**	**>3**	**M**	**Island**	**06/06/05**	**06/14/05**	**9**	**9**
617	380	>3	F	Island	06/06/05	08/30/05	86	39
618	400	>3	F	Island	06/16/05	06/24/05	9	9
619	**350**	**>3**	**M**	**Island**	**06/16/05**	**08/10/06**	**421**	**88**
620	360	>3	F	Island	06/17/05	12/27/05	194	180
621	300	≤3	F	Island	06/06/05	11/17/05	165	126
622	340	>3	M	Island	06/10/05	10/18/05	131	60

623	330	>3	F	Island	06/10/05	01/22/06	227	60
624	**500**	**>3**	**F**	**Island**	**06/06/05**	**06/10/05**	**5**	**5**
625	300	≤3	F	Island	06/10/05	08/01/05	53	16
626	250	≤3	F	Island	06/10/05	01/08/06	213	149
627	**350**	**>3**	**M**	**Island**	**04/20/06**	**04/23/06**	**4**	**2**
628	330	>3	M	Island	05/21/06	06/08/06	19	17
630	340	>3	F	Island	05/25/06	09/29/06	128	65
632	300	≤3	F	Inshore	11/13/06	01/28/07	77	61
633	330	>3	F	Inshore	01/26/07	11/08/07	287	257
634	380	>3	F	Inshore	11/14/06	04/17/07	155	135
635	300	≤3	F	Inshore	11/14/06	12/29/06	46	37
636	300	≤3	F	Inshore	11/14/06	11/24/06	11	11
637	400	>3	F	Inshore	01/17/07	08/08/07	204	147
638	400	>3	F	Island	03/10/07	11/02/07	238	169
639	300	≤3	F	Island	06/12/07	12/31/07	203	179
642	340	>3	F	Island	09/14/07	11/03/07	51	47
602607	350	>3	F	Island	06/17/05	01/14/06	212	153

3.2. Detection frequency of tagged sharks

During winter 100% of tagged males (n = 16) and females (n = 40) were detected at the Island, with similar high levels of detection on the Inshore array (94% males and 97% females). During summer, female detection rates remained high at both the Island (82%, n = 22) and the Inshore (95%), whilst male detection was lower at both the Island (22%, n = 9) and the Inshore (11%).

3.3. Residency

Tagged white sharks were monitored on the acoustic array for 975 days and detection patterns varied among individuals (Fig. 3.1). Detection period ranged from 2 - 556 days (median = 161 days) and the number of days detected ranged from 2 - 282 days (median = 73 days). The average detection period for males was 220 days (±45 days) and for females was 179 days (± 21 days). The average detection period for sharks ≤3 m was 188 days (±34 days) compared to 193 days (±25 days) for sharks >3 m. There were no significant differences in the detection period between males and females ($t = 0.92$, $df = 54$, $p = 0.8203$), nor between sharks in the two size categories, ≤3 and >3 m ($t = 0.1146$, $df = 54$, $p = 4546$). The average number of days males and females were detected in False Bay was 58 days (±10 days) and 106 days (±12 days), respectively. The average number of days sharks ≤3 m were detected was 99 days (±17 days) compared to 89 days (±11 days) for sharks >3 m. The number of days females were detected in False Bay was significantly greater than for males (t = 2.46, df = 54, p = 0.0086), but there was no significant difference in the number of days detected between the two size categories (t = 0.47, df = 54, p = 0.6816).

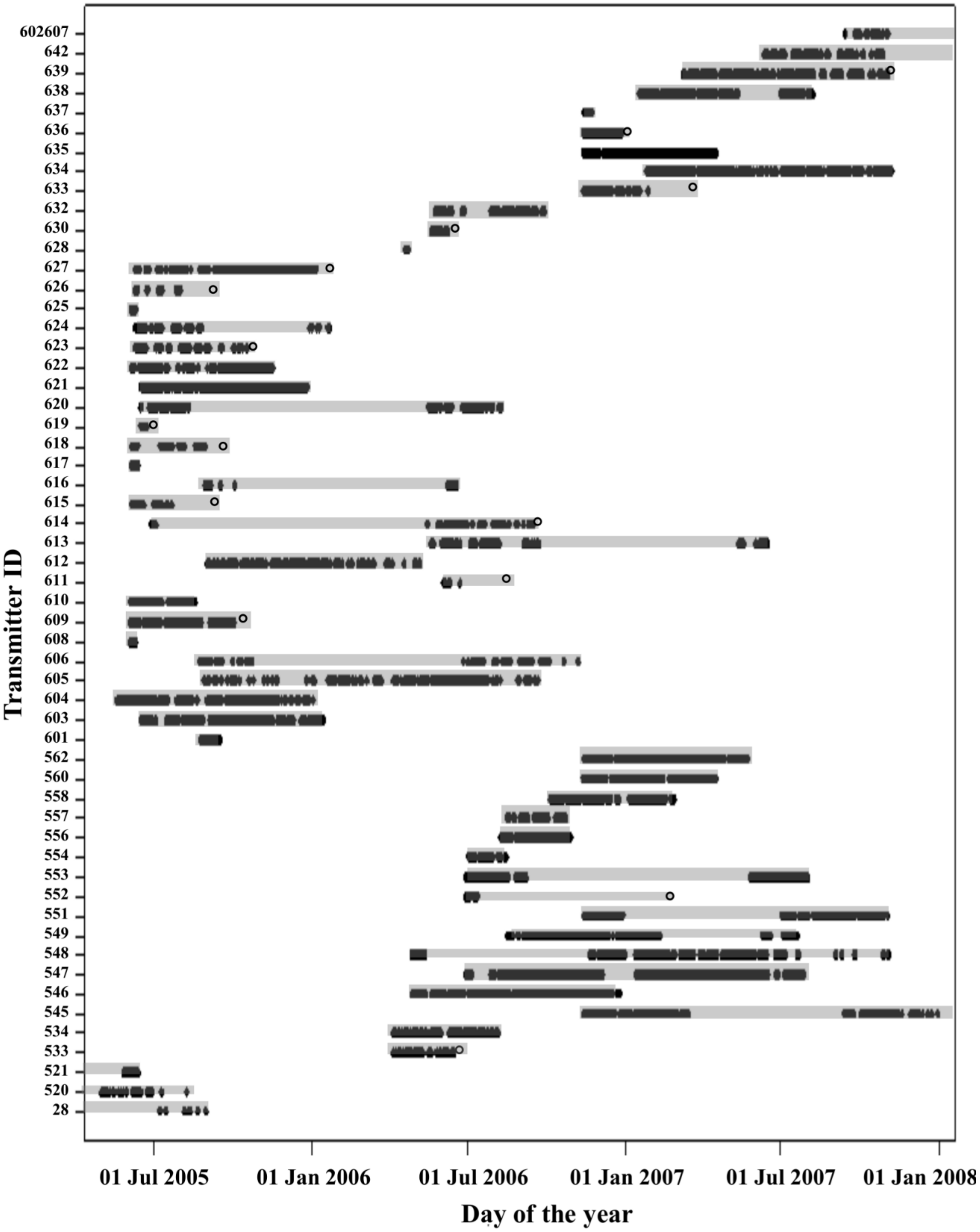

Figure 3.1. Timeline of the daily detections of acoustic tagged individual white sharks in False Bay from 1 May 2005 - 31 December 2007. The first point indicates the date the shark was tagged and black points indicate individual detections. Total time at liberty is represented by grey bars and open circles indicates detection on a receiver outside of False Bay (at Gansbaai, Mossel Bay or Algoa Bay).

3.4. Effects of season, size and sex on shark presence within False Bay

Generalized linear mixed effects models (GLMMs) were used to examine the influence of season, sex and size on white shark presence at Seal Island versus the Inshore. Table 3.2 shows the various stages of the model building procedure. Variables were initially considered independently of one another (Stage I). Of these initial models, the model including season was selected as the best (assessed using AIC and BIC, as described in methods section 2.7.2). Stages II and III built on the initial model, with each additional explanatory variable considered in turn. Finally, in Stage IV, interaction terms were considered. The likelihood ratio test was used to determine whether the best model at each successive stage was significantly better than the previous best model. The final model included season, sex and an interaction term between season and sex (Table 3.2).

Table 3.2. Generalized linear mixed effects models constructed for determining which variables best explain patterns of white shark presence at the Island vs. Inshore. Bold indicates the model selected for the next stage, using the criteria specified in the previous paragraph.

	Model Description	AIC	BIC	Lrtest	Lrtest (p-value)
Stage I	1) Sex	17658.55	17681.87	NA	NA
	2) Season	**11974.60**	**12013.46**	**NA**	**NA**
	3) Size	17669.11	17692.43	NA	NA
	4) Area Tagged	17655.29	17678.61	NA	NA
Stage II	**5) Season + Sex**	**11960.15**	**12006.79**	**5 vs. 2**	**16.45 (<0.0001)**
	6) Season + Size	11974.79	12021.43	NA	NA
	7) Season+ Area Tagged	11968.96	12015.6	NA	NA
Stage III	**8) Season + Sex + Size**	**11961.24**	**12015.65**	**8 vs. 5**	**0.9 (0.339)**
	9) Season + Sex + Area tagged	**11959.02**	**12013.43**	**9 vs. 5**	**3.13 (0.0767)**
Stage IV	**10) Season + Sex + Season:Sex**	**11865.59**	**11935.54**	**10 vs. 5**	**100.56 (<0.0001)**

A summary of the results from the final model (excluding year, as explained below) is provided in Table 3.3. For each season and sex combination, the likelihood of a white shark visit occurring at the Island versus Inshore is described, using predicted odds ratios and their corresponding 95% confidence intervals. Odds ratios that are greater than 1 indicate an increased likelihood of an Island visit, whilst those that are less than 1 indicate a decreased likelihood. All odds ratios were statistically significant, with the exception of that for males in spring. The model results indicate that there is a marked seasonal effect, and that this effect differs, depending on the sex of the shark (Table 3.3).

For males, Island visits are more likely year round, with peak likelihood in the winter months, when males are 32 times more likely to be seen at the Island than Inshore. However, female visits to the Island are less likely than Inshore visits in summer and spring. The large amount of variability observed for the males may be explained by the scarcity of observed visits to either region (Island or Inshore) in the summer and spring months: the only observed movements in these months are for a single male shark, frequenting the Island.

Table 3.3. Results from the generalized linear mixed effects model showing the likelihood (odds ratios and their 95% confidence intervals) of male and female white sharks being at the Island vs. Inshore across seasons. Bold indicates significant values.

Season	**Odds ratios (95% confidence intervals)**	
	Males	**Females**
Summer	**12.86 (4.19 - 39.51)**	**0.06 (0.04 - 0.09)**
Autumn	**10.77 (4.9 - 23.64)**	**2.35 (1.47 - 3.77)**
Winter	**32.37 (15.44 - 67.90)**	**6.73 (4.23 - 10.68)**
Spring	**1.89 (0.87 - 4.12)**	**0.17 (0.10 - 0.27)**

Due to tagging only taking place on the Inshore during the summer of 2006/2007, the area tagged and year was confounded, and thus the effects of year (and its interaction with season), were considered only at the end of the model-building procedure. Small effects of year were observed, but I excluded this variable from the final model because the same trends were observed in all three years of observation (both seasonal and sex and the interaction of the two), as per the model accounting for year (Table 3.4) and thus the inclusion of year and its interaction with season would overcomplicate the model (Johnson and Omland 2004).

Table 3.4. Results from the generalized linear mixed effects model (with year) showing the likelihood (odds ratios and 95% confidence intervals) of white sharks being at the Island vs. Inshore across seasons. Bold indicates significant values.

Year	Season	Odds ratios (95% confidence intervals)	
		Males	Females
2005	Summer	1.52 (0.31 - 7.40)	**0.02 (0.01 - 0.07)**
	Autumn	**74.31 (22.02 - 250.82)**	**15.27 (5.89 - 39.61)**
	Winter	**29.11 (12.70 - 66.72)**	**13.10, (7.31- 23.48)**
	Spring	1.15 (0.51 - 2.57)	**0.17, (0.09 - 0.30)**
2006	Summer	**11.77 (3.77 - 36.71)**	**0.03 (0.02 - 0.06)**
	Autumn	**8.46 (3.85 - 18.63)**	**0.33, (0.19 - 0.59)**
	Winter	**31.48 (14.84 - 66.78)**	**2.71 (1.57, 4.68)**
	Spring	**2.86 (1.24 - 6.59)**	**0.08 (0.05 - 0.14)**
2007	Summer	**-**	**0.06 (0.03 - 0.10)**
	Autumn	**196.53 (36.75 - 1051.07)**	**2.52 (1.48 - 4.29)**
	Winter	**179.41 (34.86 - 923.46)**	**5.04 (2.93 - 8.65)**
	Spring	**-**	**0.35 (0.20 - 0.62)**

Figure 3.2 shows the proportion of visits to the Inshore and Island regions in each month for all sharks. There is a clear seasonal pattern, with peaks in visits to the Island in the autumn and winter months (March - August), and at the Inshore region during spring and summer (September - February). This general trend was evident across all three years of the study (Fig. 3.3) and was most pronounced in the summer (Inshore) and winter (Island) months. The relationship between season and frequency of visits was much less clear in autumn and spring (e.g. February - April, 2006 and October - December, 2007, Fig 3.3.) with sharks exhibiting intermediate and alternating proportions of visits to each region.

Both males and females exhibited seasonal variation in the average proportion of visits to the island and inshore regions of False Bay (Fig. 3.5) with both sexes more likely to be detected at the Island during winter and on the Inshore in spring and early summer. Females persisted on the Inshore into late summer and autumn, while males, despite visiting the island less during spring, summer and autumn, were seldom detected on the Inshore at this time of year (i.e. January - April). No males were detected in either region during December. Seasonal patterns of an increase in the proportion of visits to the Island during winter and the Inshore during summer were consistent for both size categories of shark (Fig. 3.6).

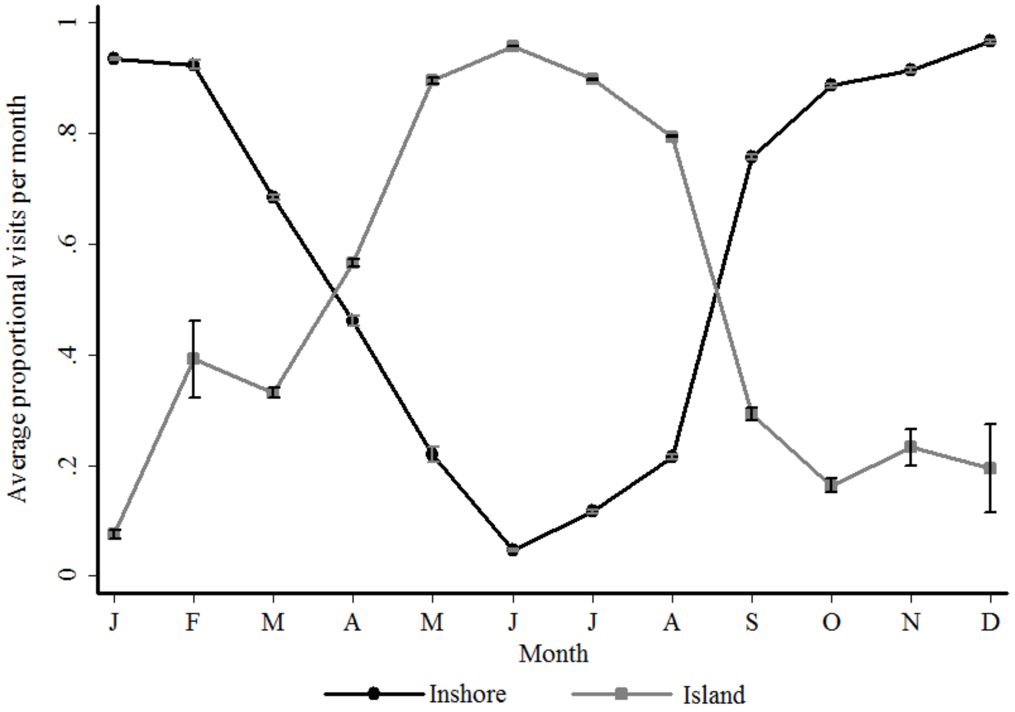

Figure 3.2. Average (± s. d.) proportion of visits per month by white sharks to the Inshore (black line) and Island (gray line) regions of False Bay from 1 May 2005 - 31 December 2007.

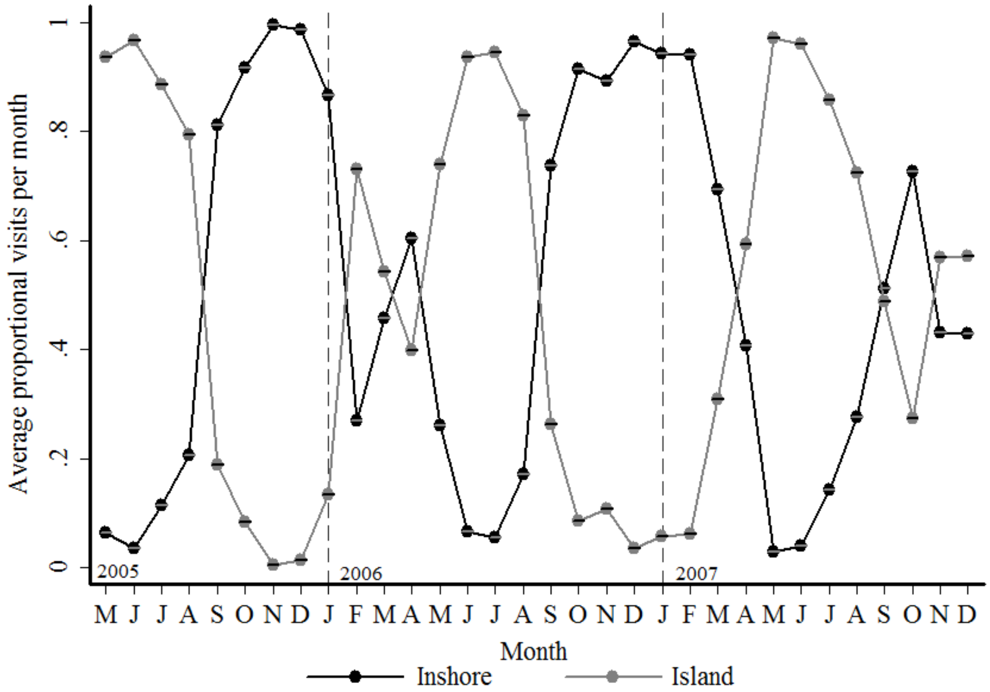

Figure 3.3. Average (± s. d.) proportion of visits per month by white sharks to the Inshore (solid line) and Island (gray line) regions of False Bay in 2005, 2006 and 2007.

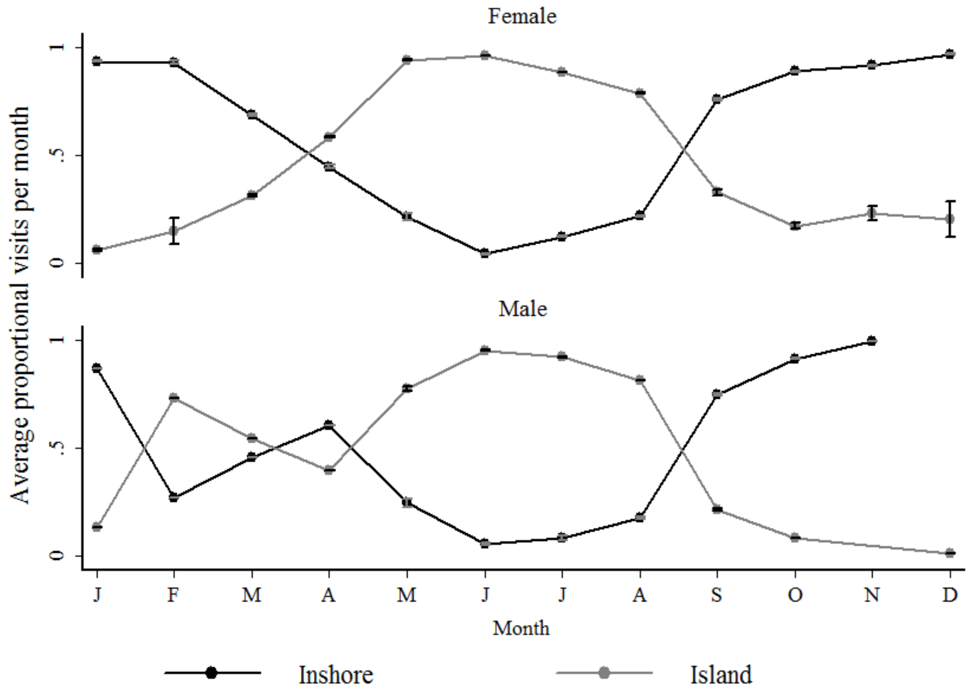

Figure 3.5. Average (+ s. d.) proportion of visits per month by male and female white sharks to the Inshore (black line) and Island (grey line) regions of False Bay from 1 May 2005 - 31 December 2007.

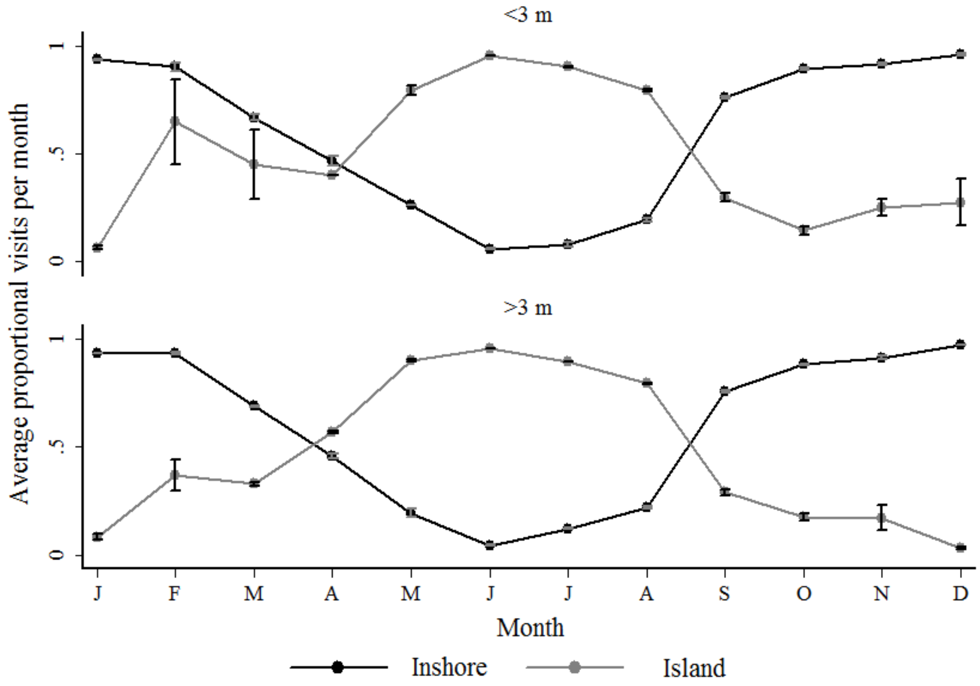

Figure 3.6. Average (+ s. d.) proportion of visits per month for ≤3 and >3 m white sharks to the Inshore (black line) and Island (grey line) regions of False Bay from 1 May 2005 - 31 December 2007.

CHAPTER 4

RESULTS 2:

Spatial and temporal patterns of presence and predation by white sharks during autumn and winter at Seal Island

The sight of a 1000 kg shark launching itself completely out of the water after a seal, 14 years ago, paved the path I find myself on today.

Photo credit Morne Hardenberg

Summary

A total of 68 individual sharks were detected on Island receivers over 1349 days from 1 May 2004 – 31 December 2007 (Table 2.1, Fig. 2.2). Overall, residency periods for males and females, and for ≤3 m and >3 m sharks, were similar. Most detections and the number of tagged sharks detected were on the South side of the Island. I used a generalized linear mixed effects model to explore the influence of time of day, sex, size, year, area tagged and chumming, on the detection frequency at the South versus the North side of the Island. The model revealed a significant effect of time of day, sex and year on the detection probability. All sharks were more likely to be detected at the South side of the Island at sunrise. Predatory events by white sharks on Cape fur seals were spatially and temporally clustered at the south and southwestern sides of the Island and at sunrise, respectively. Observed patterns of predation mirrored the spatial and temporal presence of tagged sharks.

4.1. Sex and size of tagged sharks

The data for this chapter include an additional 12 sharks (seven females, five males) tagged between May 2004 and May 2005 at the Island (Table 4.1). Analyses were thus based on a total of 68 tagged white sharks between 1 May 2004 and 31 December 2007 (2004, n = 15, 2005, n = 23; 2006, n = 25; 2007, n = 5) (see Chapter 3, Table 3.1). Sharks were tagged in all months except February and December and were mostly in the >3 m category (67.6%, 46 of 68) and were mostly female (67.6%, 46 of 68). Twenty-nine (42.6%) sharks were monitored over more than one year.

Table 4.1. Summary of tag deployments on white sharks in False Bay between 1 April 2004 - 31 December 2004. Data include Shark ID number, total length (TL) (estimated to nearest 0.5 m), size category, sex, area tagged, date of tagging, last date the tag was recorded in False Bay, detection period (days) and total number of days detected in False Bay.

Shark ID	TL (cm)	Size category	Sex	Area tagged	Date tagged	Date of last acoustic detection in False Bay	Detection period (days)	No. of days detected in False Bay
26	360	>3	M	Seal Island	07/22/2004	09/12/2004	53	39
27	260	≤3	F	Seal Island	08/11/2004	11/03/2004	85	23
29	300	≤3	M	Seal Island	08/31/2004	11/02/2004	64	6
30	320	>3	F	Seal Island	09/19/2004	12/21/2004	94	19
31	310	>3	M	Seal Island	07/28/2004	11/16/2004	112	31
32	340	>3	F	Seal Island	06/10/2004	08/17/2004	69	43
33	250	≤3	F	Seal Island	06/10/2004	10/22/2004	135	34
34	300	≤3	M	Seal Island	06/10/2004	09/04/2004	87	51
37	350	>3	M	Seal Island	06/10/2004	07/21/2004	42	26
38	370	>3	F	Seal Island	06/16/2004	07/24/2004	39	30
39	320	>3	F	Seal Island	06/17/2004	12/25/2004	192	76
522	500	>3	F	Seal Island	04/25/2004	08/13/2004	111	8

4.2. Detection frequency of tagged sharks at Seal Island during autumn and winter

All the tagged sharks (n = 68) were detected at the Island, with 98.5% (67 of 68) detected at the South side and 91.1% (62 of 68) detected at the North side. The majority (97.8%, 45 of 46) of females and 100% (n = 22) males were detected on the South side. The single female shark (Shark #632) that was not detected at the Island was tagged on the Inshore at Strandfontein on 13 November 2006 and was last recorded on 28 January 2007 in False Bay and subsequently outside of the study area (Gansbaai) on 14 March 2007.

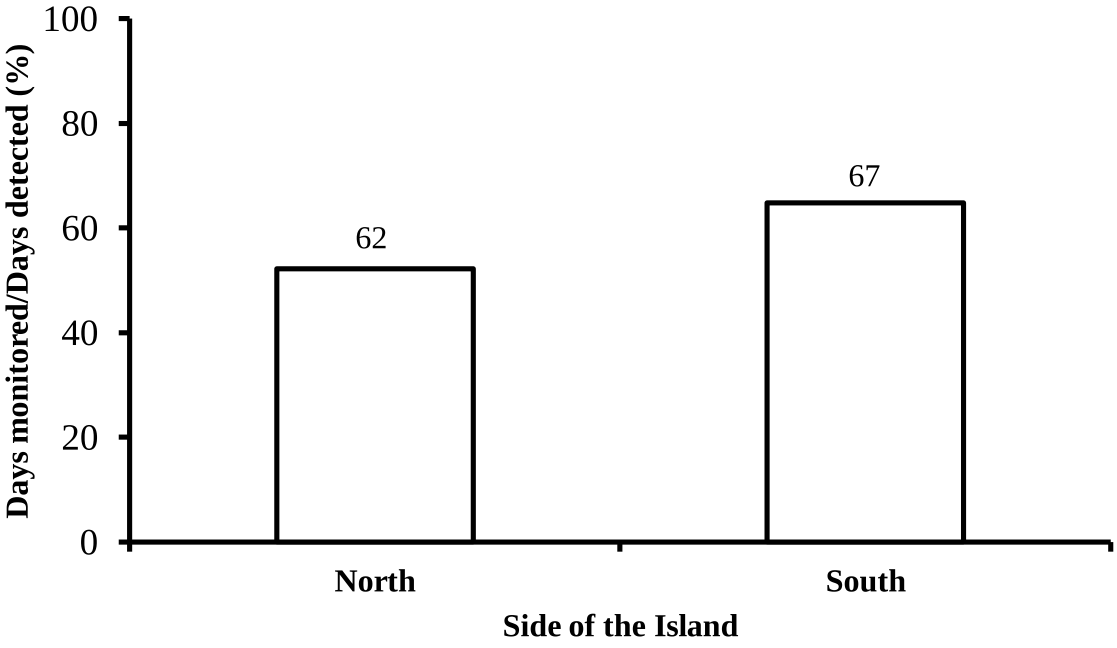

Figure 4.1. Percentage of days monitored that tagged white sharks were detected on the north and south sides of Seal Island. The numbers on top of each bar represent the maximum number of tagged sharks detected over the monitoring period at both sides.

The average number of tagged sharks detected per day on the South and North sides of the Island was 3.2 (±2.22; range 1 – 13) and 2.65 (±1.67; range 1 – 10) respectively. These rates of detection differed significantly from one another ($z = -2.768$, $p = 0.0056$, $n = 1515$).

The average number of tagged sharks detected per time of day category (for each day) on the South side of the Island differed significantly (Chi-square = 340.75, df = 3, $p = 0.001$, $n = 7643$). The highest average number of tagged sharks detected was at sunrise 3.01 (±1.29; range 2 – 10), compared to 2.85 (±2.86; range 2 – 10) during the day, 2.52 (±0.91; range 2 – 8) at sunset and 2.34 (0.71; range 2 – 7) during the night.

4.3. Residency

Tagged white sharks were monitored on the Island acoustic array for 1349 days and a total of 172,426 acoustic detections were recorded on the two Island receivers (North = 42,900, 24.88%; South = 129,526, 75.12%). Detection period ranged from 1 - 556 days (median = 120 days) and the number of days detected ranged from 1 - 149 days (median = 38 days). The average detection period for males was 185 days (±37 days) and for females was 154 days (±19 days). The average detection period for sharks ≤3 m was 164 days (±29 days) and for sharks >3 m was 164 days (±22 days). There were no significant differences between the detection period between males and females (t = 0.81, df = 66, p = 0.4193), or between sharks in the two size categories ≤3 and >3 m (t = 0.080, df = 66, p = 0.9936). The average number of days that males (45±7 days) and females (43 ±5 days) were detected at the Island was not significantly different (t = 0.16, df = 66, p = 0.8711). Similarly the average number of days sharks ≤3 m were detected (37 ±7 days), was not significantly different (t = 1.12, df = 66, p = 0.2663) to the average for sharks >3 m (47 ±5 days). Tagged sharks were present on consecutive days at the Island for an average of four days (±3 days) and for a maximum of 21 consecutive days.

4.4. Generalized linear mixed effects model

I used GLMMs to examine the influence of time of day, sex and size on white shark presence at the North vs. South side of the Island. Table 4.1 shows the various stages of the model building procedure. Variables were initially considered independently of one another (Stage I). Of these initial models, the model including time of day was selected as the best (assessed using AIC and BIC as described in methods section 2.7.3). Stages II and III built on the initial model, with each additional explanatory variable considered in turn. Finally, in Stage IV to VI, interaction terms were considered. The likelihood ratio test was used to determine whether the best model at each successive stage was significantly better than the previous best model. The final model included time of day, sex, year and an interaction term between time of day and sex (Table 4.2).

Table 4.2. Generalized linear mixed models to explore variables influencing shark presence at the North versus South of Seal Island. Bold indicates the model selected for the next stage.

	Model description	**AIC**	**BIC**	**Lrtest**
Stage I	**1) Time of Day**	**10355.82**	**10392.02**	**NA**
	2) Sex	10530.96	10552.68	NA
	3) Size	10538.83	10560.55	NA
	4) Chumming	10539.08	10560.8	NA
	5) Area Tagged	10534.07	10555.79	NA
Stage II	6) Time of Day	10355.82	10392.02	NA
	7) Time of Day + Sex	**10350.18**	**10393.62**	**8 vs. 1**
	8) Time of Day + Size	10357.32	10400.76	NA
	9) Time of Day + Chumming	10357.53	10400.97	NA
	10) Time of Day + Area Tagged	10352.43	10395.87	NA
Stage III	**11) Time of Day + Sex**	**10350.18**	**10393.62**	**12 vs. 8**
	12) Time of Day + Sex + Size	10351.85	10402.53	NA
	13) Time of Day + Sex + Chumming	10351.9	10402.58	NA
	14) Time of Day + Sex + Area Tagged	10348.76	10399.44	NA
Stage IV	15) Time of Day + Sex	10350.18	10393.62	NA
	16) Time of Day + Sex + Time of Day : Sex	**10346.29**	**10411.45**	**17 vs. 12**
Stage V	17) Time of Day + Sex + Time of Day : Sex	10346.29	10411.45	NA
	18) Time of Day + Sex + Time of Day : Sex + Year	**10320.48**	**10407.36**	19 vs. 17
Stage VI	**19) Time of Day + Sex + Time of Day : Sex + Year**	**10320.48**	**10407.36**	**20 vs. 19**
	20) Time of Day + Sex + Time of Day : Sex + Year + Time of Day: Year	10323.87	10475.91	NA
	21) Time of Day + Sex + Time of Day : Sex + Year + Sex: Year	10325.58	10434.18	NA
	22) Time of Day + Sex + Time of Day : Sex + Year + Time of Day: Year + Sex : Year	Does not converge		

Summary of the results from the final model are provided in Table 4.3 and Table 4.4. For each time of day and sex combination, the likelihood of a white shark visit at the North vs. South is described, using predicted odds ratios and their corresponding 95% confidence intervals. Odds ratios that are greater than 1 indicate an increased likelihood of a South visit, whilst those that are less than 1 indicate a decreased likelihood. All odds ratios were statistically significant, with the exception of that for night vs. sunrise and 2007 vs. 2004. The model results indicate that there is a significant time of day effect, with both sexes and both size categories more likely to be on the South side at sunrise (Table 4.3). The model results indicate that this is more likely for males (up to 3.5 times more likely) than for females, and that more South vs. North visits were likely in 2005 and 2006, compared to 2004, and less likely for 2007. The presence of chumming was included as a control variable; however, its inclusion did not contribute to explaining the observed patterns.

Table 4.3. Results from the generalized linear mixed effects model, showing the likelihood (odds ratios and 95% confidence intervals) of white sharks being present at the North versus South of the Island. Bold indicates significant values.

	Odds ratios (95% confidence intervals)	
Time of day	**Males**	**Females**
Day vs. Sunrise	**0.46 (0.32-0.52)**	**0.44 (0.38-0.51)**
Sunset vs. Sunrise	**0.53 (0.39-0.72)**	**0.48 (0.41- 0.58)**
Night vs. Sunrise	0.80(0.69-1.05)	**0.54 (0.46- 0.63)**

Table 4.4. Results from the generalized linear mixed effects model showing the likelihood (odds ratios and 95% confidence intervals) of white sharks being present across the 2.5 study years. Bold indicates significant values.

Year	**All Sharks**
2005 vs. 2004	**1.80 (1.25- 2.61)**
2006 vs. 2004	**2.09 (1.29- 3.38)**
2007 vs. 2004	1.04 (0.62- 1.75)

Figure 4.2 shows that both males and females had a higher proportion of visits to the South and North sides of the Island for the different time of day categories for autumn and winter months. A similar trend was apparent for both size categories (Fig. 4.3). Thus, regardless of sex and size, sharks consistently used the South side of the Island more than the North side and this trend was most evident at sunrise.

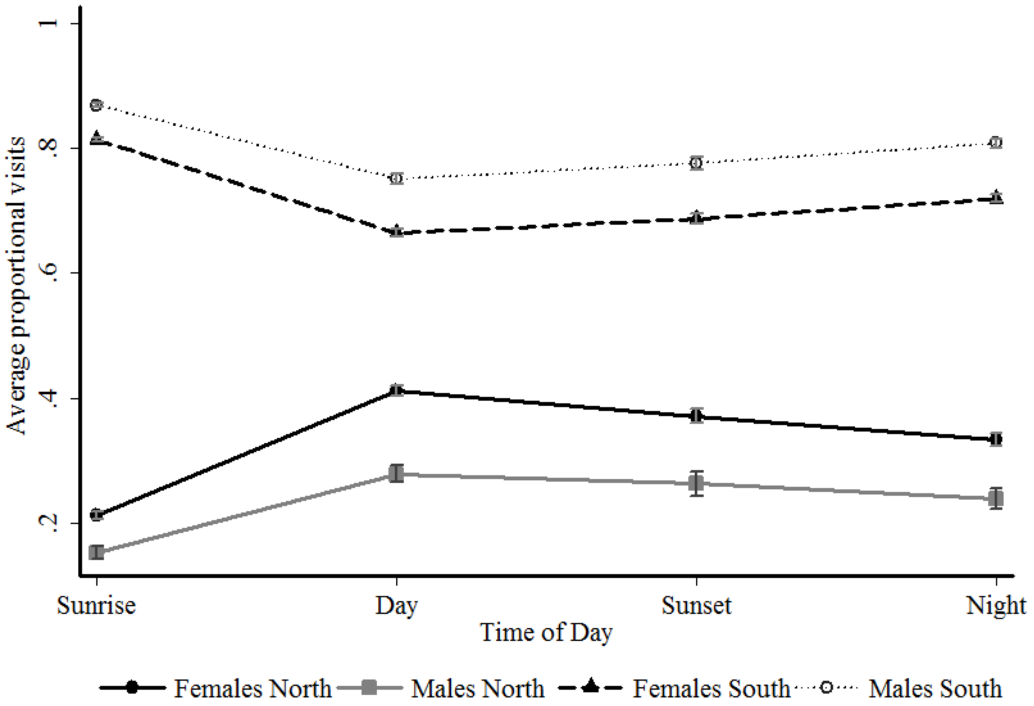

Figure 4.2. Average (+ s. d.) proportion of visits to the North and South side of Seal Island for male and female sharks for each time of day category (March - August) from May 2004 - December 2007.

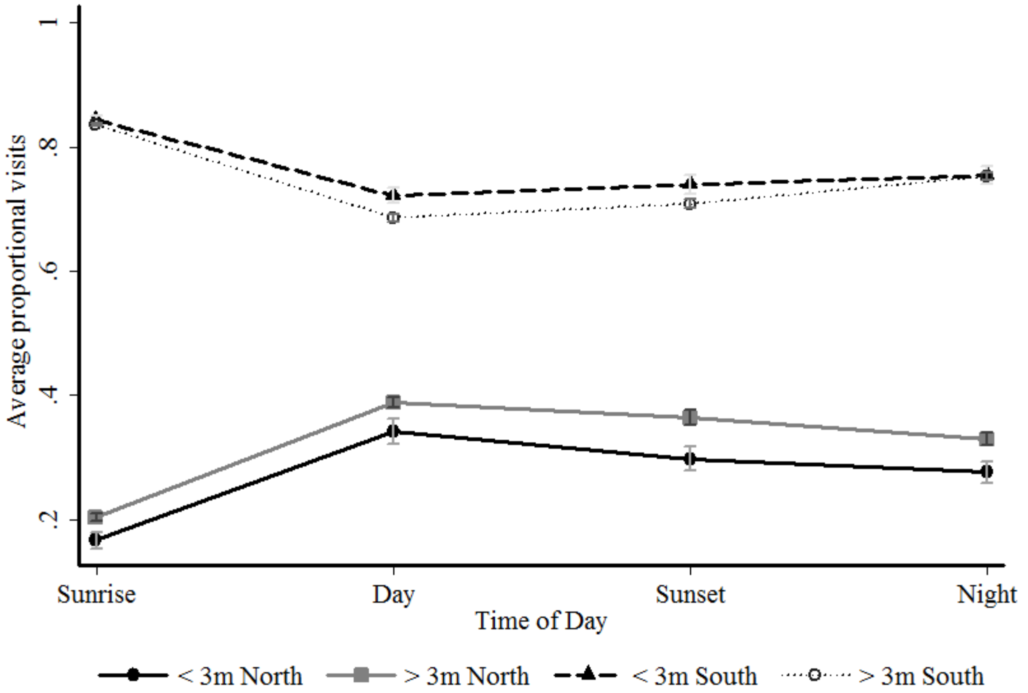

Figure 4.3. Average (+ s. d.) proportion of visits to the North and South side of Seal Island for ≤3 m and >3 m sharks for each time of day category (March - August) from May 2004 - December 2007.

4.5. Predatory events around Seal Island

A total of 72 data collection trips were made to Seal Island from June - September 2003 and June - October 2004, resulting in a total of 401.9 hours of *ad libitum* observations. This yielded a total of 498 predatory events or 1.24 predatory events per observational hour. The outcome of 78.6% (n = 390) of predatory events was verified, with 51.5% (n = 201) successful, 47.4% (n = 185) unsuccessful, 0.51% (n = 2) aborted and 0.51% (n = 2) scavenging. The average number of predatory events recorded per day was 6.33 (range 0 - 33). Extrapolated over the peak period of shark activity at the Island (March - August) for a given year (e.g. 2004) this equates to a minimum of 1164.7 attacks on Cape fur seals, of which 599.8 (or 0.78% of the Island's estimated population of 77 000 seals) are predicted to be successful.

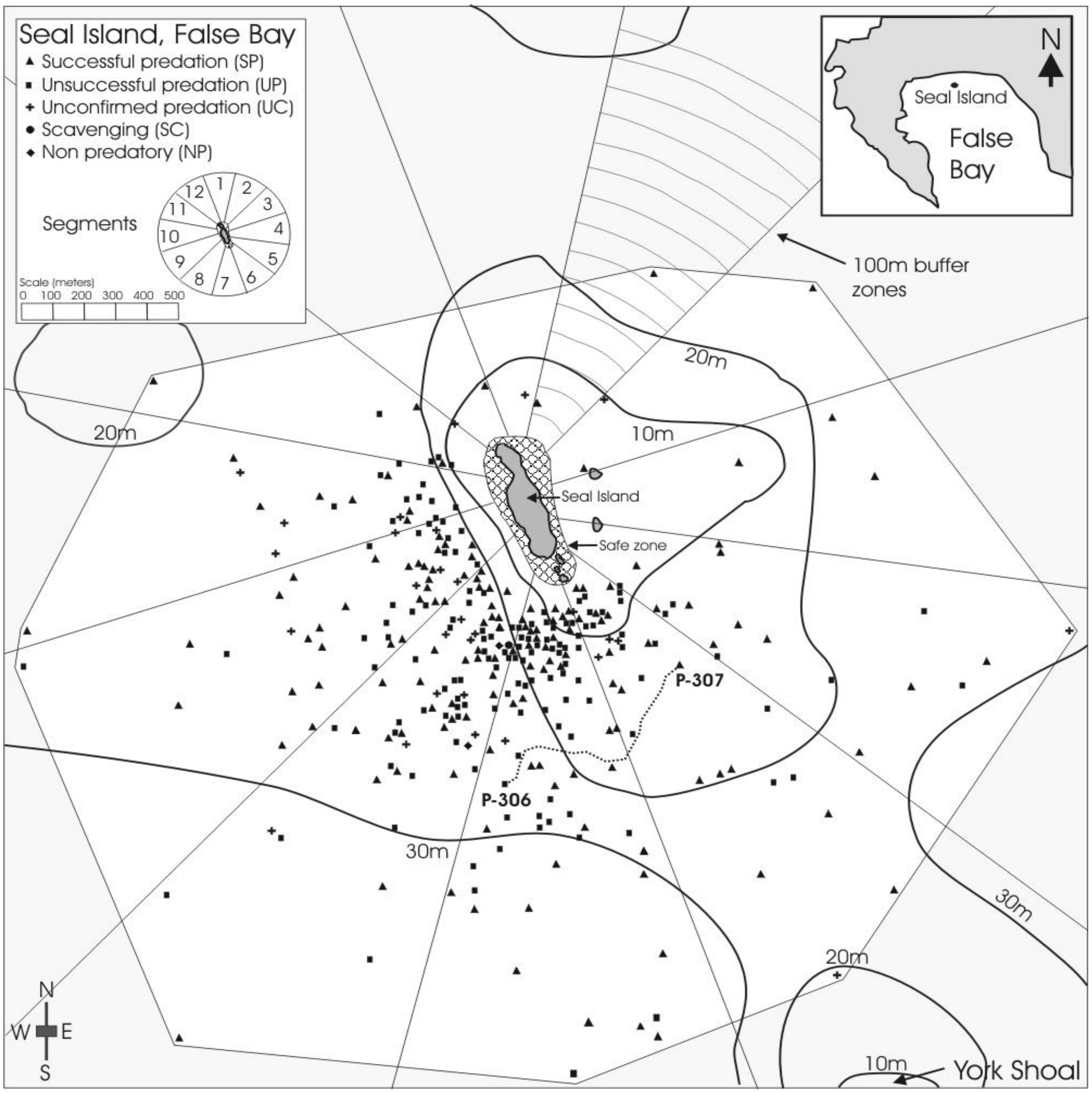

Figure 4.4. GPS locations of all predatory events (see legend) at Seal Island, False Bay from July - September 2003 and June - October 2004. The map includes the 'safe zone' around Seal Island, which is a cordon of shallow water in which predations were not observed. Also shown are bathymetry and spatial sectors that were used to investigate the effects of depth and spatial distribution on the frequency and success of predatory events. A single segment (right of center at top of figure) has concentric rings at 100m intervals. The polygon connects the outer-most predatory events and denotes the danger zone for seals around Seal Island. A portion of the 100 m concentric zones is illustrated (in segment 2).

4.6. Spatial and temporal patterns of predation

The distribution of predatory events was not evenly distributed around the island (Chi-square = 157, df = 11. p< 0.001, n = 318) (Fig. 4.4 and 4.5) with a higher than expected number of predatory events per hour in the southern and southwestern sectors (segments 6, 7, 8, 9, 10) and a lower than expected number of predatory events per hour in the northern and eastern segments (segments 1, 2, 3, 4, 5, 11, 12) (Fig. 4.5). The likelihood that an attack was successful was, however, independent of the segment in which it occurred (Chi-square = 17.1, df = 11, p> 0.05, n = 292) (Fig. 4.5).

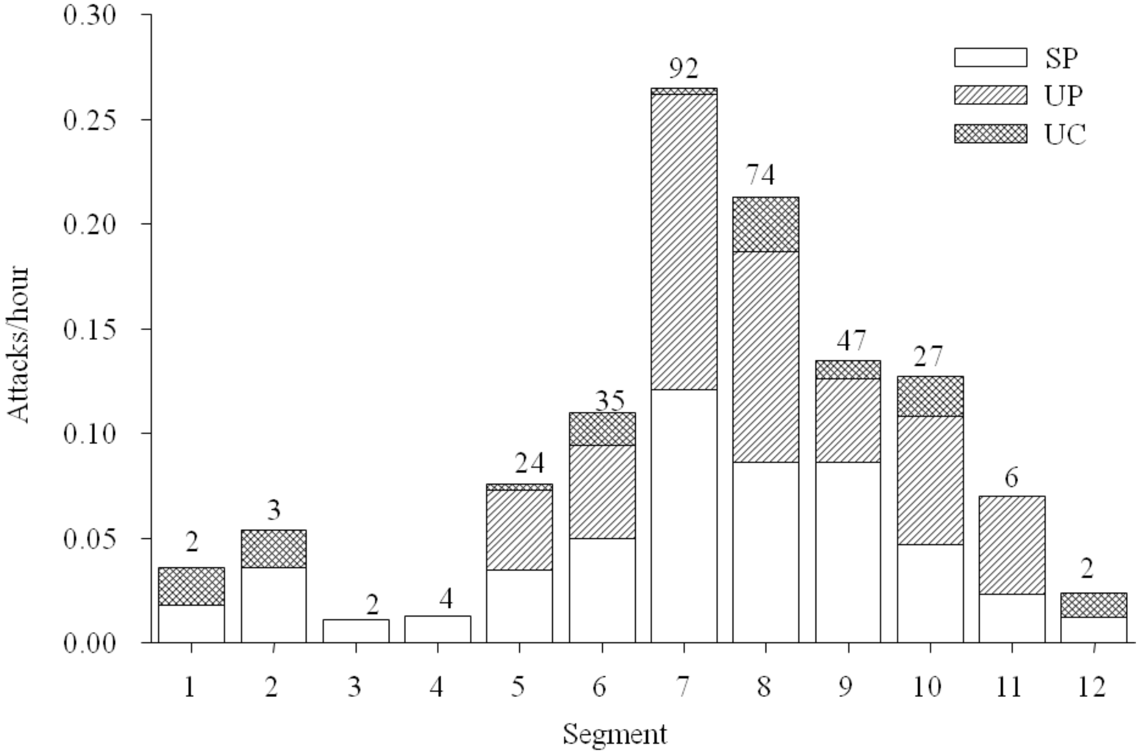

Figure 4.5. Frequency of attacks per hour in each of the 12 segments around Seal Island from July - September 2003 and June - October 2004. SP-successful predation, UP-unsuccessful predation and UC-unconfirmed predation. The numbers above each bar represent the total number of predatory events recorded in that segment.

The number of predatory events per hour varied with distance from the island (Chi-square = 237.5, df = 14, p< 0.001, n = 310) (Fig. 4.6), with more predatory events per hour than expected occurring within the 100-199, 200-299 and 300-399 m distance categories from the Island. There were very few predatory events (n = 6) in the areas closest to the Island (0-99 m), which is adjacent to a cordon of shallow water. The likelihood that an attack was successful was independent of distance from the island (Chi-square = 17.2, df = 14, p> 0.05, n = 285).

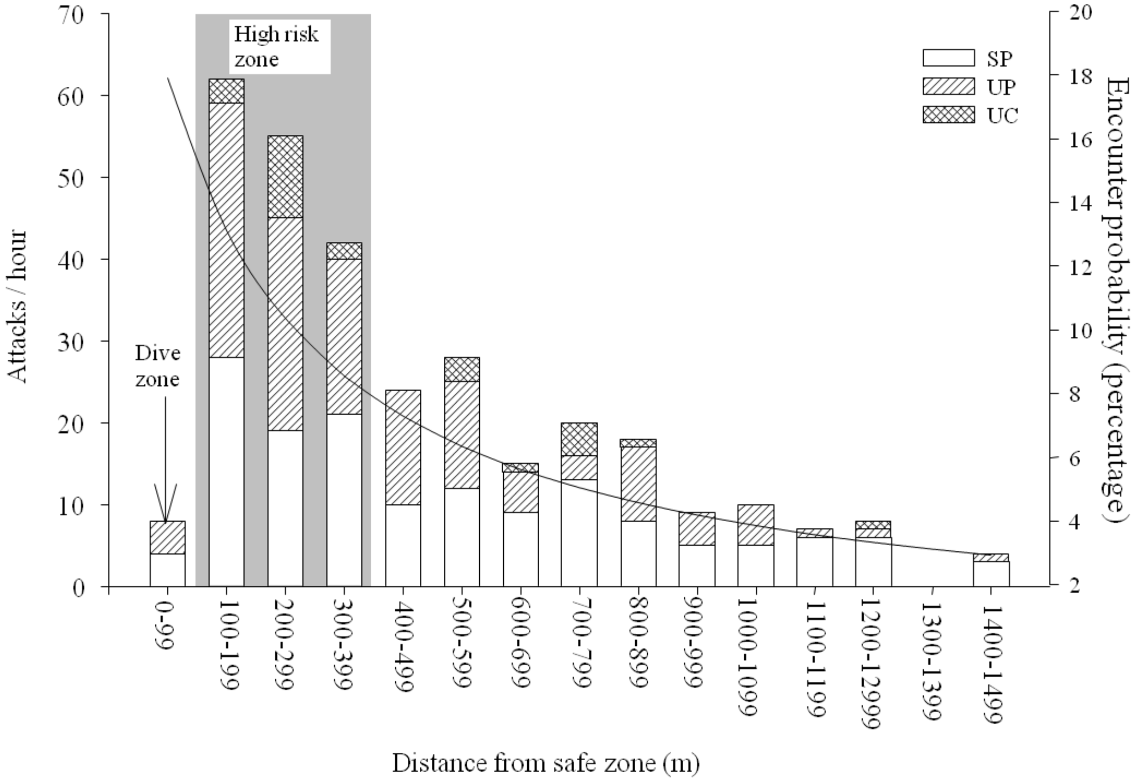

Figure 4.6. Number of predatory events per hour with consecutive 100 m distance intervals from Seal Island from July - September 2003 and June - October 2004. SP-successful predation, UP-unsuccessful predation and UC-unconfirmed predation. The solid line represents the theoretical probability of a shark encountering a seal within each 100 m zone.

The number of predatory events per hour was significantly influenced by water depth (Chi-square = 14.13, df = 2, p< 0.01, n = 320), with the lowest number of predatory events per hour recorded within the 0-10 m isobath. However, when controlling for the proportion of each depth present within the study area, the number of predatory events per hour was significantly higher than expected within the 10 m isobath. Predatory events per hour were higher than expected in water depth of 21-30 m (54.2% of the study area). The likelihood that an attack was successful was independent of depth (Chi-square = 0.3, df = 2, p> 0.05, n = 296).

Predation events varied significantly with time of day (Chi-square = 671.13, df = 13, p< 0.05, n = 495) (Fig. 4.7). Most predatory events (52.3%) were initiated within the first hour after sunrise and predation rates declined rapidly thereafter to 15.2% by 09h30 (Fig. 4.7). Predatory events within the first hour after sunrise (SP = 58.8%, n = 211) were more likely to be successful than at any other hour in the day (SP = 45.6%, n = 171) (Chi-square = 4.25, df = 13, p< 0.05, n = 382, Yates correction for continuity applied (Zar 1998) (Fig. 4.7).

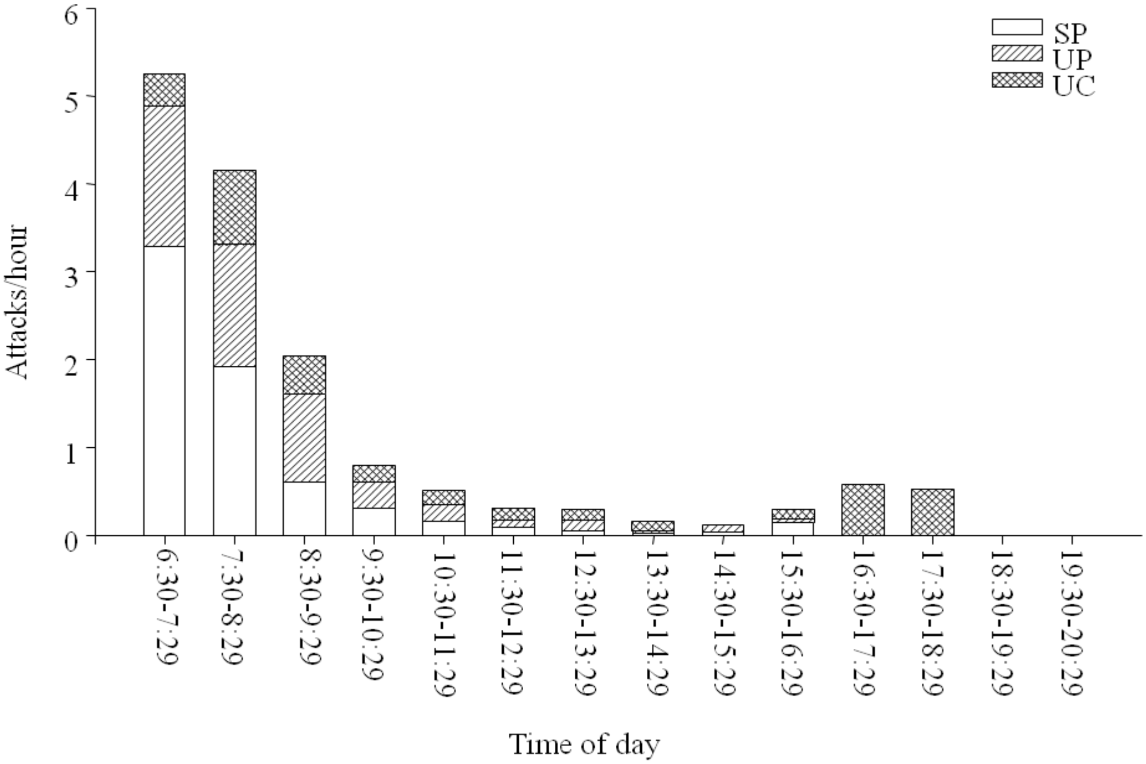

Figure 4.7. Number of predatory events per hour in hourly time intervals at Seal Island from July - September 2003 and June - October 2004. SP-successful predation, UP-unsuccessful predation and UC-unconfirmed predation.

4.7. Duration of attacks

A total of 272 predatory events were observed from start to finish and were used in this analysis. The average duration of a predatory event was 1 min (±0.0006, range 1-12 min). The frequency distribution of the duration of predatory events was highly skewed, with 91% (n = 248) being ≤1 min and only 9% (n = 25) lasting longer than 1 min. The average duration of successful predations was 1 min (±0.001, range 1-12 min, n = 80), which was similar for unsuccessful predations, which lasted on average 1 min (±0.004, range 1-4 min, n = 132). However, more successful predations lasted from 1 - 2 minutes, compared to unsuccessful predations, which were mostly less than one minute in duration (Chi-square = 12.38, df = 5, $p < 0.05$, n = 212).

4.8. Size of attacked seals

The size category of the seal attacked was determined for only 24% (n = 119) of all predatory events. Most predatory events were on young-of-the-year seals (88%), with significantly fewer attacks initiated on the two other size classes (Chi-square = 0.92, df = 3, $p < 0.05$, n = 111) (Fig. 4.8.). Due to the small sample sizes of attacks on sub-adults/adult seals (n = 15) and bull seals (n = 1), no analysis on success rate in relation to age category could be carried out.

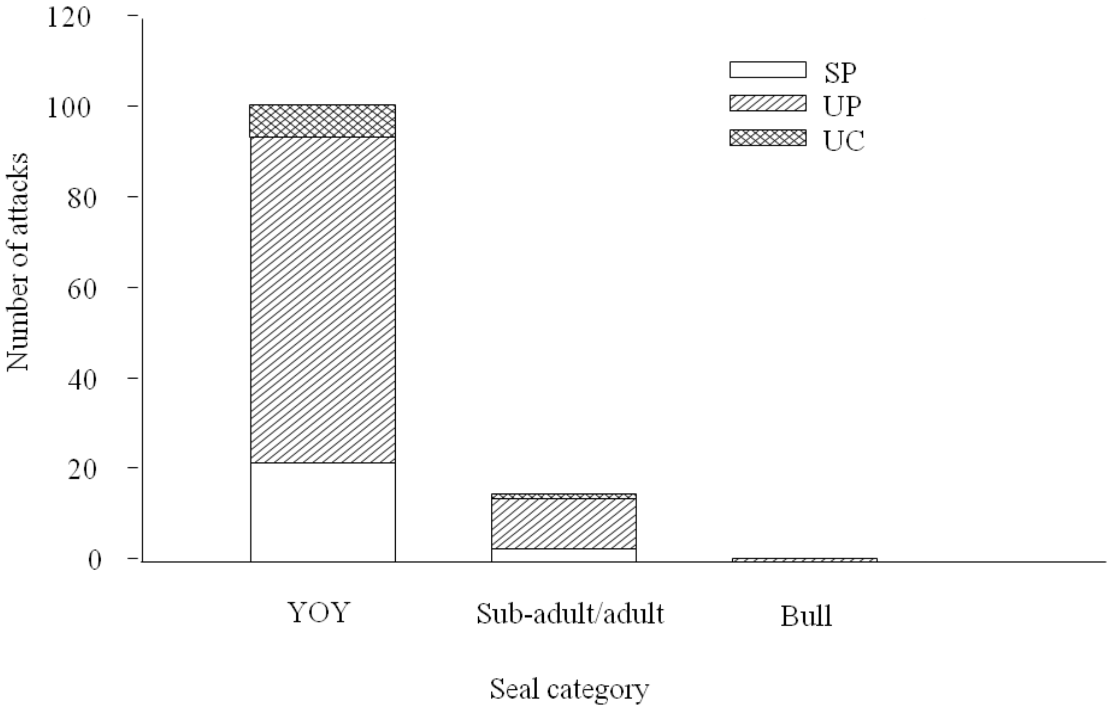

Figure 4.8. Number of predatory events initiated by white sharks on three seal size categories from July - September 2003 and June - October 2004. SP-successful predation, UP-unsuccessful predation and UC-unconfirmed predation.

CHAPTER 5

RESULTS 3:

Effect of habitat type, size and sex on white shark presence within the Inshore region of False Bay

This 5 m female white shark was oblivious to the commotion she was causing on land as she slowly swam along the beach with her tail brushing the sand from side to side.

Photo credit Enrico Gennari

Summary

A total of 56 individual sharks were detected on Inshore and Island receivers over 975 days from 1 May 2005 – 31 December 2007 (Table 2.1, Fig. 2.1). Females were detected significantly more than males along the Inshore region. Shark presence was highest at sites along the northern shore of False Bay e.g. Strandfontein and Muizenberg, and lowest along the western and eastern headlands of the Bay e.g. Cape Point and Pringle Bay. I used a generalized linear mixed effects model to explore the influence of habitat type, sex, size, time of day, distance from shore, range of receiver and year on the detection frequency along the Inshore region of False Bay. The model revealed a significant effect of habitat type, sex, time of day and range of receiver on the detection probability, with females more likely to be detected at sandy beach habitats and all sharks more likely to be detected during the day-time. An annual average of one shark bite was recorded on recreational water users in False Bay (2000-2012), and four white shark mortalities were recorded since 2000.

5.1. Sex and size of tagged sharks

A total of 53 white sharks were tagged with acoustic transmitters in False Bay between 1 May 2005 and 31 December 2007 (2005, n = 23; 2006, n = 25; 2007, n = 5). Additionally, three sharks tagged in 2004 at Seal Island as part of a long-term study (see Chapter 4), returned in 2005 and were included in the analysis, bringing the total number of acoustically monitored sharks for the study period to 56 (Table 3.1). Most sharks were tagged at Seal Island (80%, 45 out of 56 individuals) with only 20% (11 out of 56) tagged in the Inshore region (Table 3.1). Inshore tagging was only conducted during the summer of 2006/2007 and only female sharks were encountered in the 11 tagging sessions. Sharks fell predominantly into the >3 m category (71%, 40 of 56) and were mostly female (69.1%, 39 of 56). Tagged animals in this study (based on their estimated size) likely represent mostly juveniles and sub-adults.

5.2. Detection frequency of tagged sharks

The total number of detections recorded on Inshore receivers was 145,286 (Table 5.1.). On average 4843 (±6309) detections and 171 (±167) days were recorded per receiver.

The average number of tagged sharks detected per receiver was 22 (±11). The average number of females detected per receiver was 19 (±10) and of males was three (±3).

Tagged white sharks were detected on all receivers over the monitoring period (Fig. 5.1). The sites with the highest number of detections for female sharks were Muizenberg (84.6%, 33 out of 39), Fish Hoek, Kalk Bay and Macassar (79.5%, 31 out of 39 for all three beaches**)** and Strandfontein **(**77%**,** 30 out of 39). The sites with the highest number of male sharks were Macassar (75%, 12 out of 16) and Koeel Bay (68.8%, 11 out of 16). A single male shark was detected in Muizenberg (6%) and only two males (12%) were ever detected in Fish Hoek during the study period. Only Macassar and Koeel Bay had at least one male detected in all four seasons, while all sites (except Cape Point) had females detected in every season.

Tagged white sharks were detected at all monitored sites along the Inshore region of False Bay (Fig. 5.1), but the relative rates of utilisation of each site differed (Fig. 5.2). The highest average number of visits was recorded at Strandfontein, followed by Muizenberg and Macassar, all of which are beach habitats along the northern shore of False Bay. The least amount of activity was recorded at the eastern (Hangklip and Pringle Bay) and western headlands (Cape Point and Partridge Point) of the Bay.

Table 5.1. Summary of the detections at each site within the Inshore region of False Bay over the monitoring period 1 May 2005 - 31 December 2007.

Site	**Site code**	**Total detections**	**Total days sharks detected**	**Days detected/ days monitored**	**Total sharks detected**	**Total females detected**	**Total males detected**
Cape Point	RKI	53	19	0.02	11	9	2
	RKO	61	9	0.01	5	3	2
Fish Hoek	FHNI	2189	150	0.15	21	21	0
	FHNO	3181	218	0.22	29	28	1
	FHSI	1481	118	0.12	17	17	0
	FHSO	5549	216	0.22	30	29	1
Gordon’s Bay	GBI	710	37	0.04	10	10	0
	GBO	651	70	0.07	21	17	4
Hangklip	HKI	34	9	0.02	8	4	4
	HKO	27	11	0.02	11	8	3
Kalk Bay	KLBI	2178	170	0.17	27	26	1
	KLBO	7678	314	0.32	35	30	5
Koeel Bay	KBI	358	26	0.02	10	7	3
	KBO	1051	86	0.09	27	16	11
Macassar	MI	1170	76	0.23	13	10	3
	MO	5272	298	0.31	41	29	12
Muizenberg	MBC	5083	127	0.25	15	14	1
	MJB	5418	120	0.28	13	13	0
	MSB	5198	167	0.32	16	16	0
	MZV	13805	408	0.42	32	32	0
Partridge Point	PPN	384	52	0.05	16	14	2
	PPS	308	47	0.05	17	14	3
Pringle Bay	PBI	166	13	0.02	12	8	4
	PBO	120	17	0.03	17	10	7
Simonstown	STI	5576	203	0.21	27	23	4
	STO	6058	239	0.24	31	25	6
Strandfontein	SF2	18583	562	0.57	38	31	7
	SF3	25081	381	0.54	32	29	3
	SFI4	11535	321	0.45	29	29	0
	SFO1	16328	659	0.67	47	35	12

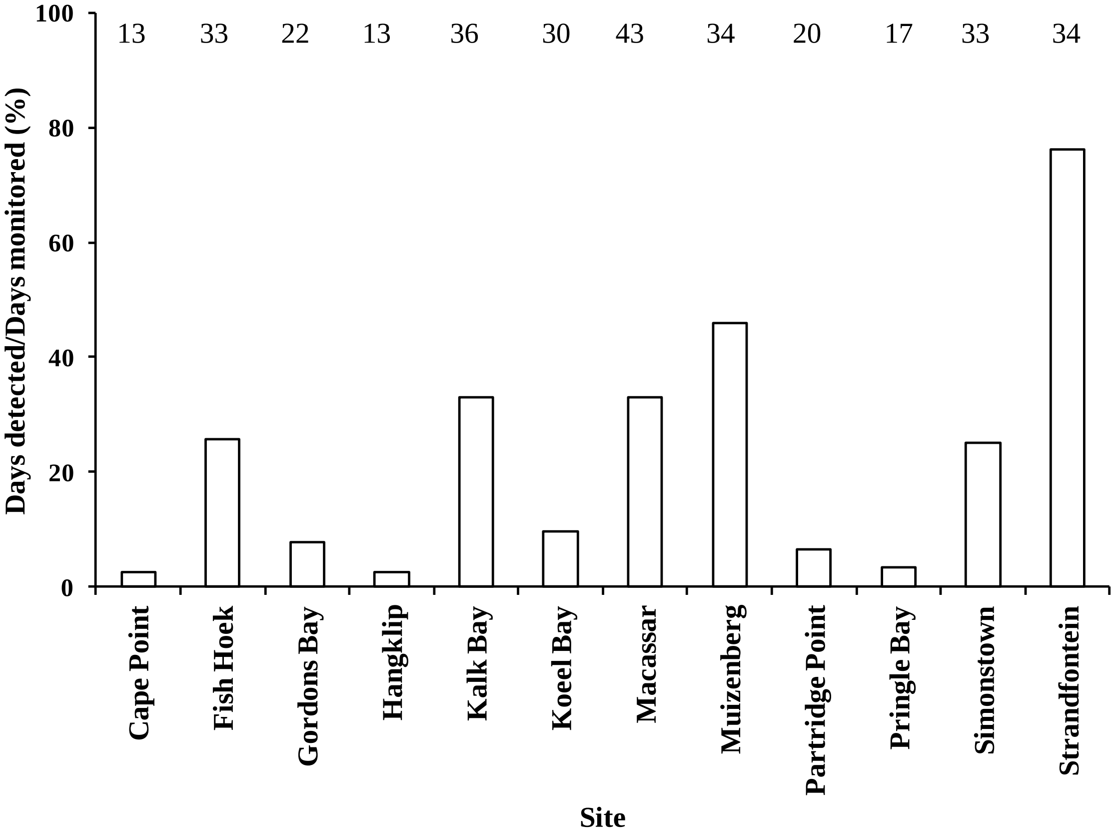

Figure 5.1. Numbers of days that tagged white sharks were detected for each Inshore site in False Bay, standardized by the monitoring period for each receiver (expressed as a percentage). The numbers above each bar represent the maximum number of tagged sharks detected over the monitoring period (1 May 2005 - 31 December 2007) at each site.

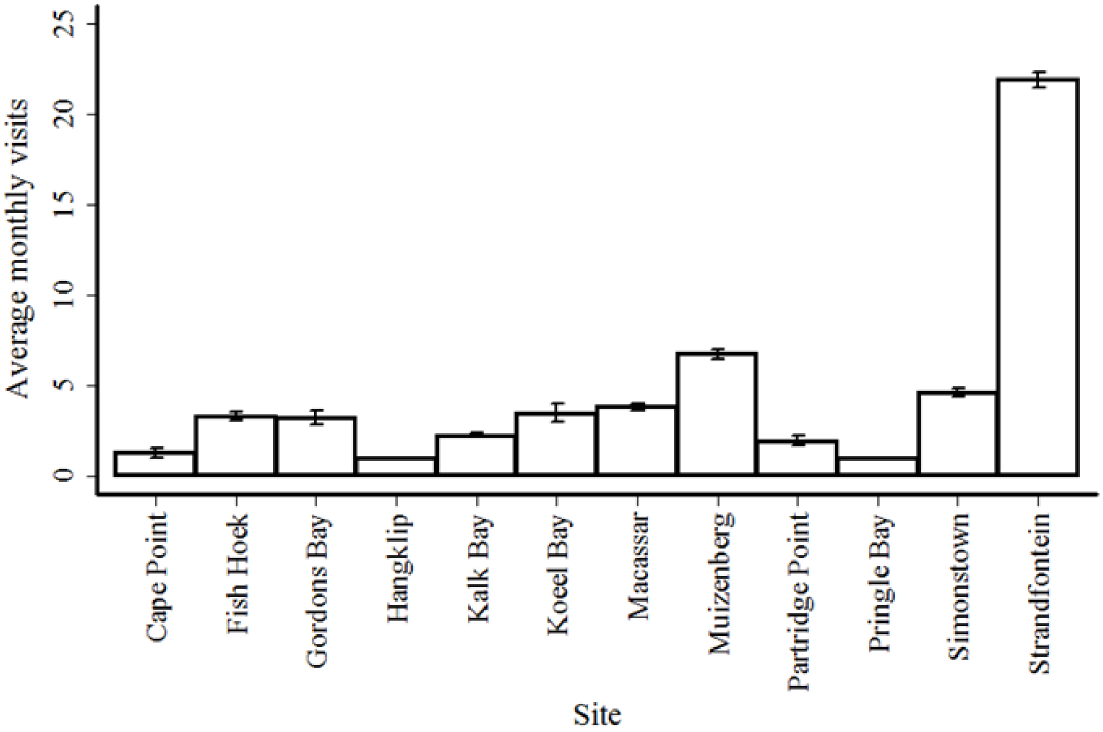

Figure 5.2. Average (+ s. d.) number of monthly visits by tagged white sharks to each of the 12 Inshore sites in False Bay for all years combined for the monitoring period 1 May 2005 - 31 December 2007.

5.3. Number of tagged sharks detected per day and number of consecutive days individual sharks were present per site

The number of tagged sharks recorded per day varied by site, with the highest number of tagged sharks detected for Strandfontein and the lowest for Partridge Point (Table 5.2). At all sites, except Strandfontein and Muizenberg, only a single shark was detected on a given day ≥60% of time (Fig. 5.3).

Table 5.2. The average (±SD), minimum (excluding zero) and maximum number of tagged sharks recorded per day at each of the 12 Inshore sites.

Site	Average (±SD)	Min	Max
Cape Point	1.08±0.28	1	2
Fish Hoek	1.50±0.79	1	5
Gordon's Bay	1.10±0.35	1	3
Hangklip	1.07±0.26	1	2
Kalk Bay	1.67±0.97	1	7
Koeel Bay	1.19±0.40	1	2
Macassar	1.49±0.81	1	6
Muizenberg	2.09±1.27	1	6
Partridge Point	1.06±0.25	1	2
Pringle Bay	1.10±0.30	1	2
Simonstown	1.36±0.69	1	5
Strandfontein	3.42±2.38	1	12

The average number of consecutive days that sharks were present at each site ranged from 1 (±1) for Cape Point and Hangklip to 4.55 (±4.54) for Strandfontein (Fig. 5.4). Strandfontein was the site with the highest maximum number of consecutive days when tagged sharks were present (27), followed by Muizenberg (13) and Macassar (8). The sites where sharks were present for the least number of consecutive days were Cape Point and Hangklip (1 day each).

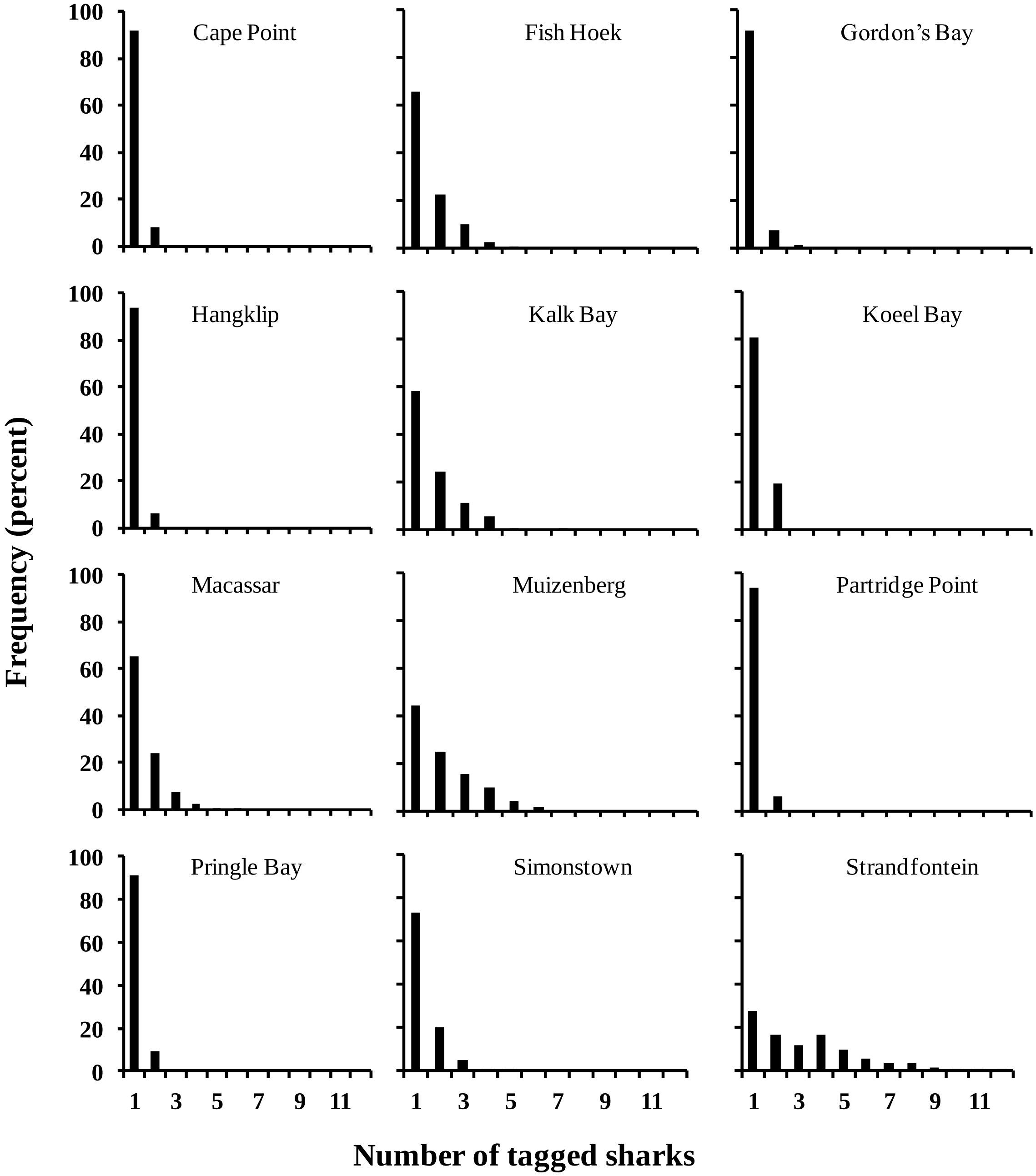

Figure 5.3. Frequency plots of the number of tagged sharks detected per day per Inshore site in False Bay for the monitoring period 1 May 2005 - 31 December 2007.

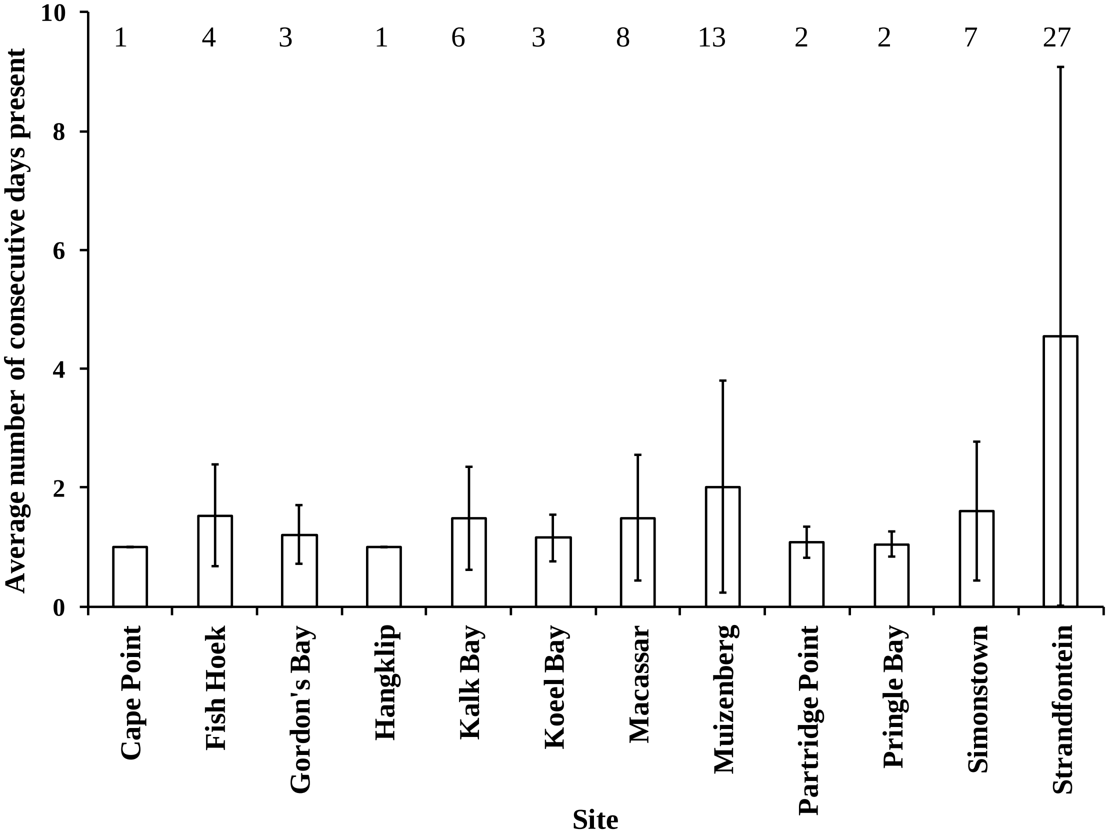

Figure 5.4. Average number (+ s. d.) of consecutive days on which white sharks were detected at each of the 12 Inshore sites in False Bay over the monitoring period 1 May 2005 - 31 December 2007. The numbers at the top of the graph represents the maximum number of consecutive days over which sharks were present at each site.

5.4. Effect of habitat type, size and sex on shark presence within the Inshore sites of False Bay

I used GLMMs to examine the influence of habitat type, size and sex on white shark presence along the Inshore sites of False Bay. The range of each receiver was included in the model as a control variable. Table 5.3 shows the various stages of the model building procedure. Variables were initially considered independently of one another (Stage I). Of these initial models, the model including ‘habitat + time of day’ was selected as the best fitting (assessed using AIC and BIC as described in methods section 2.7.4). Stages II to VII built on the initial model, with each additional explanatory variable considered in turn. Finally, interaction terms were considered in the last two stages. The likelihood ratio test was used to determine whether the best model at each successive stage was significantly better than the previous best model. The final model included habitat, time of day, range, sex and an interaction term between habitat and sex (Table 5.3). The final model was chosen to be the most parsimonious based on the lower BIC.

Table 5.3. Model building procedure using generalized linear mixed effects models and likelihood ratio tests to explore the effects of habitat type (beach, rocky, mixed, harbour), sex (male and female), time of day (sunrise, day, sunset, night) and receiver range (≤500 m, >500 m) on the number of visits to each acoustic receiver along the Inshore region of False Bay during spring and summer. Bold indicates the model selected for the next stage.

	Model description	**AIC**	**BIC**	**Lrtest**	**Lrtest (p-value)**
Stage I	1) Habitat	6855.668	6880.582	NA	
	2) Habitat + Sex	6835.901	6865.799	NA	
	3) Habitat + Size	6856.796	6886.693	NA	
	4) Habitat + Time of Day	**6683.431**	**6723.294**	NA	
	5) Habitat + Distance	6850.023	6879.92	NA	
	6) Habitat + Range	6735.305	6765.202	NA	
	7) Habitat + Year	6856.305	6891.185	NA	
	8) Habitat + Area Tagged	6856.243	6886.141	NA	
Stage II	9) Habitat + Time of Day	6683.431	6723.294	NA	
	10) Habitat + Time of Day + Sex	6662.428	6707.274	NA	
	11) Habitat + Time of Day + Size	6684.488	6729.334	NA	
	12) Habitat + Time of Day + Distance	6680.713	6725.559	NA	
	13) Habitat + Time of Day + Range	**6568.573**	**6613.419**	**13 vs. 4**	**116.86 (<0.0001)**
	14) Habitat + Time of Day + Year	6683.242	6733.07	NA	
	15) Habitat + Time of Day + Area Tagged	6683.885	6728.731	NA	
Stage III	16) Habitat + Time of Day + Range	6568.573	6613.419	NA	
	17) Habitat + Time of Day + Range + Sex	**6547.653**	**6597.482**	**17 vs. 13**	**22.92 (<0.0001)**
	18) Habitat + Time of Day + Range + Size	6569.595	6619.424	NA	
	19) Habitat + Time of Day + Range + Distance	6565.569	6615.397	NA	
	20) Habitat + Time of Day + Range + Year	6567.673	6622.484	NA	
	21) Habitat + Time of Day + Range + Area Tagged	6569.393	6619.221	NA	
Stage IV	22) Habitat + Time of Day + Range + Sex	6547.653	6597.482	NA	
	23) Habitat + Time of Day + Range + Sex + Size	6548.844	6603.655	NA	
	24) Habitat + Time of Day + Range + Sex + Distance	6545.656	6600.467	24 vs. 17	4 (0.0456)
	25) Habitat + Time of Day + Range + Sex + Year	6546.079	6605.873	25 vs. 17	5.57 (0.0616)
	26) Habitat + Time of Day + Range + Sex + Area Tagged	6549.461	6604.272	NA	
Interactions I	27) Habitat + Time of Day + Range + Sex	6547.653	6597.482	NA	
	28) Habitat + Time of Day + Range + Sex + Habitat*Sex	**6524.81**	**6589.587**	**28 vs. 17**	**28.84 (<0.0001)**
	29) Habitat + Time of Day + Range + Sex + Habitat*Time of Day	6536.613	6631.287	NA	
Interactions II	**30) Habitat + Time of Day + Range + Sex + Habitat*Sex**	**6524.81**	**6589.587**	**NA**	
	31) Habitat + Time of Day + Range + Sex + Habitat*Sex + Habitat*Time of Day	6513.788	6623.411	31 vs. 28	29.02 (<0.0006)

Summaries of the results from the final model are provided in Tables 5.4, 5.5 and 5.6. Incident rate ratios and their corresponding 95% confidence intervals are displayed for each habitat and sex combination, time of day and range of receivers. Incidence rate ratios greater than 1 indicate an increased likelihood of a visit, whilst those less than 1 indicate a decreased likelihood. All incidence rate ratios were statistically significant, with the exception of those for males when comparing mixed vs. beach and rocky vs. beach (Table 5.4). The model results indicate that there are significant habitat and time of day effects (Table 5.4 and Table 5.5). For females, the number of visits to beach habitats is greater than those at harbour, mixed and rocky habitats, while for males there was a preference of beach habitat over harbour habitat (Table 5.4). There was no significant difference in the number of visits between males and females at either mixed or rocky habitats (95% confidence interval crosses 1). The number of visits was highest during the day, followed by night, sunrise and then sunset (Table 5.5). As expected, the likelihood of a visit was greater at receivers with greater (>500 m) receptive areas (Table 5.6).

Table 5.4. Results from the generalized linear mixed effects model showing the likelihood (incident rate ratios and 95% confidence intervals) of male and female white sharks being present in different habitats (beach, mixed, harbour, rocky), along the Inshore region of False Bay. Bold indicates significant values.

	Incidence rate ratios (95% confidence intervals)	
Habitat	**Males**	**Females**
Mixed vs. Beach	0.82 (0.5-1.34)	**0.22 (0.20-0.24)**
Harbour vs. Beach	**0.39 (0.2-0.73)**	**0.23 (0.22-0.25)**
Rocky vs. Beach	0.68 (0.31-1.49)	**0.16 (0.12-0.22)**

Table 5.5. Results from the generalized linear mixed effects model showing the likelihood (incident rate ratios and 95% confidence intervals) of white sharks being present at different times of day (sunrise, day, sunset, night), along the Inshore region of False Bay. Bold indicates significant values.

Time of Day	**Incident rate ratios (95% confidence intervals)**
Day vs. Sunrise	**1.3** (1.22-1.38)
Sunset vs. Sunrise	**0.84** (0.78-0.9)
Night vs. Sunrise	1.09 (1.02-1.17)

Table 5.6. Results from the generalized linear mixed effects model showing the likelihood (incident rate ratios and 95% confidence intervals) of white sharks being present at receivers of different reception range (≤500 and >500 m), along the Inshore region of False Bay. Bold indicates significant values.

Range of receiver	Incident rate ratios (95% confidence intervals)
>500 m vs. ≤500 m	**1.65 (1.50-1.81)**

White sharks did not use the Inshore areas of False Bay uniformly. Both female and male sharks had higher average number of visits to beach habitat (Fig. 5.5) relative to harbour, mixed and rocky habitats. For females, there was a marked seasonal pattern for beach visits, which peaked during spring and summer months (September - February). A similar, but less pronounced pattern was evident for males, which showed a peak in the number of visits in April and October. There were no clear patterns in the use of mixed, harbour and rocky habitats for either sex, with the exception of a small peak in visits for females to mixed and harbour habitats in summer (Fig. 5.5).

Both size classes of shark had a higher average number of visits to beach habitat in the spring and summer months (Fig. 5.6) relative to all other habitat types. There were no clear patterns in the use of Inshore habitat types during the winter months, or for mixed, harbour and rocky habitats during the rest of the year. Sharks ≤3 m had another peak in the number of visits to the beach habitat in May and had a higher average number of visits compared to >3 m sharks in October.

The average number of visits for all tagged sharks was highest for beach habitat across all times of day, with peaks during day and night and lows during sunrise and sunset (Fig. 5.7). There were no clear temporal patterns in average visitation in any of the other habitat types (mixed, harbour, rocky).

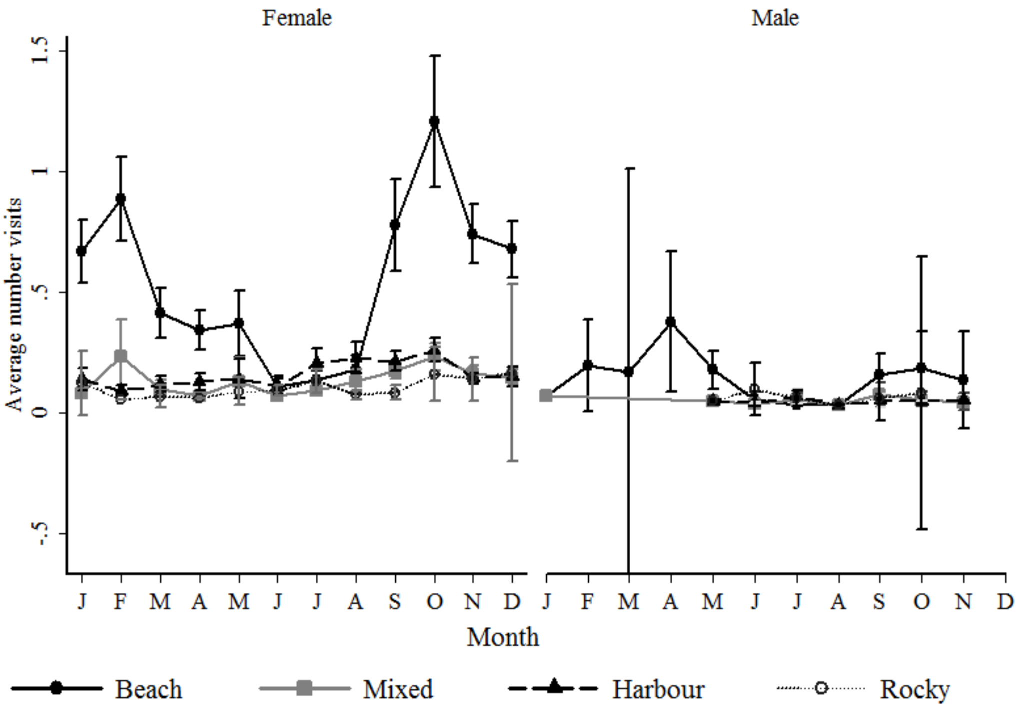

Figure 5.5. Average (± s. d.) number of visits by female and male white sharks to each of the four habitat types (beach, mixed, harbour, rocky) for each month of the year (January - December) across all years for the monitoring period 1 May 2005 - 31 December 2007.

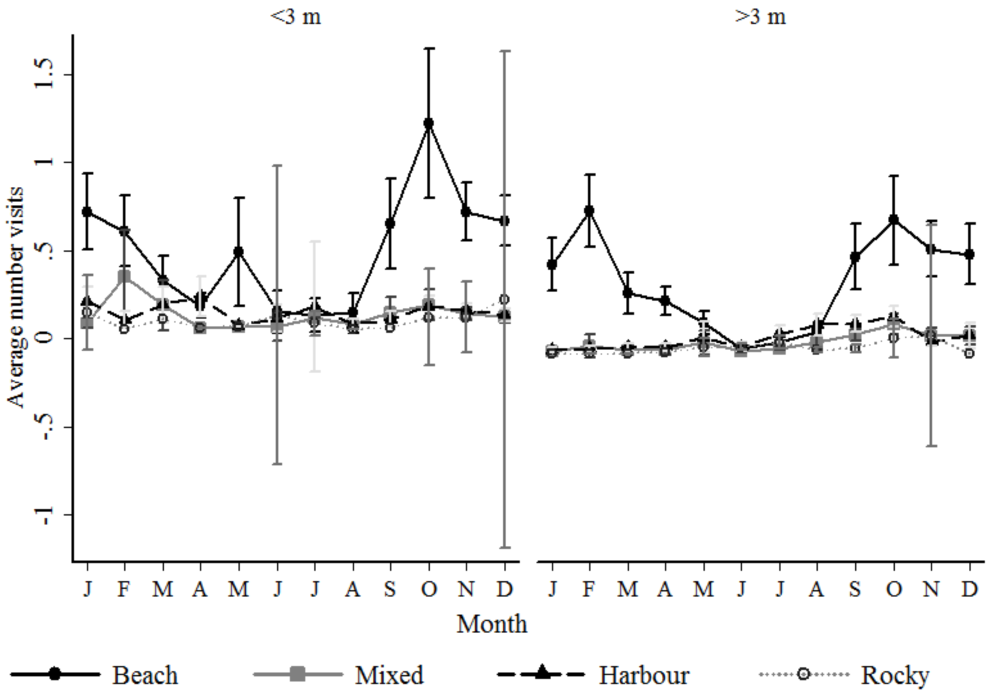

Figure 5.6. Average (± s. d.) number of visits by small (≤3 m) and large (>3 m) white sharks to each of the four habitat types (beach, mixed, harbour, rocky) for each month of the year (January - December) across all years for the monitoring period 1 May 2005 - 31 December 2007.

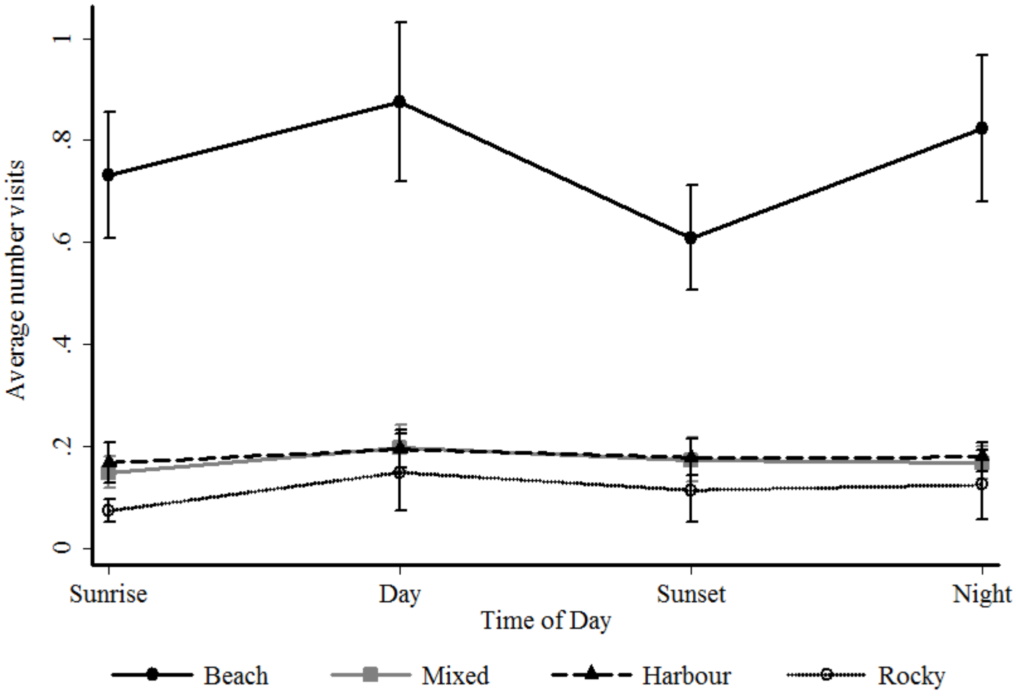

Figure 5.7. Average (± s. d.) number of white shark visits by time of day (sunrise, day, sunset, night) to each of the four habitat types (beach, mixed, harbour, rocky) for spring and summer months (September - February) across all years for the monitoring period 1 May 2005 - 31 December 2007.

5.5. White shark-human interactions

5.5.1. White shark bites

Since 2000, an annual average of one shark bite (n = 12), of which four (33.3%) were fatal, have been recorded on water users or small craft in False Bay (Table 5.7). Fish Hoek had the most bites (50%, 6 out of 12) and fatalities (75%, 3 out of 4).

Table 5.7. Summary of white shark bites in False Bay, South Africa from 2000 to 2012.

No.	Date	Location	Activity	Injury	Source
1	09/13/2002	Fish Hoek	Surf ski rider	None, surf ski rudder	(Cliff 2006)
2	04/05/2004	Muizenberg	Surfer	Major, right leg amputated	(Cliff 2006)
3	11/15/2004	Fish Hoek	Swimmer	Fatal, body not recovered	(Cliff 2006)
4	06/04/2005	Miller's Point	Spear fisherman	Fatal, body not recovered	(Cliff 2006)
5	10/01/2005	Fish Hoek	Surf ski rider	None, ski front	(Cliff 2006)
6	12/15/2005	Simonstown	Sea kayak	None, kayak	(Oelofse pers. com)
7	07/29/2006	Fish Hoek	Surf ski rider	None, surf ski	(Kock pers.com)
8	08/13/2006	Sunrise Beach	Swimmer	Major, leg severely bitten	(Oelofse pers. com)
9	11/07/2007	Strand	Surfer	Minor, right foot lacerated	(Kock pers. obs.)
10	01/12/2010	Fish Hoek	Swimmer	Fatal, body not recovered	(Oelofse 2010)
11	09/28/2011	Fish Hoek	Swimmer	Major, leg bitten off	(Oelofse 2011)
12	04/19/2012	Koeel Bay	Surfer	Fatal, leg bitten off	(Oelofse 2012)

5.5.2. White shark deaths

Since 2000, four white shark deaths have been reported in False Bay. In 2000 a dead white shark was found floating in Simonstown harbour with no external injuries (Fallows pers. com). On 25 October 2008 a 4.6 m male white shark was found on the beach at Macassar. Before authorities could retrieve the carcass, the head with the jaws was cut off and removed, but subsequently returned. There were no obvious external injuries on the body of the shark and the cause of death could not be determined. On 11 March 2012 a 4.3 m female white shark was accidentally caught in the ropes of a whelk cage set on the seafloor off Fish Hoek beach. In October of 2011 a 3 m male white shark was found dead on the rocks near Pringle Bay. It was suspected the shark was caught by a rock and surf angler, based on presence of two fishing hooks lodged inside the corner of its mouth and chaff marks on the body, possibly from fishing line.

CHAPTER 6

DISCUSSION

Living with white sharks in Cape Town has many challenges, but the more we understand about their behaviour, the better equipped we are to make informed management and conservation decisions.

Photo credit Morne Hardenberg

Although South Africa has long been recognised as a centre of global white shark abundance, little is known about their habitat use and residency patterns in these waters. Such information is essential for developing effective management strategies that reduce conflict between sharks and humans, without impacting adversely on the sustainability of this endangered species (Bonfil *et al*. 2005, Dudley 2012). In this study, I have used acoustic tagging to provide the first detailed investigation of white shark distribution patterns at different temporal and spatial scales in the largest Bay in South Africa, False Bay. Here, I discuss the results, within the context of our current knowledge on white sharks and other elasmobranchs, before concluding the thesis with recommendations for conservation and management plans aimed at achieving a sustainable white shark population with reduced human conflict.

6.1. Residency, habitat use and sexual segregation in False Bay

While white sharks are certainly capable of long-distance coastal and oceanic migrations, this study demonstrates that they also exhibit a high degree of fidelity to specific areas. Tagged white sharks, representing mostly immature animals (juveniles and sub-adults), were detected in False Bay in all months of the year and across all years. White shark use of the Bay varied significantly with both the season and the sex of the shark, but not with shark size. In autumn and winter, both males and females of different sizes aggregated at the Cape fur seal colony (Seal Island), where they were observed to feed predominantly on young-of-the-year seals. In the spring and summer months there was marked sexual segregation, with females frequenting the Inshore region and males seldom being detected at any acoustic stations in False Bay. Further corroborating this result is the observation that, out of eleven field trips to tag sharks on the Inshore over the 2006/2007 summer season, only female sharks were encountered and tagged. Together, these results suggest both a high level of residency and a strong annual rhythm of habitat use within this coastal region.

Numerous shark species aggregate seasonally, either for foraging or reproductive purposes. Whale sharks *Rhincodon typus* (Robinson *et al*. 2013), sevengill sharks *Notorynchus cepedianus* (Barnett *et al*. 2010), sixgill sharks *Hexanchus griseus*

(Andrews *et al*. 2009), salmon sharks *Lamna ditropis* (Hulbert *et al*. 2005) and tiger sharks *Galeocerdo cuvier* (Heithaus *et al*. 2002), all follow seasonal shifts in prey resources. Aggregations related to reproduction are less well known, and due to the difficulties associated with recording reproductive behaviour in large, far-ranging marine organisms, it is difficult to determine the relative importance of different geographic regions for feeding and/or reproduction. However, specific breeding aggregations have been described for ragged tooth sharks (*Carcharhinus taurus*) (Dicken *et al*. 2006) and bull sharks (*Carcharhinus leucas*) (Brunnschweiler and Baensch 2011). It is hoped that improved tracking technology, including SPOT tags, will improve our understanding of global movement patterns for white sharks and possibly identify areas where white sharks mate and/or give birth (Ocearch Global Shark Tracker, online at http://www.ocearch.org/tracker).

Predictable seasonal aggregations have been confirmed in all of the main centres of white shark abundance, including the Central California and the Southern California Bight, USA (Klimley 1985, Klimley and Anderson 1996, Jorgenson *et al*. 2010), Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2008, 2012, Nasby-Lucas and Domeier 2012), Neptune Islands, Australia (Bruce *et al*. 2006) and Seal Island, Gansbaai, Mossel Bay and Algoa Bay, South Africa (Martin *et al*. 2005, Bonfil *et al*. 2005, Johnson and Kock 2006). Elasmobranch aggregations form in response to refuging (Sims 2005, Sims *et al*. 2005), reproduction (Lucifora *et al*. 2005, Ebert and Ebert 2005), and foraging (Bethea *et al*. 2004, Lucifora *et al*. 2005), and may be segregated by sex, size, and/or maturity status (Sims *et al*. 2001, Bethea *et al*. 2004, Ebert and Ebert 2005, Sims 2005). In white sharks, aggregations have mostly been attributed to foraging (Tricas and McCosker 1984, Ainley *et al*. 1985, Klimley *et al*. 1992, Pyle *et al*. 1996, Martin *et al*. 2005, Hammerschlag *et al*. 2006) and to a lesser extent reproduction (Weng *et al*. 2007a, Jorgenson *et al*. 2010, 2012, Domeier 2012), with considerable debate as to their relative importance in some areas (Jorgenson *et al*. 2010, 2012, Domeier 2012). White shark aggregations at pinniped rookeries are well-established and almost unanimously considered to reflect convergence of predators on a seasonally abundant, high-quality food resource (Strong *et al*. 1996, Klimley *et al*. 1992, Pyle *et al*. 1996, Goldman and

Anderson 1999, Malcolm *et al*. 2001, Bruce *et al*. 2005, Martin *et al*. 2005, Domeier and Nasby-Lucas 2007, Laroche *et al*. 2008).

Seal Island, False Bay is a known white shark aggregation site and the convergence of sharks over autumn and winter is generally attributed to the seasonal increase in the abundance of predator-naïve seals (Laroche *et al*. 2008, de Vos 2010, Chapters 3 and 4). However, this study further identified the Inshore region of False Bay as another important and frequently-used region by female white sharks ranging in size from 1.7–5 m. Few studies have looked at habitat use along Inshore areas not associated with seal colonies. Recently Bruce and Bradford (2012a) reported temporary seasonal residency of newborn and juvenile sharks near beaches in eastern Australia, identifying two primary residency sites (periods of residency at these two sites ranged from 21 - 122 days) along a coastal stretch of 2000 km. This is similar to our finding of temporary (seasonal) residency in the Inshore habitat, but differs in being sex-biased rather than size-biased. Bruce and Bradford (2012a) attributed Inshore residency to food availability (e.g. Australian salmon) and because most of the sharks using this habitat were young-of-the-year and juvenile sharks, they classified these Inshore areas as nursery grounds.

Perhaps the most remarkable findings of this study are the high levels of site fidelity shown by the same tagged sharks at the Island in winter and the Inshore in summer, despite the close proximity of these two areas and given the large areas over which white sharks may range. Similar patterns of white sharks aggregating around seal colonies in winter and Inshore sites in summer have been documented in other areas of the Western Cape, South Africa, including Gansbaai (Towner *et al*. 2013) and Mossel Bay (Johnson *et al*. 2009, Jewell *et al*. 2012).

Sexual segregation in habitat use appears to be common among sharks (Klimley 1987, Wearmouth and Sims 2008), with adult males and females within a species using different habitats either within the same, or different, geographic regions (Sims 2005). Habitats may be selected differentially by the sexes for social, thermoregulatory or food-related reasons (Wearmouth and Sims 2008). Seasonal migration between two distinct habitats has been shown for white sharks within the northeastern Pacific, but these two habitats are hundreds of kilometers apart. In that study, mature and sub-adult white sharks show predictable seasonal aggregations at pinniped rookeries were they were tagged (Domeier and Nasby-Lucas 2008), before migrating offshore to common pelagic habitats (Domeier and Nasby-Lucas 2008, Jorgensen *et al*. 2010). In central California, sex-specific visitation patterns at aggregation sites are thought to be linked to the 12-18 month gestation period of females, who only visit every second year, whilst males return annually (Anderson and Pyle 2003). A similar pattern has been observed at Guadalupe Island, Mexico and has also been attributed to the sex-specific differences in the reproductive cycle (Domeier and Nasby-Lucas 2007). At the Neptune Islands, Australia, shark occurrence is biased towards males and more males are observed in months with cooler water temperatures and more females in months with warmer water temperatures, giving rise to the hypothesis that the sexual segregation is related to water temperature (Robbins 2007, Robbins and Booth 2012). These studies propose that warmer waters may facilitate optimum growth of developing embryos, and increase somatic growth rates, which together may enhance lifetime female reproductive success (Klimley 1987, Sims *et al*. 2001). Conversely, it has been suggested that male sharks may select cooler waters for optimal sperm production (Kime and Hews 1982).

The causes of white shark aggregations and of the marked sexual segregation found in the Inshore region of False Bay are not known. However, the shift from the Island in autumn and winter to the Inshore region in spring and summer by females mirrors the seasonal peak in abundance of juvenile seals (Laroche *et al*. 2008, de Vos 2010) and of migratory teleost and elasmobranch species (Clarke *et al*. 1996a, 1996b, Lamberth 2006), respectively in False Bay. While I have no data for social interactions between white sharks in False Bay and how these may vary seasonally, I do have information on shark presence and seasonal variation in both water temperature and prey availability within the Bay and hence further discussion of the possible impacts of these variables may prove heuristic.

Water temperatures within the Bay are highest in spring and summer with the highest temperatures typically recorded along the Inshore region (Clark *et al*. 1996a). White shark presence along the Inshore region of False Bay in spring and summer is known to be influenced by sea surface temperature and lunar phase, with more sharks detected in warmer waters (≥18 °C) and at new moon (Weltz *et al*. 2013). The warmer water results in blooms of surf-zone diatoms, which are associated with an increase in abundance and diversity of teleosts and chondrichthyans (Atkins 1970, Lamberth *et al*. 1995, Clarke *et al*. 1996a, 1996b), both of which are common prey for white sharks (Tricas and McCosker 1984, Cliff *et al*. 1989). While the diet of white sharks on the Inshore areas of False Bay has not been quantified, there are many anecdotal observations of them feeding on seasonally-abundant fish, such as white steenbras (*Lithognathus lithognathus*) and yellowtail (*Seriola lalandi*), in addition to various elasmobranch species frequently caught by fishermen in False Bay during the summer months (pers. obs.). Given the close association between prey abundance and shark distribution (Sims and Quayle 1998, Sims *et al*. 2003, Dicken *et al*. 2006, Wirsing *et al*. 2007, Barnett and Semmens 2012), it is possible that the combination of increased difficulty in catching 'more experienced' juvenile seals at the island (de Vos 2010), and an increase in the availability of fish species in the Inshore region, may drive the marked seasonal shift from the Island to the Inshore region of False Bay. This explanation is well supported by the literature that seeks to explain seasonal shifts in predator presence in a variety of both terrestrial (e.g. Hopcraft *et al*. 2005) and marine (e.g. Barnett and Semmens 2012) ecosystems.

The hypothesis that white shark movement patterns in False Bay are driven by seasonal shifts in prey availability and catchability does not, however, explain why males were seldom detected in False Bay outside of the winter months and why they were seldom detected along the Inshore region. Recent unpublished satellite tag data (Ocearch Global Shark Tracker, online at http://www.ocearch.org/tracker) suggests that males of all sizes (ages) disperse along the Southern African coast during spring and summer. Thus, their lack of detection on the False Bay acoustic array would not appear to be a sampling error, but rather a reliable measure of their absence from the region in general and the Inshore in particular. This suggests very strong resource partitioning by a highly mobile predator.

In general, these results are strikingly similar to those reported for sevengill sharks *Notorynchus cepedianus* in Tasmania, where males and females were present at coastal sites during summer, but during winter, males move out of the coastal areas, migrating north, while some females remain at the coastal site (Barnett *et al*. 2010). These authors concluded that the lack of behavioural evidence for reproduction in these coastal areas and the absence of smaller size classes (<150 cm) suggests that, similar to my study, the best explanation for sex-biased site fidelity and migration patterns is the partitioning of food resources (Barnett *et al*. 2010, 2011). This fine-scale habitat partitioning is particularly noteworthy, given the highly mobile nature of these large sharks.

6.2. Spatial and temporal patterns of presence and predation by white sharks at Seal Island during autumn and winter

While the predatory behaviour of white sharks around pinniped colonies has received considerable attention (Klimley *et al*. 1992, Klimley and Anderson 1996, Klimley *et al*. 1996, Pyle *et al*. 1996, Martin *et al*. 2005, Hammerschlag *et al*. 2006, Kock and Johnson 2006, Laroche *et al*. 2008), few studies have integrated acoustic data with behavioural observations of predation by white sharks, to determine whether there is competition between the sexes and sizes of white sharks and how this impacts on possible sex/size based segregation around this concentrated food resource.

Seal breeding colonies provide a seasonally predictable, abundant food source for white sharks (Laroche *et al*. 2008, Semmens *et al*. 2013, Kock *et al*. 2013, Chapter 3) which arrive at Seal Island in April/May and depart in August/September (Chapter 3). There was, however, a high degree of individual variation in residency at the Island with the number of consecutive days each shark was present ranging from 1-21 days (median = 3). These residency periods are considerably shorter than those reported for the North Neptune Islands, Australia, where the number of consecutive days present ranged from 1-52 (median = 6.5), but are similar to those reported from the South Neptune Islands, Australia, where the number of consecutive days present ranged from 1-34 (median = 2) (Bruce and Bradford 2012b). Given that in both Bruce and Bradford (2012b) and my study our acoustic array design ensured total coverage of the island groups, it is possible to compare these findings. Bruce and Bradford (2012b) concluded that the differences in residency between the North and South Neptune Islands were as a result of increased white shark cage diving effort at the North Neptune Islands, compared to the South Neptune Islands. However, Bruce and Bradford (2012b) did not account for seal abundance or catchability between these two island groups, and thus it is not possible to discuss their findings within this context. It is, however, interesting to note that the residency of white sharks at Seal Island, False Bay which experiences moderate levels of ecotourism (Laroche *et al*. 2007), is similar to the South Neptune Islands, where no white shark cage diving takes place. Given the large distance between the Neptune Islands and the mainland, it is also possible that residency is higher at the North Neptune Islands because the costs of commuting to other foraging areas are higher. By contrast, Seal Island, False Bay is very close (approx. 6 km) to the Inshore region, which may result in reduced residency as sharks explore other habitats in between visits to the island.

Both the total number of predation events at Seal Island, and the proportion of these that are successful, have been shown to peak at sunrise (Hammerschlag *et al*. 2006) and the results of this study support this observation (Chapter 4). This temporal bias in predation effort and success is assumed to result from the increased abundance of naïve seals in the water at sunrise (de Vos 2010) and the optimal light conditions that exist at sunrise for a counter-shaded, ambush predator approaching surface swimming seals from depth (Strong *et al*. 1996, Kock 2002, Martin *et al*. 2005, Hammerschlag *et al*. 2006, Laroche *et al*. 2008, de Vos 2010, de Vos and O'Riain 2010, Martin and Hammerschlag 2012). If the sharks are not initially successful, they seldom engage in prolonged pursuit of the prey and give up the attack quickly. This is very similar to the strategy used by terrestrial ambush predators, such as lions and leopards, and contrasts with pursuit predators such as wild dogs (Vanak *et al*. 2013).

In general, the patterns of predation presented in Chapter 4 support the results of Martin *et al*. (2005) and Hammerschlag *et al*. (2006), where predation events are spatially clustered on the South and south western areas of the Island, within 500 m of Seal Island, with a clear peak and higher success rate at sunrise. My results do not, however, support their finding that white sharks were more successful to the South of the Island, or that the chances of a successful attack increased with distance from the Island. Conversely, I found no difference in success rates around the Island, nor with increasing distance from the Island. It is possible that these differences reflect our different methods, with Martin *et al*. (2005) and Hammerschlag *et al*. (2006) focusing their observational effort to the South of the Island at sunrise, whilst I sampled all areas around the Island evenly and across all times of the day, randomly selecting both the Island segment and interval before commencing observations (Chapter 2). While Martin *et al*. (2005) and Hammerschlag *et al*. (2006) were able to confirm predation events in areas adjacent to the southern segment, the error in both detection rate and confirmation of whether such events were successful would have increased with distance from their boat, in the absence of equal sampling in all areas across all times. In addition, successful predations have more cues for detection (i.e. breaching, birds scavenging on remains and the sharks feeding on the surface) and last longer than unsuccessful predations. Furthermore, all data from Seal Island so far indicate that white sharks maximize their chances of encountering seals and concentrate their predation attempts when physical conditions maximize the chances of success. This is clearly evident from both the data presented here and that of Laroche *et al*. (2008), both of which show a strongly non-random pattern of attacks and presence, with strong temporal peaks and distinct spatial patterns around the Island, associated with factors such as light intensity, bottom topography and seal abundance. Therefore, the findings from Martin *et al*. (2005) that show success rate is greater further away from the Island and in areas less patrolled by white sharks are not consistent with this strategy. If this were indeed the case, one would expect an equal distribution pattern of attacks across the time of day and around the Island, which is not what the tracking data show (Chapter 4).

The results of this study, demonstrated that, regardless of sex or size, white sharks over-dispersed on the South side of the Island at sunrise, where seal movement to and from the island is highest (Laroche *et al*. 2008, de Vos 2010) and consequently encounter rates and predation events peaked (Martin *et al*. 2005, Hammerschlag *et al*. 2006, Chapter 4). Intriguingly, while males and females both showed a preference for being on the South side at sunrise, males visited the south significantly more often (80% of their time while at the island) than females (60% of their time while at the island). This may indicate that social interactions between males and females are influencing their respective use of the Island and females may have to balance wanting to maximize encountering a seal, with more frequent encounters with males. However, in the absence of direct or indirect (e.g. by using Crittercams) observations of behavioural interactions between the sexes, the reason for this spatial bias at the island between the sexes, remains a mystery. Chapter 3 showed that male and female white sharks exhibited sexual segregation, with females using the Inshore areas of False Bay during spring and summer and males noticeably absent. This may indicate that males and females require different resources. It is therefore also possible that the relative importance of seals in the diet of white sharks is greater for males than for females.

There were no significant differences in overall residency patterns for sharks of either size category, or between males and females, at the Island (Chapter 4). Furthermore, the lack of any size-based habitat use difference in sharks visiting the south side of the Island at sunrise does not support the hypothesis proposed by Goldman and Anderson (1999) that smaller sharks are more naïve than larger sharks concerning the spatial and temporal distribution of food around the Island. Furthermore, the lack of difference in the size of sharks visiting the more productive southern side of the Island at sunrise does not support the theory proposed by Anderson and Goldman (1996) that larger sharks may competitively exclude smaller sharks from small areas with high concentrations of seals. This original hypothesis has been cited numerous times in the scientific literature (e.g. Martin *et al*. 2005, Speed *et al*. 2010, Bruce and Bradford 2012a, Jewell *et al*. 2012), but until now, the theory has not been tested with appropriate data. While it remains possible that on a very fine spatial scale, social hierarchies are possible, my data shows that in general, small and large sharks are present simultaneously in prime hunting areas. Lastly, the lack of data on the relative predation success of different sized/sex sharks at the Island confounds the ability to verify the relative importance of seals in the diet of small versus larger sharks. This has been suggested to be greater for larger white sharks (Cliff *et al*. 1989, Hussey *et al*. 2012). Heithaus *et al*. (2006) similarly found no difference in microhabitat use between smaller (<3.25 m) and larger (>3.25 m) tiger sharks. Interestingly, very small white sharks (<2 m) have been observed at Seal Island swimming in close proximity to large (4 m) individuals and interacting around the bait in a relative relaxed manner (personal observation). It thus does not appear that these smaller sharks are threatened by the larger sharks in the area. It is more likely, that larger sharks (with larger gape size) are more capable of exploiting larger prey items, which may account for the absence of very small (<2 m) sharks at the Island.

Lack of competition between conspecifics at concentrated food resources is supported by the observation that white sharks scavenging on cetacean carcasses rarely show aggression towards one another (or to other shark species feeding concurrently on the carcass) and often feed side by side (Dudley *et al*. 2000, Curtis *et al*. 2006, Fallows *et al*. 2013). Other shark species where a range of size classes share the same habitat exhibit resource partitioning to reduce competition, for example adult leopard sharks (*Triakis semifasciata*) feed inside nursery areas, but shift from a fish egg diet to crustacean prey as they age (Ebert and Ebert 2005). It is possible that the small size of juvenile Cape fur seals upon entry to open waters, relative to juvenile elephant seals (*Mirounga angustirostris*), allows white sharks of all sizes (except perhaps young-of-the-year) to catch and consume this particular marine mammal. In support of this suggestion is the result that over 88% of the all the attacks recorded at Seal Island were on juvenile seals de Vos (2010) and there are many records of small (2 m) juvenile white sharks performing breach attacks on these juveniles.

Potential impact of ecotourism on white shark presence and behaviour

Seal Island is a popular destination for white shark ecotourism and filming activities, which include chumming, shark-cage diving and towing of seal decoys (Laroche *et al*. 2008). While not a primary goal of this study, I did include the potential impact of chumming on shark presence at Seal Island by including it as a factor in the GLMM. Encouragingly, chumming did not contribute significantly to explaining the variation in white shark presence and so was excluded from the final model (Chapter 5). These results support similar findings by Laroche *et al*. (2008), which revealed that white sharks had very little contact time with the cage-diving boats at the Island and their visits to these boats declined with time over the winter season.

It is not possible, at this stage, to conclude that the full suite of ecotourism activities at Seal Island have no adverse impacts on natural predator/prey interactions. Of concern is the practice of permit (typically 3-5 boats) and non-permit holders (up to eight boats on a single day) approaching closer than the permitted 80 m to a predatory event that is in progress. Although difficult to prove, personal observations suggest that the close presence of a boat may impact directly on the outcome of a predation event, with sharks having been observed to abort an attack and seals using the boat as a refuge. Boats also follow seals commuting to and from the Island, in the hope that they will witness a predation event. This may impact on both the seals ability to detect a shark and evade it and the sharks' ability to detect a seal and capture/consume it. I thus urge further research into these and other potential impacts (e.g. towing decoys) on this ecologically and financially important predator-prey system, in addition to improved policing of existing regulations.

Extraordinary predation rates and possible impacts on seals

The calculated predation rate by white sharks on seals at Seal Island represents a conservative estimate, as many attacks occur at night and underwater, where they are not detected by boat-based observers. Currently predation rates at Seal Island are substantially higher (1.24 predatory events per hour) than observed at any other pinniped rookery worldwide (Pyle *et al*. 1996, Fallows *et al*. 2012, Dicken *et al*. 2013, Wcisel 2013). Reasons for this are not fully understood yet, but may be a result of a unique combination of seal abundance, shark abundance, bathymetry around the island and the position of the island within the Bay, which together combine to increase the catchability of seals.

Seal Island is the largest island breeding colony for Cape fur seals in South Africa (Kirkman *et al*. 2006) and its position, relative to the seals' offshore feeding areas, forces them to traverse a predictable route from the South side of the Island (de Vos 2010).

Tracking data show that white sharks patrol these areas significantly more than other sites around the island (Laroche *et al*. 2008, Chapter 4). Furthermore, Seal Island has one of the largest concentrations of white sharks in the world, with a recent population estimate of >700 sharks (Hewitt 2013). It's therefore possible that the high predation rate could be explained by the relative abundance of both seals and sharks. However, this does not explain the high predation rate relative to other sites along the South African coast that also have large concentrations of both seals and sharks e.g. Gansbaai (Towner *et al*. 2013). Unlike Gansbaai, there are no refugia around Seal Island, False Bay, in the form of kelp beds (*Ecklonia maxima*) or extensive reef systems which may offer protection to departing and returning seals (Wcisel 2013). Therefore, in addition to abundant seals, abundant sharks, coupled with predictable seal movement, the lack of refugia, combined with a steep drop-off means that seals are exposed to attack from below, resulting in an ideal scenario for the white sharks' ambush hunting strategy (Strong *et al*. 1996).

Although the predation rate is amongst the highest recorded by white sharks on seals anywhere in the world, it is nevertheless unlikely that white sharks are having a significant impact on seal density at Seal Island since the minimum estimated predation rate equates to only 0.78% (599.8 seals) of the Island's estimated population of 77 000 seals. Instead, it is more likely that the seal population is constrained by the limited haul-out space on the Island (Kirkman *et al*. 2006). An annual average of 2484 seal pups are found dead on beaches in False Bay during the seal breeding season (November – January), having been washed off the lower sections of the Island in the adverse weather conditions associated with the strong summer southeasterly winds (Kirkman *et al*. 2006). The seal population in False Bay is thus stable and appears to be limited by density dependent effects, rather than top-down control by white shark predation (Kirkman *et al*. 2006). This is important for white shark conservation in the area, as it suggests that one of their primary food sources is both predictable in space and sustainable in numbers. Although it is unlikely that white sharks are impacting seal density, it has been shown that they have had a marked sub-lethal effect on the spatio-temporal movement patterns (de Vos 2010) and behaviour (de Vos and O'Riain 2010, 2013) of seals commuting to and from Seal Island.

6.3. Effect of habitat type, size and sex on white shark presence within the Inshore region of False Bay

It has been well established that juvenile and sub-adult white sharks use coastal areas extensively (Dewar *et al*. 2004, Bonfil *et al*. 2005, Weng *et al*. 2007b, Johnson *et al*. 2009, Bruce and Bradford 2012a, Jewell *et al*. 2012). However, little is known about the fine-scale habitat use of coastal areas that are not associated with pinniped colonies. This is the first study to characterize white shark habitat use on the inshore region of False Bay, which includes a number of popular recreational beaches that have a history of white shark bite incidents.

Tagged white sharks were detected in all of the four major habitats (beach, rocky, mixed and harbour) that I categorised along the Inshore region of False Bay. However, the highest mean proportion of sharks, as estimated from the mean number of monthly visits and consecutive days present, was recorded for sandy beach habitat, despite my acoustic array including a higher proportion of both rocky and mixed habitat types. Importantly, and similar to the findings presented in Chapter 3, the use of the different Inshore habitats was significantly influenced by the sex, but not the size, of the shark. Males were only rarely detected in any Inshore regions of False Bay (visiting Muizenberg and Fish Hoek beaches once and twice respectively throughout the entire study period), while females were regular visitors to beach habitats and had higher levels of fidelity to Strandfontein beach in summer (27 consecutive days, Chapter 5) than Seal Island in winter (21 consecutive days, Chapter 4). The high white shark activity at the Strandfontein site is noteworthy, compared to adjacent and other beach sites in False Bay (Chapter 5). Furthermore, up to 12 tagged sharks were recorded on a single day at Strandfontein, while the most recorded at any other beach site was 6 and the highest at Seal Island was 13.

The marked preference of white sharks for beach habitat, specifically for the Strandfontein site, along the Inshore region in False Bay is similar to recent findings by Johnson *et al*. (2009), Jewell *et al*. (2012) and Bruce and Bradford (2012). Johnson *et al*. (2009) and Jewell *et al*. (2012) reported high fidelity at discrete beach sites near Mossel

Bay, South Africa. Jewell *et al*. (2012) provided fine-scale movement patterns in nearby Mossel Bay by actively tracking 13 white sharks over an accumulated 782 hours. Sharks showed a strong preference for a discrete area of just 1.05 km² corresponding to a beach with an adjacent deeper-water flat reef system. Johnson *et al.* (2009) suggest that this coastal beach habitat is used primarily for resting and socializing, in between foraging visits to a nearby seal colony. Johnson *et al*. (2009) base their conclusion on the slow rate of movement by sharks along the Inshore aggregation area. However, movement rates alone do not allow one to discriminate between different functional behaviours (e.g. foraging versus resting). Bruce and Bradford (2012a) demonstrated that although juvenile white sharks ranged along the east coast of Australia over a distance of more than 2000 km, they also showed high residency to two sites. Like at Mossel Bay, and similar to the northern shore of False Bay (this study), both the Australian sites, Port Stephens and Corner Inlet, are adjacent to long open beach systems. Bruce and Bradford (2012a) suggest that juvenile white sharks are using this inshore beach habitat primarily for foraging, a view supported by Werry *et al.* (2012), who quantified white shark catches in the gill nets used for bather safety along this coast. Bruce and Bradford (2012a) suggest that white sharks use an energy-conserving ‘sit and wait’ foraging strategy to encounter passing shoals of seasonally abundant fish e.g. Australian salmon (*Arripis trutta*), Australasian snapper (*Pagrus auratus*) and smooth hound sharks (*Mustelus antarcticus*) following predictable movement paths along the beachfront.

I cannot provide any direct behavioural evidence that might help elucidate whether sharks are using beach habitat primarily to rest or feed, but numerous personal observations and those relayed to me by local fisherman, do suggest that, similar to Bruce and Bradford (2012a), white sharks may be combining periods of limited movement with foraging. Their behaviour may thus be defined as both resting and foraging, which supports a sit and wait ambush approach to prey travelling along the coast. This suggestion is further corroborated by Shark Spotters positioned along a number of False Bay’s beaches, who typically record the behaviour of sharks in beach habitat as either commuting (moving through the beach area) or patrolling, possibly for food (swimming backwards and forwards in the beach area) (Kock *et al*. 2012). During inshore surveys by boat and aerial flights along False Bay's northern region, white sharks have also been observed to be almost stationary at the surface for extended periods of time (Kock, personal observation).

In summary, therefore, the available evidence suggests that female white sharks in this study are using the Inshore areas of False Bay to both forage and rest. The general absence of males from beaches in False Bay suggests that it is not likely to be a suitable habitat for socializing in this species. In support of this conclusion is that studies on other large, coastal marine predators such as coastal dolphins, propose that habitat selection patterns occur principally as a function of distribution, movement and abundance of prey species, and secondly to refuges from predators, and lastly to socializing and resting (Stevick *et al*. 2002, Ribeiro *et al*. 2007). It is clear that new methods, including cameras attached to animals (e.g. Crittercam, sensu Heithaus *et al*. 2002, acoustic 'business' card tags, sensu Holland *et al*. 2009 or acoustic pH transmitters, sensu Papastamatiou *et al*. 2007) will have to be used to ultimately derive behavioural activity profiles for white sharks in different habitat types.

In considering factors that may explain why white sharks appear to prefer beach habitat during the spring and summer months, one needs to consider possible reasons for why they avoid the other habitats in False Bay. Numerous studies have demonstrated a negative relationship between increasing habitat complexity and predator foraging success in aquatic environments (e.g. Gotceitas and Colgan 1989). Rocky and mixed areas with dense kelp beds provide refugia for smaller prey and may also obstruct the movement, and thus ability, of large sharks to successfully capture prey in these habitats. Due to their large size, white sharks are better suited to foraging in uncluttered habitats (Wcisel 2013), such as the open water around Seal Island, or the sandy substrates typical of coastal beaches such as Strandfontein. Terrestrial ambush predators, like lions, track the seasonal distribution and abundance of their preferred prey, but on a fine-scale select habitat where prey is easier to catch, rather than areas where prey densities are highest (Hopcraft *et al.* 2005). Future studies should attempt to gather more information on the key variables (e.g. prey availability, diet, anthropogenic disturbance and key oceanographic variables) predicted to influence white shark use of the Inshore region in False Bay during the spring and summer months.

There was a clear diel pattern of detection within the Inshore region of False Bay, with the average number of white shark visits highest during the daytime and lowest at sunrise. This is different to Seal Island, where the peak in activity was at sunrise (Chapter 4). The peak at the Island has been attributed to presenting ideal conditions for both encountering their target prey (naïve seal pups) and successfully catching them (low light levels) (Hammerschlag *et al*. 2006, Laroche *et al*. 2008, de Vos 2010). Johnson *et al*. (2009) also found a peak in white shark activity close to shore during the day and concluded that the sharks were resting, and left the Inshore region to feed on seals at dusk and dawn at a nearby seal colony. However, unlike with my study, they did not look at differences in seasonal habitat use (in addition to time of day), which varied markedly with broad scale habitat use in my study, and thus direct comparisons with False Bay are of limited value.

Diel movement patterns have generally found that other species of sharks increase their activity and home range at night, which has been attributed to increased foraging activity (for a review see Speed *et al*. 2010). Sixgill sharks (*Hexanchus griseus)* inhabit deeper waters during the day and shallower waters during the night, presumably to follow prey (Andrews *et al*. 2009). Similarly, prickly sharks (*Echinorhinus cookie*) were sedentary during the day and active at night with a clear crepuscular peak in activity, suspected to be related to hunting (Dawson and Starr 2009). However, as I am unable to confirm whether the Inshore region is primarily used by white sharks for hunting or resting, the primary reason for the peak presence during the day remains unresolved.

The influence of acoustic receiver receptive range

The highest numbers of detections was recorded on receivers with greater (>500 m) receptive range. To account for the data being biased by receptive range, I included it as an explanatory variable in the model (Chapter 5). The result was that the receptive range was a significant, and the model predicted that shark visits were more likely on receivers with greater receptive range than ones with smaller (≤500 m) range. However, even though this was the case, the explanatory variables of habitat type, time of day and the interaction between habitat type and sex were still significant explanatory variables.

Harbours as chumming areas

I predicted increased white shark activity adjacent to harbour sites, especially Kalk Bay, the largest of the fishing harbours, due to the large chum slicks produced by on-site fish processing. These activities are particularly prevalent during the spring and summer months, when seasonal fish, such as, snoek (*Thyrsites atun*), yellowtail (*Seriola lalandi*) and smaller sharks e.g. smooth hounds (*Mustelus mustelus*), are more abundant (Lamberth *et al*. 1995, Clarke *et al*. 1996a). Jewell *et al.* (2012) showed that two out of their thirteen tagged white sharks frequented the area immediately adjacent to the Mossel Bay fishing harbour, spending a few hours in the area patrolling close by, or even inside, the harbour or around a sardine purse-seine fishing vessel in the process of cleaning its hold. I also found that on occasion sharks frequented the area near the harbours, with up to seven tagged sharks detected at Kalk Bay harbour on a single day, and individual sharks detected for up to six consecutive days at the harbor receivers (Chapter 4). However, these were exceptions, with shark presence at harbours being lower on average than at either beach or mixed habitats. Together, these results suggest that fish processing at these sites is not associated with long-term, increased shark presence, but may provide temporary (hours or days) attraction to passing white sharks.

Spatial overlap in the Inshore region between humans and white sharks

The spring and summer spatial (Inshore) and temporal (day time) peaks in white shark presence on the Inshore have implications for both humans and sharks. The peak in female use of the Inshore region in the summer months corresponds with the annual peak in human recreational activities (van Herwerden *et al*. 1989, Engelbrecht 2013). Since 2000, 12 white shark bites, of which four (33.3%) were fatal, have been recorded on water users in False Bay, with Fish Hoek beach having the most bites (50%) and fatalities (75%). Although rare, attacks put tremendous pressure on management authorities like the Department of Environmental Affairs, Oceans and Coasts Branch and the City of Cape Town municipality, to implement lethal control programs e.g. drums lines or gill nets like those employed along the KwaZulu-Natal coast (Dudley and Cliff 1993). Cape Town municipality has, however, opted to support a non-lethal policy at this stage (Nel and Peschak 2006); but rather aims to reduce the spatial overlap between sharks and recreational beach users through both a Shark Spotter programme (Kock *et al*. 2012), and a non-lethal exclusion net at Fish Hoek beach (22 March 2013 Media Release, online at: http:/www.capetown.gov.za). However, as is evidenced in other countries (e.g. Australia and Reunion), frequent shark attacks may see politicians adopt lethal policy decisions which are not supported by the best available science, but rather are driven by perceived popular opinion (Neff 2012). It is for this reason that both of our local conflict mitigation measures are supported by strong environmental awareness and education campaigns.

Although the numbers of shark incidents are rare, it is interesting to note that there is no clear relationship between shark presence and the risk of a shark attack. Strandfontein has very little water user activity, which may explain the current low rate of incidence; however, Muizenberg had more than double the number of visits by white sharks, compared to Fish Hoek, and has had only a single incident in the last decade, compared to Fish Hoek, which had two fatalities and one major incident. I propose that it may be the marked differences in the bathymetry of the two beaches, with Fish Hoek having a steeper drop-off than Muizenberg, which influences the distance of the backline of waves from the shore. Data from the Shark Spotter programme reveals that most (> 70%) of white shark sightings are just behind the surf zone, beyond the breaking waves (Kock *et al*. 2012). Thus, a steeper beach profile brings white sharks closer to recreational users, who typically swim up to, but seldom beyond, the backline. By contrast, Muizenberg has a very gradual slope and the backline is thus very far from shore, greatly reducing the number of bathers in this zone and hence reducing the physical proximity of white sharks and people.

Threats to white sharks in False Bay

The high use of the Inshore region during spring and summer also has implications for the sharks. This is the region that is most heavily impacted by fishing, pollution, and disturbance from coastal development. While the Cape fur seal population in False Bay seems to be stable (Kirkman *et al*. 2006), the same cannot be said for coastal fish populations (Penney 1991, Griffiths 2000) and other shark populations in False Bay e.g. soupfin sharks (*Galeorhinus galeus*) (Best *et al*. 2013). It is possible that loss or changes in distribution of prey could impact the abundance, and spatial and temporal movements of white sharks in False Bay, in addition to inadvertently driving sharks to seek alternative prey sources.

As long-lived, apex predators, white sharks are particularly susceptible to elemental and organic contaminant uptake and accumulation via the food web (Gelsleichter and Walker 2010, Mull *et al*. 2012, 2013). High levels of contaminants have been shown to have deleterious effects on aquatic vertebrates, from impairment of reproduction and growth to possible immune suppression (Cross 1988, Hose *et al*. 1989, Gelsleichter *et al*. 2006). Currently, the extent of contaminant exposure in white sharks in South African waters and its potential physiological effects are not well understood. A recent study from California, USA showed that young of the year and juvenile white sharks had high levels of contaminants, but it is not yet clear how this may impact survival or reproductive fitness (Mull *et al.* 2013). Given that white sharks, especially females, spend so much time in polluted coastal waters in False Bay the evidence for bioaccumulation of toxins and the potential impacts on the sharks should be a research priority, with white sharks providing a potential sentinel role for pollution of coastal waters by urban run-off of known contaminants.

Since 2000, four white shark deaths have been reported in False Bay. In most cases, the cause of death could not be verified, although it is suspected they were as a result of either beach-seine bycatch or shore-angling. Since 2005, there has been a significant increase in shark catches in the recreational fishery in False Bay (Best *et al*. 2013), possibly as a consequence of a point system implemented by the Western Province Shore Angling Association that incentivizes anglers to target the largest fish species available on the Inshore (Dicken *et al*. 2006). Sport fishermen thus target large sharks occurring along False Bay's inshore areas e.g. bronze whalers (*Carcharhinus brachyurus*) and ragged tooth sharks (*Carcharhinus taurus*). However, due to the high spatial overlap between these species and white sharks, the latter are regularly caught as bycatch. A number of reports and photographs have appeared in fishing forums and on social media pages (Sealine website, online at http://www.sealine.co.za) over the last seven years, depicting anglers posing with white sharks they had caught and landed (Fig. 6.1). While most fishermen state that they would release a white shark as by-catch, post-release mortality is unknown. Given the extended fight times often reported, the need to drag the shark out of the water and the use of gaffs to secure it, it is highly likely that the impacts of shoreline fishing on white sharks is high. In a landmark case in February 2013, a fisherman was successfully prosecuted in South Africa for catching a white shark in Mossel Bay, dragging it out of the water and posing for a photograph (Cape Times, 5 February 2013). This will hopefully serve as a deterrent to others deliberately targeting white sharks for sport.

Figure 6.1. Juvenile white sharks caught by sport fishermen in False Bay. Images like these get posted on social media websites like Facebook and in fishing forums.

6.4. Management considerations for False Bay

The seasonal aggregation of white sharks at coastal sites and pinniped colonies, coupled with occasional large-scale coastal and oceanic migrations, demands coordinated regional and international management plans for effective conservation (Bonfil *et al*. 2005, Dulvy *et al*. 2008). White sharks are currently afforded full protection in South African waters (Fergusson *et al*. 2009). However, an exemption is in place along the KwaZulu-Natal coastline which allows for the use of shark nets and drumlines to capture and kill large sharks, including protected species, as part of the long-standing bather protection programme (Dudley and Simpfendorfer 2006). Additionally, international agreements are in place, which restrict trade i.e. they are listed on Appendix II of the Convention for International Trade in Endangered Species and under the Convention on Migratory Species (Fergusson *et al*. 2009). There is, however, an urgent need for neighbouring countries, such as Mozambique and Madagascar, to be included in these management plans to ensure regional coordination and effectiveness of conservation efforts.

Establishing the connectivity between coastal aggregation sites and migration pathways along the Southern African coast is an essential first step in improving existing regional and international conservation plans. This research is well under way, with long-term monitoring of white shark presence and behaviour currently in progress at four well established aggregation sites along the southern African coastline - False Bay (Kock *et al*. 2013), Gansbaai (Towner *et al*. 2013), Mossel Bay (Jewell *et al*. 2012) and Algoa Bay (Dicken and Booth 2013). In addition, 2012 saw the initiation of a large, internationally coordinated research program (Ocearch) that aims to provide data on the movement patterns, isotope ecology and reproduction of white sharks off the coastline of Southern Africa. Together, these projects, in addition to the long-term monitoring of culled white sharks (numbers, sex, size and gut contents of killed white sharks) in KwaZulu-Natal (Sharks Board), provide management and conservation authorities with a wealth of information to make informed policy decisions for the sustainable management of the white shark population in southern African waters.

In this study I have confirmed False Bay as a globally-important aggregation site for white sharks, with juvenile and sub-adult white sharks of both sexes showing high levels of fidelity to the Bay. However, sharks that spend considerable periods in coastal habitats are particularly vulnerable to anthropogenic impacts, due to their proximity to human populations, where fishing pressure and habitat degradation is typically high (Holland *et al*. 1999, Heupel *et al*. 2009, Speed *et al*. 2010, Bruce and Bradford 2012a). In addition, conflict with humans as a result of occasional attacks arguably poses one of the greatest threats to white shark populations around the world. Lethal control programs, like gill nets and drumlines, specifically target large sharks (Cliff and Dudley 1992). In South

Africa, lethal control for bather safety is used along the KwaZulu-Natal coastline and currently the average number of white sharks caught in the shark nets is 25 per year, with eight more caught on the drumlines (Cliff and Dudley 2011). The nets and drumlines also capture and impact a range of non-target species, such as harmless (to humans) shark species, turtles, whales and dolphins (Cliff and Dudley 2011). Although the likelihood of being attacked by a shark is extremely low, the white shark’s seasonal distribution along popular recreational coastlines, natural opportunistic predatory tactics and large size, almost guarantees some level of human-shark conflict (Curtis *et al*. 2012, Kock *et al*. 2013). In False Bay, there has been an average of one shark attack per year since 1960, with six fatalities in the last decade (Cliff 2006, Kock *et al*. 2012, Weltz *et al*. 2013).

Shark attacks can have negative impacts on the recreational pursuits and economies of local communities, which can in turn impact management policies through public lobbying – often through an emotive media platform (Muter *et al*. 2012). There are a number of examples which highlight these negative impacts on local communities in False Bay. The Fish Hoek Lifesaving Club’s Mile Surf-Swim challenge started in 1962 and was the biggest and longest-standing annual ocean open-water swimming race in the country. It ran for 44 years until 2006, when it was cancelled as a direct result of a high profile lethal shark attack and frequent non-lethal encounters at Fish Hoek and surrounding beaches (M. Schilperoot, pers. comm.). Furthermore, the Fish Hoek Surf Lifesaving club has reported declines in membership of particularly young life-savers known as “nippers”. In 2011 the Fish Hoek Life Saving Club won the right to host the annual life-saving championships, but due to the shark bite incidents, clubs from all around the country refused to attend if the event was held in Fish Hoek. The championships were subsequently moved to the much colder Atlantic waters of Camps Bay beach. In 1999/2000 surf skiing and paddling became a popular form of recreation in Cape Town and one would often see a long train of paddlers on the water between Muizenberg and Fish Hoek. Local paddling schools reported a decline in business following a spate of non-lethal, but high profile attacks on these water craft (D. Mocke, pers. comm.).

Recent research documenting recreational (i.e. bathers, surfers and paddlers) water use patterns at two of Cape Town's most popular beaches (Fish Hoek and Muizenberg) reveals that shark sightings and shark bites have a significant impact on water users (Engelbrecht 2013). Following a fatal shark incident in False Bay, bather and surfer numbers declined significantly for up to two months after the incident at both beaches. Surf school owners have felt these effects on their business income and have recently taken out liability insurance to safe-guard their businesses from losses caused as a result of shark attacks (R. Davis, pers. comm.). Together these clear impacts associated with shark presence and occasional shark incidents with humans requires careful management, with frequent stakeholder participation in conflict management options.

Figure 6.2. A Shark Spotter overlooks Fish Hoek beach in False Bay from an adjacent mountain vantage point, ready to close the beach if a white shark enters the bather area.

A major problem faced in the field of conservation and management of predators that are in conflict with humans is the often strongly-divided public opinion (Knight 2000). At the one extreme predators, such as, white sharks may be regarded with fear and hatred by those who see them as wilful man-eaters, while at the other extreme they may be viewed with admiration, reverence and sympathy by those who consider their current plight and conflict to be wholly human-induced (Muter *et al*. 2012). Quite where the majority perception lies in the various global conflict hotspots remains unclear, but what is clear is that lethal shark attacks are invariably followed by renewed discussion on the need to consider lethal alternatives to existing non-lethal bather-protection methods (Kock *et al*. 2012). It is for this reason that existing research on conflict species, such as white sharks, must be widely and frequently disseminated to the public. Such information may help to educate the public about the essential ecological role that white sharks fulfil in marine ecosystems, in addition to countering the many sources of inaccurate and sensationalist propaganda that white sharks and other large predators (e.g. lion, wolves and bears) attract. Key to such educational campaigns is the constant reminder of the exceptionally low probability of an encounter with a white shark, despite the frequent close proximity of white sharks to a diverse array of recreational pursuits by large number of people in the Inshore region.

Shark eco-tourism and wildlife documentaries are believed to be playing an important role in improved public education and awareness of white sharks, while simultaneously generating non-consumptive revenue. In Gansbaai, South Africa the white shark cage diving industry (WSCD) generated R30 million over a 12-month period (Hara *et al*. 2003) and further educated thousands of tourists about the conservation challenges that white sharks face, both locally and globally. These revenue streams need to be translated into more effective monitoring and enforcement of existing guideline for tourism, research and management of white sharks at coastal aggregation sites. Ultimately the inclusion of all coastal aggregation sites within marine protected areas (MPA's) may be the single most important management intervention for ensuring the sustainable conservation and management of white shark populations with the associated eco-tourism rewards.

Figure 6.3. People from all over the world come to see white sharks breach on seals at Seal Island, False Bay. Photo credit Morne Hardenberg

The inclusion of Seal Island and Strandfontein within the False Bay MPA

False Bay currently has a network of five MPA's (Fig. 6.3). However, with the exception of the small MPA located on the northeastern corner of False Bay (Helderberg MPA), no beach habitats, fall within the existing MPA network, nor is Seal Island included in the MPA system. This study has confirmed that white sharks have very high levels of fidelity to both Seal Island and Strandfontein beach and I would thus argue strongly for their immediate inclusion within False Bay's limited MPA network. Such a move would not only increase monitoring and control of activities which may directly threaten white sharks e.g. trek net fisheries, line-fisheries and shore angling, but also the ongoing loss of prey species that appears to drive such high levels of fidelity to these sites. Furthermore, it has been demonstrated that marine reserves can benefit marine megafauna, and that megafauna can help establish target areas and boundaries for ecosystem reserves (Hooker and Gerber 2004). Resistance to extending the MPA to include these sites may come from both commercial and recreational users of these sections of False Bay and hence this proposal will have to be subject to a detailed risk assessment and extensive consultation with all of the relevant stakeholders.

Until these sites are afforded improved conservation status, it is essential to address known threats to white sharks along the Inshore. Perhaps highest on the list of known threats is the capture of white sharks by shore-based fisherman, either deliberately or as by-catch when fishing for other shark species. The banning of capture gear e.g. large hooks, large baits and steel traces in areas with high while shark fidelity (e.g. Strandfontein) may reduce these risks, although the enforcement of such bans remains problematic.

Other fisheries in False Bay that do accidentally catch white sharks are the beach seine nets (trek nets), with on average one white shark caught per year, which is usually released (Lamberth 2006). In 2012, a 4.3 m female white shark was accidentally caught and died by becoming entangled in a trap used for an experimental whelk fishery and positioned off Fish Hoek beach. Simple adjustments to these nets could have prevented them from entangling large sharks, or other large marine mammals. It is, therefore, my recommendation that before new or experimental fishery gear is deployed, it should be inspected by the relevant authorities to ensure minimal entanglement risk to vulnerable marine life.

Figure 6.4. Current marine and other nature reserves in the Cape Town and False Bay region.

Future threats to white sharks in False Bay include the potential farming of white shark prey species, such as yellowtail (*Seriola lalandi*) in the area (DAFF 2011). These farms may attract sharks (e.g. Papastamatiou *et al*. 2010) and pose a threat to human safety, or pose a direct threat to sharks due to entanglement, or an indirect threat due to conflict with farmers. Other threats include further coastal development and the many associated negative activities that are associated with a burgeoning human population living in a coastal city (e.g. pollution).

Figure 6.5. A 4.3 m female white shark caught in an experimental fishery targeting whelks on the 11 March 2012 in Fish Hoek, False Bay. Photo credit Adrian Hewitt

6.5. Conclusion

White sharks are high-order trophic level predators and predate on a wide range of prey species (Cortes 1999, Hussey *et al*. 2012). It is therefore hypothesized that they play important roles in the structuring of biological communities, by influencing community composition and the relative abundance of prey species (Cortes 1999, Stevens *et al*. 2000, Myers and Worm 2003, Speed *et al*. 2010, Ruppert *et al*. 2013). A reduction in white shark density is therefore expected to lead to the release of mesopredator populations, an increase in competing taxa, and ultimately, a reduction or imbalance in species under the influence of predation, as has been demonstrated following the removal of other top predators (Fogarty and Murawski 1998, Pace *et al*. 1999, Speed *et al*. 2010, Ruppert *et al*. 2013). The results from this thesis are already being used to devise more site-specific and effective management for white sharks of False Bay. In addition, regular public presentations of the findings presented are helping to educate the public, particularly those most directly affected by white shark presence and occasional bite incidents. It is hoped that the combination of existing conflict mitigation methods (i.e. shark spotters and barrier nets) at popular beaches, in addition to ongoing public education, will translate into a sustainable and better tolerated white shark population off the coastline of southern Africa. Ultimately an internationally coordinated conservation effort should be developed for this global ranging species, by taking a strategic, pro-active, and comprehensive approach to white shark research and management.

REFERENCES

Abrahams, M.V. (1995). The interaction between antipredator behaviour and antipredator morphology: experiments with fathead minnows and brook sticklebacks. *Canadian Journal of Zoology,* 73:2209-2215.

Adams, D.H., Mitchell, M.E. & Parsons, G.R. (1994). Seasonal occurrence of the white shark, *Carcharodon carcharias,* in waters off the Florida west coast, with notes on its life history. *Marine Fisheries Review,* 56:24.

Ainley, D., Henderson, R., Huber, H., Boekelheide, R., Allen, S. & McEltroy, T. (1985). Dynamic of white shark/pinniped interactions in the Gulf of the Farallones. *Memoirs of the Southern California Academy of Sciences*, 9:109-122.

Anderson, S.D. & Goldman, K. (1996). Photographic evidence of white shark movements in Californian waters. *California Fish and Game,* 82:182-186.

Anderson, S.D. & Pyle, P. (2003). A temporal, sex-specific occurrence pattern among white sharks (*Carcharodon carcharias*) at the South Farallon Islands, California. *California Fish and Game*, 89:96-101.

Andrews, K.S., Williams, G.D. & Levin, P.S. (2010). Seasonal and ontogenetic changes in movement patterns of sixgill sharks. *PLoS ONE,* 5:e12549.

Applegate, S.P. & Espinosa-Arrubarrena, L. (1996). The fossil history of *Charcharodon* and its possible ancestor, *Cretolamna*: A study in tooth identification. Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.19-36.

Atkins, G.R. (1970). Winds and current patterns in False Bay. *Transactions of the Royal Society of South Africa,* 39(2):139-148.

Ballance, L.T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science,* 8:262-274.

Barnett, A. & Semmens, J.M. (2012). Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. *Oikos,* 121(6):882-890. doi: 10.1111/j.1600-0706.2011,2000.x.

Barnett, A., Abrantes, K.G., Seymour, J. & Fitzpatrick, R. (2012). Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLoS ONE,* 7(5):e36574. doi:10.1371/journal.pone.0036574.

Barnett, A., Abrantes, K.G., Stevens, J.D. & Semmens, J.M. (2011). Site fidelity and sex-specific migrations in a mobile apex predator: implications for conservation and ecosystem dynamics. *Animal Behaviour.* doi:10.1016/j.anbehav.2011.02.011.

Barnett, A., Stevens, J.D., Frusher, S.D. & Semmens, J.M. (2010). Seasonal occurrence and population structure of the broadnose sevengill shark *Notorynchus cepedianus* in coastal habitats of south-east Tasmania. *Journal of Fish Biology,* 77:1688-1701.

Bascompte, J., Melian, C.J. & Sala, E. (2005). Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102:5443-5447.

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. (1975). Sharks of the east coast of southern Africa. Part V. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. *Oceanographic Research Institute, Durban, Investigatory Reports*, 39:22-26.

Baum, J.K. & Myers, R.A. (2004). Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters,* 7:135-145.

Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Animal Ecology,* 78(4):699-714.

Baum, J.K., Myers, R.A., Keller, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, 299:389-391.

Bennett, B.A. (1993). Aspects of the biology and life history of white steenbras *Lithognathus lithognathus* in southern Africa. *South African Journal of Marine Science*, 13:83-96.

Benoit-Bird, K.J. & Au, W.W.L. (2003). Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology*, 53(6):364-373.

Bertram, B.C.R. (1978). Living in groups: predators and prey. In: Krebs, J.R. & Davies, N.B. (Eds). *Behavioural ecology: an evolutionary approach* (4th ed). Oxford: Blackwell. p.64-96.

Best, L.N. (2013). The historical exploitation of chondrichthyans in False Bay, South Africa and assessment of their conservation status. MSc Thesis. Zoology Department, University of Cape Town.

Bethea, D., Buckel, J. & Carlson, J. (2004). Foraging ecology of the early life stages of four sympatric shark species. *Marine Ecology Progress Series*, 268:245-264.

Bizzarro, J.J., Robinson, H.J., Rinewalt, C.S. & Ebert, D.A. (2007). Comparative feeding ecology of four sympatric skate species off central California, USA. *Environmental Biology of Fishes*, 80:197-220.

Block, B.A. & Carey, F.G. (1985).Warm brain and eye temperatures in sharks. *Journal of Comparative Physiology B,* 156:229-236.

Bonfil, R., Francis, M., Duffy, C., Manning, M. & O'Brien, S. (2010). Large-scale tropical movements and diving behaviour of white sharks, *Carcharodon carcharias*, tagged off New Zealand. *Aquatic Biology,* 8:115-123.

Bonfil, R., Meyer, M.A., Scholl, M.C., Johnson, R.L., O'Brian, S., Oosthuizen, W.H., Swanson, S., Kotze, D. & Patterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science,* 301:100-103.

Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, 68:371-394.

Boustany, A., Davis, S., Pyle, P., Anderson, S., Le Boeuf, B.J., & Block, B.A. (2002). Expanded niche of white sharks. *Nature*, 415:35-36.

Bozodogan, H. (1987). Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika* 52(3):345-370.

Branstetter, S. (1990). Early life-history implications of selected Carcharhinoid and Lamnoid sharks of the Northwest Atlantic. In: Pratt Jr, H.L., Gruber, S.H. & Taniuchi, T. (Eds). Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries, U.S. Dept. of Commerce , NOAA Technical Report, NMFS 90, 17-28.

Brown, J.S., Kotler, B.P. & Bouskila, A. (2001). The ecology of fear: Foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici*, 38:71-87.

Bruce, B.D. (1992). Preliminary observations on the biology of the White Shark, *Carcharodon carcharias*, in South Australian waters. *Australian Journal of Marine and Freshwater Research*, 43:1-11.

Bruce, B.D. (2008). The biology and ecology of the white shark (*Carcharodon carcharias*). In: Camhi, M.D. & Pikitch, E.K. & Babcock, E.A. (Eds). *Sharks of the open ocean: biology, fisheries and conservation*. Oxford: Blackwell Scientific. p.69-81.

Bruce, B.D. & Bradford, R.W. (2012a). Habitat use and spatial dynamics of juvenile white sharks , *Carcharodon carcharias*, in Eastern Australia. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.225-254.

Bruce, B.D. & Bradford, R.W. (2012b). The effects of shark cage-diving operations on the behaviour and movements of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. *Marine Biology*, 160(4):889-907

Bruce, B.D, Stevens, J.D. & Bradford, R.W. (2005). Site fidelity, residence times and home range patterns of white sharks around pinniped colonies. Report to the Australian Government Department of the Environment and Heritage. CSIRO Marine and Atmospheric Research, Hobart.

Bruce, B.D., Stevens, J.D. & Malcolm, H. (2006). Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Marine Biology*, 150(2):161-172. doi:10.1007/s00227-006-0325-1.

Brunnschweiler, J.M. & Baensch, H. (2011). Seasonal and long-term changes in relative abundance of bull sharks from a tourist shark feeding site in Fiji. *PLoS ONE* 6(1): e16597. doi:10.1371/journal.pone.0016597

Burgess, G.H., Buch, R.H., Carvalho, F., Garner, B.A. & Walker, C.J. (2010). Factors contributing to shark attacks on humans: A Volusia County, Florida, case study. In: Carrier, J.C., Musick, J.A. & Heithaus, M.R. (Eds). *Sharks and their relatives:*

II. Biodiversity, adaptive physiology, and conservation. Boca Raton: CRC Press. p.541-565.

Burgess, G.H. & Callahan, M. (1996). Worldwide patterns of white shark attacks on humans. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.457-469.

Cailliet, G., Natanson, L., Weldon, B. & Ebert, D. (1985). Preliminary studies on the age and growth of the white shark *Carcharodon carcharias*, using vertebral bands. *Memoirs of the Southern California Academy of Sciences*, 9:49-60.

Camhi, M.D., Fordham, S.V. & Fowler, S.L. (2008). Domestic and international management for pelagic sharks. In: Camhi, M.D. & Pikitch, E.K. & Babcock, E.A. (Eds). *Sharks of the open ocean: biology, fisheries and conservation*. Oxford: Blackwell Scientific. p.418-444.

Carey, F.G., Kanwisher, J.W., Brazier, O., Gabrielson, G., Casey, J.G. & Pratt, H.L. (1982). Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia*, 1982(2): 54-260.

Carlson, J.K., Heupel, M.R., Bethea, D.M. & Hollensead, L.D. (2008). Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). *Estuaries and Coasts*, 31(5):931-940.

Caro, T. & Sherman, P.W. (2011). Endangered species and a threatened discipline: behavioural ecology. *Trends in Ecology & Evolution*, 26:111-118.

Casey, J. & Pratt, H. (1985). Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Southern California Academy of Science Memoirs*, 9:2-14.

Castro, J.I. (2012). A summary of observations on the maximum size attained by the white shark, *Carcharodon carcharias*. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.85-90.

Chapple, T.K., Jorgenson, S.J., Anderson, S.D., Kanive, P.E., Klimley, A.P., Botsford, L.W. & Block, B.A. (2011). A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. *Biological Letters*, 7:581-583.

Clark, B.M, Bennett, B.A. & Lamberth, S.J. (1996a). Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series*, 131:35-47. doi:10.3354/meps131035.

Clark, B.M., Bennett, B.A. & Lamberth, S.J. (1996b). Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. *Marine Ecology Progress Series*, 131:17-34. doi:10.3354/meps131017.

Cliff, G. (2006). A review of shark attacks in False Bay and the Cape Peninsula between 1960 and 2005. In: Nel, D.C. & Peschak, T.P. (Eds). 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 Annexure 1: 20-31.

Cliff, G., Compagno, L.J.V., Smale, M.J., van der Elst, R.P. & Wintner, S.P. (2000). First records of white sharks, *Carcharodon carcharias* from Mauritius, Zanzibar, Madagascar and Kenya. *South African Journal of Science*, 96:365-367.

Cliff, G. & Dudley, S.F.J. (1992). Protection against shark attack in South Africa, 1952-1990. *Australian Journal of Marine and Freshwater Research,* 43:263-272.

Cliff, G. & Dudley, S.F.J. (2011). Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. *Marine and Freshwater Research,* 62:700–709. doi: 10.1111/j.1365-3032.1995.tb00818.x.

Cliff, G., Dudley, S.F.J. & Davis, B. (1989). Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science,* 8: 131-144.

Cliff, G., van der Elst, R.P., Govender, A., Witthuhn, T.K. & Bullen, E.M. (1996). First estimates of mortality and population size of white sharks on the South African coast. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.393-400.

Compagno, L.J.V. (1984). Sharks of the world, Part 1: Hexanchiformes to Lamniformes. FAO Fisheries Synopsis 125(4).

Compagno, L.J.V. (1991). Government protection for the great white shark (*Carcharodon carcharias*) in South Africa. *South African Journal of Marine Science*, 87:284-285.

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.

Compagno, L.J.V., Dando, M. & Fowler, S. (2005). *Sharks of the world*. Princeton: Princeton University Press.

Compagno, L.J.V., Marks, M. & Fergusson, I. (1997). Threatened fishes of the world, *Carcharodon carcharias*. *Environmental Biology of Fishes*, 50:61-62.

Cortes, E. (1999). Standardized diet compositions and trophic levels of sharks. ICES *Journal of Marine Science,* 56:707-717.

Creel, S., Christianson, D., Lily, S. & Winnie, J.A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science*, 315:960.

Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis*, 150:3-17.

Cross, J.N. (1998). Evidence for impaired reproduction in white croaker (*Genyonemus lineatus*) from contaminated areas off Southern California. *Marine Environmental Research,* 24(1–4):185–188.

Curtis, T.H., Kelly, J.T., Menard, K.L., Laroche, R.K., Jones, R.E., *et al*. (2006). Observations on the behavior of white sharks scavenging from a whale carcass at Point Reyes, California. *California Fish & Game*, 92:113–124.

Curtis, T.H., Bruce, B.D., Cliff, G., Dudley, S.F.J., Peter, A., Kock, A.A., Lea, R.N., Lowe, C.G., McCosker, J.E., Skomal, G.B., Werry, J.M. & West, J.G. (2012). Responding to the risk of white shark attack updated statistics, prevention, control methods and recommendations. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.477-510.

Dawson, C.L. & Starr, R.M. (2009). Movements of sub-adult prickly sharks *Echinorhinus cookei* in the Monterey Canyon. *Marine Ecology Progress Series,* 386:253-262.

Department of Agriculture, Forestry and Fisheries (2011). A profile of the South African aquaculture market value chain.

de la Parra Venegas, R., Hueter, R., González Cano, J., Tyminski, J., Gregorio Remolina, J., Maslanka, M., Ormos, A., Weigt, L., Carlson, B. & Dove, A. (2011). An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean Sea. *PLoS ONE,* 6:e18994.

de Vos, A. (2010). Anti-predator behaviour by Cape fur seals *Arctocephalus pusillus pusillus* in relation to predation by white sharks *Carcharodon carcharias* around Seal Island, False Bay. PhD Thesis. Zoology Department, University of Cape Town.

de Vos, A. & O'Riain, M.J. (2010). Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. *Biology Letters*, 6:48-50.

de Vos, A. & O'Riain, M.J. (2013). Movement in a selfish seal herd: do seals follow simple or complex movement rules? *Behavioral Ecology*, 24(1):190-197.

Dewar, H., Domeier, M.L. & Nasby-Lucas, N. (2004). Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. *Environmental Biology of Fishes*. 70(2):133-143.

Dicken, M.L. (2008). First observations of young of the year and juvenile great white sharks (*Carcharodon carcharias*) scavenging from a whale carcass. *Marine and Freshwater Research*, 59:596-602.

Dicken, M. L. & Booth, A. J. (2013). Surveys of white sharks (Carcharodon carcharias) off bathing beaches in Algoa Bay, South Africa. *Marine and Freshwater Research*, 64:530–539.

Dicken, M.L., Smale, M.J. & Booth, A.J. (2006). Spatial and seasonal distribution patterns of the ragged-tooth shark *Carcharias taurus* along the coast of South Africa. *African Journal of Marine Science*, 28:603-616.

Dicken, M.L., Bradshaw, M. & Smale, M.J. (2013). White shark (*Carcharodon carcharias*)-inflicted bite wounds observed on Cape fur seals (*Arctocephalus pusillus pusillus*) at Black Rocks, Algoa Bay, South Africa. *African Zoology,* 48 (2): 418-426.

Domeier, M.L. (2012). A new life-history hypothesis for white sharks, *Carcharodon carcharias*, in the Northeast Pacific. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.199-223.

Domeier, M.L. & Nasby-Lucas, N. (2007). Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine Biology*, 150:977-984.

Domeier, M.L. & Nasby-Lucas, N. (2008). Migration patterns of white sharks (*Carcharodon carcharias*) tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series*, 370:221-237.

Domeier, M.L. & Nasby-Lucas, N. (2012). Sex-specific migration patterns and sexual segregation of adult white sharks, *Carcharodon carcharias*, in the northeastern Pacific. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.133-146.

Dotchim, M. (2006). Recreational trends and safety in waters of the Cape as it relates to risk of interactions with sharks. In: Nel, D.C. & Peschak, T.P. (Eds). 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 Annexure 1. p.130–137.

Dudley, S.F.J. (2012). A review of research on the white shark, *Carcharodon carcharias*, in southern Africa. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.511-533.

Dudley, S.F.J., Anderson-Reade, M.D., Thompson, G.S. & McMullen, P.B. (2000). Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks. *Fisheries Bulletin*, 98:646-649.

Dudley, S.F.J. & Cliff, G. (1993). Some effects of shark nets in the Natal nearshore environment. *Environmental Biology of Fishes*, 36:243–255.

Dudley, S.F.J. & Simpfendorfer, C.A. (2006). Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978-2003. *Marine and Freshwater Research*, 57(2),225-240. doi:10.1071/MF05156.

Duffy, C.A.J., Francis, M.P., Manning, M.J. & Bonfil, R. (2012). Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.147-158.

Dufois, F. & Rouault, M. (2012). Sea surface temperature in False Bay (South Africa): towards a better understanding of its seasonal and inter-annual variability. *Continental Shelf Research*, 43:24-35.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J., Musick, J.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 Conservation: Marine and Freshwater Ecosystems*, 18(5):459-482. doi: 10.1002/aqc.975.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davisdson, L.N.K., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J.V., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S. & White, W.T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3:e00590.

Ebert, D.A. & Ebert, T.B. (2005). Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. *Marine and Freshwater Research*, 56:1089.

Elwen, S.H., Findlay, K.P., Kiszkacd, J. & Weir, C.R. (2011). Cetacean research in the southern African subregion: a review of previous studies and current knowledge. *African Journal of Marine Science,* 33(3):469-493.

Engelbrecht, T. (2013). The impact of white shark (*Carcharodon carcharias*) sightings and attacks on recreational water use patterns in False Bay. Honours Thesis. University of Cape Town, Biological Sciences Department.

Estes, J.A. & Duggins, D.O. (1995). Sea otters and kelp forests in Alaska – generality and variation in a community ecological paradigm. *Ecological Monographs,* 65:75-100.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011). Trophic downgrading of planet earth. *Science,* 333:301-306.

Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science,* 282:473-476.

Fallows, C., Martin, R.A. & Hammerschlag, N. (2012). Comparisons between white shark-pinniped interactions at Seal Island (South Africa) with other sites in California. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.1059-117.

Fallows, C., Gallagher, A.J., Hammerschlag, N. (2013). White sharks (*Carcharodon carcharias*) Scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PLoS ONE* 8(4): e60797. doi:10.1371/journal.pone. 0060797

Fergusson, I., Compagno, L.J.V. & Marks, M. (2009). *Carcharodon carcharias*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. www.iucnredlist.org. Downloaded on 23 November 2013.

Ferreira, C. & Ferreira, T. (1996). Population dynamics of white sharks in South Africa. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.381-391.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13,1055-1071.

Field, I.C., Meekan, M.G., Speed, C.W., White, W., Bradshaw, C.J.A. (2011). Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. *Coral Reefs.* 30:61-71.

Fogarty, M.J. & Murawski, S.A. (1998). Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications*, 8:S6-S22.

Food and Agriculture Organisation of the United Nations. (1999). International plan of action for the conservation and management of sharks. In: FAO Fisheries and Aquaculture Department [online]. Rome. [Cited 8 November 2011]. http://www.fao.org/fishery/ipoa-sharks/en, IPAO-Sharks, FAO 1999.

Food and Agriculture Organisation of the United Nations. (2004). Report of the FAO expert advisory panel for the assessment of proposals to amend appendices I and II of CITES concerning commercially-exploited aquatic species. FAO Fisheries Reports, 748:1-51.

Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A. & Musick, J.A. (comp. and ed.). (2005). Sharks, rays and chimaeras: the status of the Chondrichthyan fishes. Status Survey. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Francis, M.P. (1996). Observations on a pregnant White Shark with a review of reproductive biology. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.157-172.

Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burnham, K.P. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*. 70:539-590.

García, V.B., Lucifora, L.O. & Myers, R.A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B*, 275:83-9.

Gelsleichter, J. & Walker, C.J. (2010). Pollutant exposure and responses in sharks and their relatives. In: Carrier, J.C., Musick, J,A, & Heithaus, M.R. (Eds). *Sharks and their relatives II*. Boca Raton, FL: CRC Press. p.491-540.

Gelsleichter, J., Walsh, C.J., Szabo, N.J. & Rasmussen, L.E.L. (2006). Organochlorine concentrations, reproductive physiology, and immune function in unique populations of freshwater Atlantic stingrays (*Dasyatis sabina*) from Florida's St. Johns River. *Chemosphere*, 63(9):1506-1522.

Goetz, S., Steinberg, D., Dubayah, R. & Blair, B. (2007). Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sensing of Environment*, 108:254-263.

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.

Goldman, K.J., Anderson, S.D., McCosker,J.E. & Klimley, A.P. (1996). Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.111-120.

Gotceitas, V. & Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia*, 80:158-166.

Griffiths, M.H. (2000). Long-term trends in catch and effort of commercial line-fish off South Africa's Cape Province: snapshots of the 20th century. *South African Journal of Marine Science*, 22:81-110.

Griffiths, C.L., Robinson, T.B., Lange, L. & Mead, A. (2010). Marine biodiversity in South Africa: an evaluation of current states of knowledge. *PLoS ONE*, 5(8):e12008. doi:10.1371/journal.pone.0012008.

Grundlingh, M. & Largier, J. (1991). Physical oceanography of False Bay: a review. *Transactions of the Royal Society of South Africa*, 47(4-5):387-400.

Gubili, C., Duffy, C.A.J., Cliff, G., Wintner, S.P., Shivji, M., Chapman, D., Bruce, B.D., Martin, A.P., Sims, D.W., Jones, C.S. & Noble, L.R. (2012). Application of molecular genetics for conservation of the white shark, *Carcharodon carcharias*, L. 1758. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.357-380.

Hammerschlag, N., Martin, R. & Fallows, C. (2006). Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environmental Biology of Fishes*, 76:341-350.

Hara, M., Maharaj, I. & Pithers, L. (2003). Marine-based tourism in Gansbaai: A socio-economic study. Final report for the Department of Environmental Affairs and Tourism (DEAT), South Africa, 55 pp.

Heithaus, M.R. (2004). Predator-prey interactions. In: Carrier, J., Musick, J. & Heithaus, M. (Eds). *Biology of sharks and their relatives*. Boca Raton, FL: CRC Press. p.487-522.

Heithaus, M.R. & Dill, L.M.. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83:480-491.

Heithaus, M.R., Dill, L.M., Marshall, G. & Buhleier, B. (2002). Habitat use and foraging behaviour of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology*, 140:237-248.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23(4):202-210.

Heupel, M.R. & Simpfendorfer, C.A. (2005). Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, 147:1239-1249.

Heupel, M.R., Reiss, K.L., Yeiser, B.G. & Simpfendorfer, C.A. (2008). Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography: Methods*, 6:327-335.

Heupel, M.R., Simpfendorfer, C.A., Collikns, A.B. & Tyminski, J.P. (2006). Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes*, 76:47-67.

Heupel, M.R., Williams, A.J., Welch, D.J., Ballagh, A., Mapstone, B.D. & Carlos, G., et al. (2009). Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fisheries Research*, 95:350-361.

Heupel, M.R., Yeiser, B.G., Collins, A.B., Ortega, L., & Simpfendorfer, C.A. (2010). Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. *Marine and Freshwater Research*, 61:1–10. doi:10.1071/MF09019

Heupel, M.R., Knip, D.M, Simpfendorfer, C.A. & Dulvy, N.K. (2014). Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*, 495:291-298.

Hewitt, A.M. (2013). Demographics of a seasonal aggregation of white sharks at Seal Island, False Bay, South Africa. Masters Thesis. University of Cape Town, Biological Sciences Department.

Holland, K.N., Meyer, C.G. & Dagorn, L.C. (2009). Inter-animal telemetry: results from first deployment of acoustic ‘business card’ tags. *Endangered Species Research*, 10:287–293.

Holland, K.N., Wetherbee, B.M., Lowe, C.G. & Meyer, C.G. (1999). Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology*, 134:665-675.

Holland, K.N., Wetherbee, B.M., Peterson, J.D. & Lowe, C.G. (1993). Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*, 1993(2):495-502.

Hooker, S.K. & Gerber, L.R. (2004). Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *BioScience*, 54(1):27-39.

Hopcraft, J.G.C., Sinclaire, A.R.E. & Packer, C. (2005). Planning for success: Serengeti lions seek accessibility rather than abundance. *Journal of Animal Ecology*, 74(5):559-566.

Hose, J.E., Cross, J.N., Smith, S.G. & Diehl, D. (1989). Reproductive impairment in a fish inhabiting a contaminated coastal environment off southern California. *Environmental Pollution*, 57:139–148. doi: 10.1016/0269-7491(89)90006-7

Hubbell, G. (1996). Using tooth structure to determine the evolutionary history of the white shark. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.9-18.

Hueter, R., Heupel, M.R., Heist, E.J. & Keeney, D.B. (2005). Evidence of philopatry in sharks and implications for the management of shark fisheries. *Journal of Northwest Atlantic Fishery Science*, 35:239-247.

Hulbert, L., Aires-Da-Silva, A.M., Gallucci, V.F. & Rice, J.S. (2005). Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. *Journal of Fish Biology*, 67:490–509

Hussey, N.E., Dudley, S.F.J., McCarthy, I.D., Cliff, G. & Fisk, A.T. (2011). Stable isotope profiles of large marine predators: viable indicators of trophic position, diet and movement in sharks. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(12): 2029-2045.

Hussey, N.E., McCann, H., Cliff, G., Dudley, S.F.J., Wintner, S. & Fisk, A.T. (2012). Size-based analysis of diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.27-50.

Jewell, O.J.D., Johnson, R.L., Gennari, E. & Bester, M.N. (2012). Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa. *Environmental Biology of Fishes*, 96(7):881-894.

Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19(2):101-108.

Johnson, R.L, Bester, M.N., Dudley, S.F.J., Oosthuizen, W.H., Meyer, M., Hancke, L. & Gennari, E. (2009). Coastal swimming patterns of white sharks (*Carcharodon carcharias*) at Mossel Bay, South Africa. *Environmental Biology of Fishes*, 85:189-200.

Jorgensen, S.J., Arnoldi, N.S., Estess, E.E., Chapple, T.K., Rückert, M., Anderson, S.D. & Block, B.A. (2012). Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon carcharias*) migration and offshore behaviour. *PLoS ONE*, 7(10):e47819. doi:10.1371/journal.pone.0047819.

Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S.D., Perle, C., van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P., and Block, B.A. (2010). Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B*, 277:679-688.

Kelly, J.T. & Klimley, A.P. (2003). The occurrence of the white shark, *Carcharodon carcharias*, at Point Reyes Headlands, California. *Bulletin of California Fish and Game*, 89(4):187-196.

Kime, D.E. & Hews, E.A. (1982). The effect of temperature on steroid biosynthesis by testes of the dogfish, *Scyliorhinus caniculus*. *Comparative Biochemistry and Physiology – Part B, Comparative Biochemistry*, 71(4):675-679.

Kirkman, S.P., Oosthuizen, W.H. & Meÿer, M.A. (2006). The seal population of Seal Island, False Bay. In: Nel, D.C. & Peschak, T.P. Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa, p.83-94. Proceedings of a specialist workshop. WWF South Africa Report Series – 2006/Marine/001 Annexure 1.

Klimley, A.P. (1985). The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Southern California Academy of Sciences*, *Memoirs,* 9:15-40.

Klimley A.P. (1987). The determinants of sexual segregation in the scalloped hammerhead *Sphyrna lewini*. *Environmental Biology of Fishes,* 18:27-40.

Klimley, A.P. & Anderson, S.D. (1996). Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias*. San Diego: Academic Press. p.365-373.

Klimley, A.P., Anderson, S.D., Pyle, P. & Henderson, R.P. (1992). Spatio-temporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia*, 3:680-690.

Klimley, A.P. & Curtis, T.H. (2006). Shark attack versus ecotourism: negative and positive interactions. In: Timm, R.M. & O'Brien, J.M. (Eds). Proceedings of the 22nd Vertebrate Pest Conference, University of California, Davis. p.33-44.

Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F. & van Sommeran, S. (2001). Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and large marine species. *Marine Biology*, 138:429-446.

Knight, J. (Ed.), (2000). *Natural enemies: People-wildlife conflicts in anthropological perspective*. London: Routledge.

Knip, D.M., Heupel, M.R. & Simpfendorfer, C.A. (2010). Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series,* 402:1-11.

Kock, A.A. (2002). Predatory activity of great white sharks (*Carcharodon carcharias*) around a Cape fur seal colony. Honours Thesis. University of Cape Town, Percy FitzPatrick Institute.

Kock, A.A. & Johnson, R.L. 2006. White shark abundance: Not a causative factor in numbers of shark bite incidences. In: Nel, D.C. & Peschak, T.P. (Eds). 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 Annexure 1:p.1-19.

Kock, A.A., O'Riain, M.J., Mauff, K., Meÿer, M., Kotze, D. & Griffiths, C. (2013). Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE*, 8(1): e55048. doi:10.1371/journal.pone.0055048.

Kock, A.A., Titley, S., Petersen, W., Sikweyiya, P., Tsotsobe, S., Colenbrander, D., Gold, H. & Oelofse, G. (2012). Shark Spotters: a pioneering shark safety program in Cape Town, South Africa. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.447-466.

Krausman, P.R. (1999). Some basic principles of habitat use. In: Launchbaugh, K.L., Sanders, K.D. & Mosley, J.C. *Grazing behavior of livestock and wildlife*. Idaho Forest, Wildlife and Range Experiment Station Bulletin 70: 85–90.

Krebs, J.R. & Davies, N.B. (Eds). (1993). *Behavioural ecology: an evolutionary approach* (4th ed). Oxford: Blackwell.

Lacroix, G.L. & Voegeli, F.A. (2000). Development of automated monitoring systems for ultrasonic transmitters. In: Moore, A. & Russell, I. *Advances in fish telemetry*. CEFAS, Suffolk, U.K. pp. 37-50.

Lamberth, S.J. (2006). White shark and other chondrichthyan interactions with the beach-seine (treknet) fishery in False Bay, South Africa. *South African Journal of Marine Science*, 28(3-4):723-727.

Lamberth, S.J., Clark, B.M. & Bennett, B.A. (1995). Seasonality of beach-seine catches in False Bay, South Africa, and implications for management. *South African Journal of Marine Science,* 15:157-167.

Laroche, R.K., Kock, A.A., Dill, L.M. & Oosthuizen, H. (2007). Effects of provisioning ecotourism activity on the behaviour of white sharks, *Carcharodon carcharias*. *Marine Ecology Progress Series*, 338:199-209.

Laroche, R.K., Kock, A.A., Dill, L.M. & Oosthuizen, H. (2008). Running the gauntlet: a predator-prey game between sharks and two age classes of seals. *Animal Behaviour*, 76:1901-1917.

Lima, S.L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, 481:25-34.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68: 619-640.

Lucifora, L.O., Menni, R.C. & Escalante, A.H. (2005). Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from north Patagonia, Argentina. *ICES Journal of Marine Science*, 62:107-115.

Luttbeg, B. & Kerby, J.L. (2005). Is scared prey as good as dead? *Trends in Ecology & Evolution*, 208:416-418.

Macdonald, I.A.W. & Cowling, R.M. (1996). Biodiversity and conservation of Table Mountain and the Cape Peninsula. *Biodiversity and Conservation*, 5:525–526.

Madden, F. (2004). Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. *Human Dimensions of Wildlife*, 9:247-257.

Malcolm, H., Bruce, B.D. & Stevens, J.D. (2001). A review of the biology and status of white sharks in Australian waters. Report to Environment Australia, Marine Species Protection Program, CSIRO Marine Research, Hobart.

Mann, J. & Watson-Capps, J.J. (2005). Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins (*Tursiops* sp.). *Animal Behaviour*, 69:899-909.

MarineBio Conservation Society. Web. Thursday, December 19, 2013. http://marinebio.org/species.asp?id=38. Last update: 1/14/2013 2:22:00 PM. Contributor(s): MarineBio.

Martin, R.A., Hammerschlag, N., Collier, R.S. & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom*, 85:1121-1135.

Martin, R.A & Hammerschlag, N. (2012). Marine predator–prey contests: Ambush and speed versus vigilance and agility. *Marine Biology Research,* 8 (1), 90-94.

McCosker, J.E. (1987). The white shark, *Carcharodon carcharias,* has a warm stomach. *Copeia* 1987(1):195-197.

McCullagh, P. & Nelder, J.A. (1989). *Generalized linear models. Monographs on statistics and applied probability 37*. London; Chapman & Hall.

Meyer, C.G., Clark, T.B., Papastamatiou, Y.P., Whitney, N.M. & Holland, K.N. (2009). Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. *Marine Ecology Progress Series,* 381:223-235. doi:10.3354/meps07951.

Morant, P.D. (1991). The estuaries of False Bay. *Transactions of the Royal Society of South Africa*, 47(4/5):629-640.

Morant, P.D. & Grindley, J.R. (1982). Estuaries of the Cape: Part II. Synopsis of available information on individual systems. In: Heydorn, A.E.F. & Grindley, J.R. Report 13 Sand (CSW 4). Stellenbosch CSIR Research Report 413. 70 pp.

Morris, D.W. (2003). Toward an ecological synthesis: the case for habitat selection. *Oecologica*, 136:1-13.

Morrissey, J.F. & Gruber, S.H. (1993). Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environmental Biology of Fishes*, 38:311-319.

Mull, C.G., Lyons, K., Blasius, M.E., Winkler, C., O'Sullivan, J.B., *et al*. (2013). Evidence of Maternal Offloading of Organic Contaminants in White Sharks (*Carcharodon carcharias*). *PLoS ONE,* 8(4): e62886. doi:10.1371/journal.pone. 0062886.

Mull, C.G., Blasius, M.E., O'Sullivan, J.B., Lowe, C.G. (2012). Heavy metals, trace elements, and organochlorine contaminants in muscle and liver tissue of juvenile white sharks (*Carcharodon carcharias*) from the Southern California Bight. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.59-75.

Musick, J.A., Burgess, G., Cailliet, G., Camhi, M. & Fordham, S. (2000). Management of sharks and their relatives (Elasmobranchii). *Fisheries*, 25:9-13.

Muter, B.A., Gore, M.L., Gledhill, K.S., Lamont, C. & Huveneers. C. (2012). Australian and U.S. news media portrayal of sharks and their conservation. *Conservation Biology,* 27 (1), 187–196.

Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423:280-283.

Nasby-Lucas, N., Dewar, H., Lam, C., Goldman, K. & Domeier, M.L. (2009). White shark offshore habitat: a behavioural and environmental characterization of the Eastern Pacific shared offshore foraging area. *PLoS ONE*, 4(12):e8163.

Nasby-Lucas, N. & Domeier, M.L. (2012). Use of photo identification to describe a white shark aggregation at Guadalupe Island, Mexico. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.381-392.

Neff, C. (2012). Australian beach safety and the politics of shark attacks. *Coastal Management*, 40:88-106.

Nel, D. & Peschak, T. (2006). 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 Annexure 1.

Nyhus, P.J., Fisher, H., Madden, F. & Osofsky, S. (2003). Taking the bite out of wildlife damage: the challenges of wildlife compensation schemes. *Conservation in Practice*, 4:37-40. doi: 10.1111/j.1526-4629.2003.tb00061.x

Owen-Smith, N. & Mills, M.G.L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs*, 76:73- 92.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14:483–88.

Papastamatiou, Y.P., Itano, D.G., Dale, J.J., Meyer, C.G. & Holland, K.N. (2010). Site fidelity and movements of sharks associated with ocean-farming cages in Hawaii. *Marine and Freshwater Research*, 61:1366−1375.

Papastamatiou, Y.P., Lowe, C.G., Caselle, J.E. & Friedlander, A.M. (2009). Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*, 90:996-1008.

Papastamatiou, Y.P., Meyer, C.G. & Holland, K.N. (2007). A new acoustic pH transmitter for studying the feeding habits of free-ranging sharks. *Aquatic Living Resources*, 20:287–290.

Pardini, A.T., Jones, C.S., Noble, L.R., Kreiser, B., Malcolm, H., Bruce, B.D., Stevens, J.D., Cliff, G., Scholl, M.C., Francis, M., Duffy, C.A.J. & Martin, A.P. (2001). Sex biased dispersal of great white sharks. *Nature*, 412:139-140.

Parra, G.J. (2005). Behavioural ecology of Irrawaddy *Ocraella brevirostris* (Owen in Gray, 1866), and Indo-Pacific humpback dolphins *Sousa chinensis* (Osbek, 1765), in northeast Queensland, Australia: a comparative study. Doctoral Thesis. School of Tropical Environment Studies and Geography. James Cook University.

Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences*, 98:3904-3908.

Penney, A.J. (1991). The interaction of net and line-fisheries, in False Bay, South Africa. *Transactions of the Royal Society of South Africa*, 47(4/5):063-681.

Pepperell, J.G. (1992). Trends in the distribution, species composition and size of sharks caught by gamefish anglers off south-eastern Australia, 1961-90. *Australian Journal of Marine and Freshwater Research*, 43:213-25.

Pratt, H.L. (1996). Reproduction in the male white shark. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.131-138.

Purdy, R.W. (1996). Paleoecology of fossil white sharks. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.67-78.

Pyle, P., Anderson, S.D. & Ainley, D. (1996). Trends in white shark predation at the South Farallon Islands, 1968-1993. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.375-380.

Rand, R.W. (1956). The Cape fur seal *Arctocephalus pusillus pusillus* (Schreber). It's general characteristics and moult. Investigative Report Division of Sea Fisheries South Africa, 21:1-52.

Rand, R.W. (1967). The Cape fur-seal (*Arctocephalus pusillus*): general behaviour on land and at sea. Investigational Report, Sea Fisheries Research Institute, South Africa, 60:1-39.

Reid, D. & Krogh, M. (1992). Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. *Australian Journal of Marine and Freshwater Research*, 43:283-296.

Ribeiro, S., Viddi, F.A., Cordeiro, J.L. & Freitas, T.R.O. (2007). Fine-scale habitat selection of Chilean dolphins (*Cephalorhynchus eutropia*): interactions with aquaculture activities in southern Chiloé Island, Chile. *Journal of the Marine Biological Association of the United Kingdom*, 87:19-128. doi:10.1017/S0025315407051594.

Robbins, R.L. (2007). Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. *Journal of Fish Biology*, 70:1350-1364.

Robbins, R. & Booth, D. (2012). Seasonal, sexual and size segregation of white sharks *Carcharodon carcharias* at the Neptune Islands, South Australia. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.287-299.

Robinson, D.P., Jaidah, M.Y., Jabado, R.W., Lee-Brooks, K., Nour El-Din, N.M., *et al.* (2013). Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in

Qatari waters of the Arabian Gulf to feed on fish spawn. *PLoS ONE* 8(3): e58255. doi:10.1371/journal.pone.0058255

Rose, D. (1996). *An overview of world trade in sharks and other cartilaginous fishes*. Cambridge: TRAFFIC Network.

Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.J. & Meekan, M.G. (2013). Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS ONE* 8(9): e74648. doi:10.1371/journal.pone.0074648

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7:153-163.

Semmens, J.M., Payne, N.L., Huveneers, C., Sims, D.W. & Bruce, B.D. (2013). Feeding requirements of white sharks may be higher than originally thought. *Scientific Reports*, 3:1471. doi:10.1038/srep01471.

Shivji, M., Chapman, D., Pikitch, E. & Raymond, P. (2005). Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. *Conservation Genetics*, 6:1035-1039.

Simpfendorfer, C.A., Heupel, M.R., White, W.T. & Dulvy, N.K. (2011). The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research,* 62:518.

Simpfendorfer, C.A. & Milward, N.E. (1993). Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes*. 37:337-345.

Sims, D.W. (2005). Differences in habitat selection and reproductive strategies of male and female sharks. In Ruckstuhl, K.E. & Neuhaus, P. (Eds). *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge: Cambridge University Press. p.127–147.

Sims, D.W., Nash, J.P. & Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alter native behavioural strategies and apparent sexual segregation. *Marine Biology,* 139: 1165-1175.

Sims, D.W. & Quayle, V.A. (1998). Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature,* 393:460-464.

Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C. & Metcalfe, J.D. (2003). Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series,* 248:187-196.

Sims, D.W., Southall, E.J., Wearmouth, V.J., Hutchinson, N., Budd, G.C. & Morritt, D. (2005). Refuging behaviour in the nursehound *Scyliorhinus stellaris* (Chondrichthyes: Elasmobranchii): preliminary evidence from acoustic telemetry. *Journal of the Marine Biological Association of the United Kingdom,* 85:1137.

Smale, M. & Cliff, G. (2012). White sharks and cephalopod prey: Indicators of habitat use? In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.51-57.

Smith, S.E., Au, D.W. & Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, 49:663-78.

Spargo, P. (1991). False Bay, South Africa: An historic and scientific overview. *Transactions of the Royal Society of South Africa,* 47:363-375.

Speed, C.W., Field, I.C., Meekan, M.G. & Bradshaw, C.J.A. (2010). Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, 408:275-293

Stephens, D.W. & Krebs, J.R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000). The effects of fishing on sharks, rays and chimaeras (*chondrichthyans*), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57:476-494.

Stevick, P.T., McConnel, B.J. & Hammond, P.S. (2002). Patterns of movement. In: Hoelzel, A.R. (Ed). *Marine mammal biology: an evolutionary approach*. Oxford: Blackwell Science. p.185–216.

Strong, W.R., Bruce, B.D., Nelson, D.R. & Murphy, R.D. (1996). Population dynamics of white sharks in Spencer Gulf, South Australia. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.401-414.

Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P. & de Marignac, J.R.C. (2001). Review of elasmobranch behavioural studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris,* around Bimini Islands, Bahamas. *Environmental Biology of Fishes,* 60:225-250. doi:10.1023/A:1007657505099.

Towner, A.V., Wcisel, M.A., Reisinger, R.R., Edwards, D. & Jewell, O.J.D. (2013). Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. *PLoS ONE,* 8(6):e66035. doi:10.1371/journal.pone.0066035.

Tricas, T.C. & McCosker, J.E. (1984). Predatory behaviour of the white shark, *Carcharodon carcharias*, and notes on its biology. *Proceedings of the California Academy of Sciences,* 43:221-238.

Uchida, S., Toda, M. Teshima, K. & Yano, K. (1996). Pregnant white sharks with near-term foetuses from Fishery Bulletin 98(2) Japan. In: Klimley, A.P. & Ainley, D. (Eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego: Academic Press. p.139-155.

van Herwerden, L., Griffiths, C.L., Bally, R., Blaine, M & du Plessis, C. (1989). Patterns of shore utilization in a metropolitan area: The Cape Peninsula, South Africa. *Ocean and Shoreline Management*, 12:331-346.

Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. (2103). Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, 94(11):2619–2631.

Voegeli, F.A., Smale, M.J., Webber, D.M., Andrade, Y., & O'Dor, R.K. 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environmental Biology of Fishes*, 60: 267-281.

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan L, Arias-Castro, E., Myers R.A. (2010). Large-scale absence of sharks on reefs in the greater-Caribbean: a footprint of human pressures. *PLoS One,* 5:e11968.

Wcisel, M. (2013). The effects white shark, *Carcharodon carcharias,* presence has on the behaviour of Cape fur seals, *Arctocephalus pusillus pusillus,* at Geyser Rock. Masters Thesis. University of Cape Town, Percy FitzPatrick Institute.

Wearmouth, V.J. & Sims, D.W. (2008). Sexual segregation in marine fish, reptiles, birds and mammals behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, 54:107-170.

Weltz, K., Kock, A.A., Winker, H., Attwood, C. & Sikweyiya, M. (2013). The influence of environmental variables on the presence of white sharks, *Carcharodon carcharias* at two popular Cape Town bathing beaches: A Generalized Additive Mixed Model. PLoS ONE 8(7): e68554. doi:10.1371/journal.pone.0068554

Weng, K.C., Boustany, A.M., Pyle, P., Anderson, S.D., Brown, A. & Block, B.A. (2007a). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology,* 152:877-894.

Weng, K.C., O'Sullivan, J.B., Lowe, C.G., Winkler, C.E., Dewar, H. & Block, B.A. (2007b). Movements, behaviour and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series,* 338:211-224.

Werry, J.M., Bruce, B., Sumpton, W., Reid, D. & Mayer, D.G. (2012). Beach areas used by juvenile white sharks, Carcharodon carcharias, in eastern Australia. In: Domeier, M.L. *Global perspectives on the biology and life history of the white shark*. Boca Raton: CRC Press. p.271-286.

White, W.T. & Potter, I.C. (2004). Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. *Marine Biology,* 145(5):1023-1032.

Wintner, S. & Cliff, G. (1999). Age and growth determination of the white shark, *Carcharodon carcharias,* from the east coast of South Africa. *Fisheries Bulletin,* 97(1):153-169.

Wirsing, A.J., Heithaus, M.R. & Dill, L.M. (2007). Can measures of prey availability improve our ability to predict the abundance of large marine predators? *Oecologia*, 153:563-568.

Wirsing, A.J., Heithaus, M.R., Frid, A. & Dill, L.M. (2008). Seascapes of evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science,* 24:1-15.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. & Gruber, S.H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy,* 40:194-204. doi:10.1016/j.marpol. 2012.12.034.

Yates, P.M., Heupel, M.R., Tobin, A.J. & Simpfendorfer, C.A. (2012). Diversity in young shark habitats provides the potential for portfolio effects. *Marine Ecology Progress Series,* 458:269-281. doi: 10.3354/meps09759.

Zuffa, M., van Grevelynghe, G., De Maddalena, A. & Storai, T. (2002). Records of the white shark, *Carcharodon carcharias* (Linnaeus, 1758) from the Western Indian Ocean. *South African Journal of Science,* 98(7-8):347-349.

Zuur, A.F., Leno, E.N. & Smith, G.M. (2007). *Analysing ecological data: statistics for biology and health.* New York: Springer.

Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.