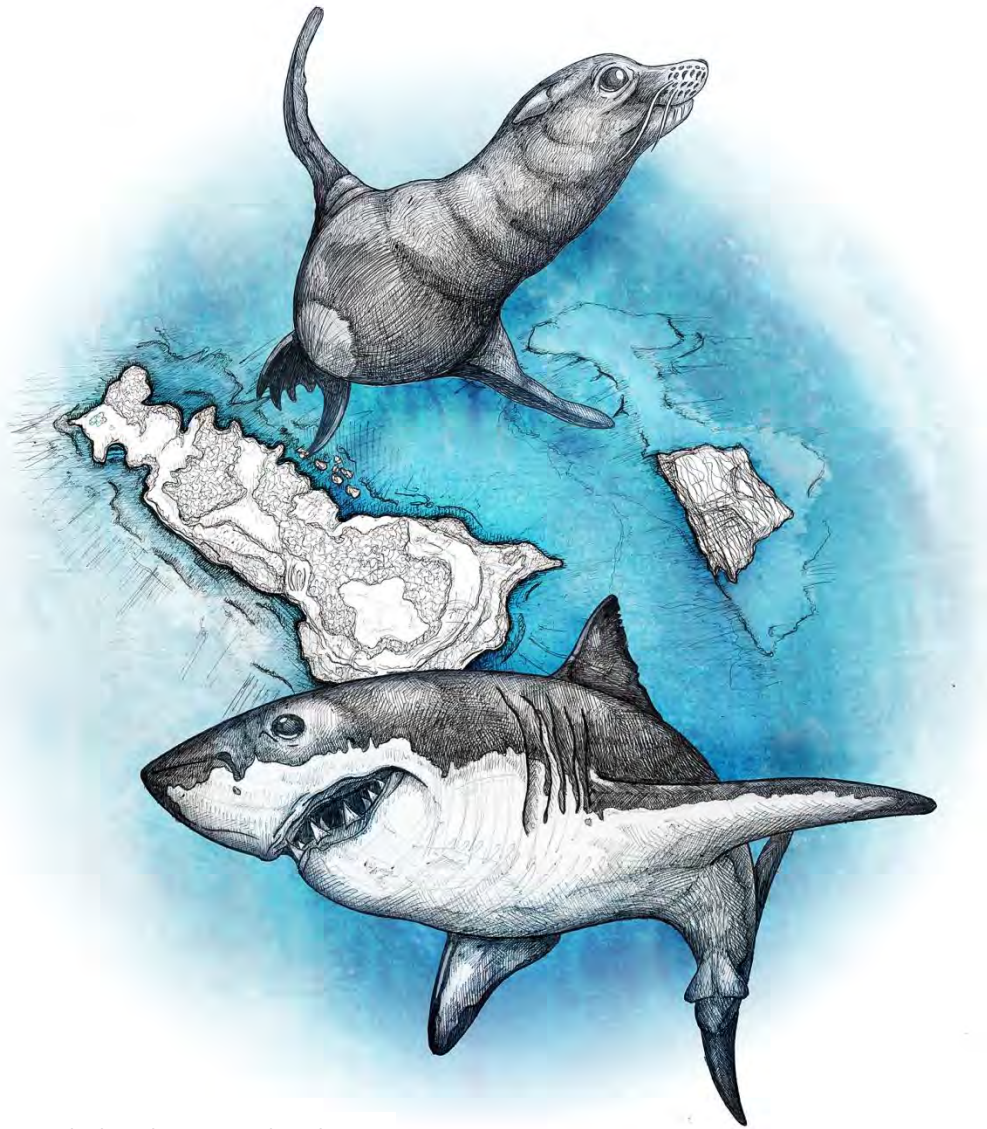


# The effects of white shark presence on the behaviour of Cape fur seals at Geyser Rock, Gansbaai, South Africa

Michelle Wcisel



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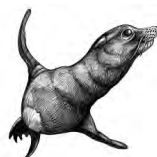
Dissertation presented for the degree of Master of Science in  
the Department of Biological Sciences  
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## Abstract

Predators and the risk associated with their presence may affect group composition, group size, movement patterns, and habitat use of prey species. The removal of predators, or their reintroduction following long periods of absence, equally can have profound impacts on their prey, triggering ecological cascades and ultimately shaping the biota of entire landscapes. While such processes are well documented in terrestrial ecosystems, similar results are absent in the marine realm, largely due to logistical difficulty. One exception to this is the study of white shark and seal interactions at coastal island rookeries, where white shark presence is seasonal, and seals exhibit marked behavioural differences between seasons. What is lacking from these studies, however, is how subsurface habitat around the islands, specifically refugia, may influence the behaviour of seals and their interactions with white sharks. I address this challenge by comparing both seal movement patterns and shark-seal interactions at Geysers Rock, Gansbaai with the established seal and shark patterns at Seal Island, False Bay. White sharks aggregate at both islands during the austral winter and seals encounter these aggregations when commuting to and from their respective rookeries to offshore foraging areas. The seascape around Geysers Rock is comparably more featured, including kelp beds and extensive shallow (5–10m depth) reef systems, whereas Seal Island is largely featureless, with neither extensive kelp nor reefs. At Geysers Rock, predations by white sharks were rarely observed (0.1 predations/hour) compared to Seal Island (1.24 predations/hour) and lacked the focused spatiotemporal peak at sunrise to the south of the island. Seals at Geysers Rock did not show a relationship between group formation and season, which was clearly demonstrated at Seal Island. This suggests that seals at Geysers Rock may be less reliant on group formation (safety in numbers) and selfish herd tactics within such groups to reduce predation risk. Rather, seals at Geysers Rock avoided deep open water patches during winter and shifted their movement patterns to and from the island to sectors with greater subsurface habitat heterogeneity. While I was limited in quantifying spatiotemporal patterns of predation risk around Geysers Rock (predation events were rare and widely dispersed), these results strongly suggest that seals actively avoid deep open water and show a preference for high structural complexity sectors during the risky winter months when shark presence is highest. This finding represents a habitat-escape tactic unidentified in previously studied white shark/pinniped systems. Together these results provide empirical support for both the risk-allocation hypothesis and refugia hypotheses within marine predator-prey systems.

## Declaration

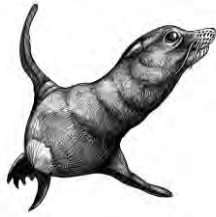
I, Michelle Weisel, confirm that the work presented in this dissertation is my own. Where information has been derived from other sources, I confirm that this has been indicated in the dissertation.

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Michelle Weisel

University of Cape Town

## Acknowledgments



“Don't worry about what is behind you, next to you, or what it looks like ahead. Just concentrate on the piece of water you are on right now.” - Albert Scholtz

This dissertation would not have been possible without a team of people who were, for whatever reason, dedicated to see me succeed with various aspects of my journey.

Foremost is my forgiving family; Lori, Dale and Amie. Mom, you continue to be my source of strength, and only through your encouragement was I able to reach the places I have – from my first dorm room to South Africa. Dad, you taught me that nothing will come to you without hard work and I am forever grateful for my tom-boy upbringing. By mastering a quad (you'll have to fill in the model and year) by age 7, I had the confidence to skipper a 600hp semi-rigid zodiac by age 26. Amie, I have always been inspired by your ability to transform, adapt, and give it your all. Your enthusiasm for life reminded me to also have fun! My family's combined patience and unconditional support allowed me to find my path at a snail's pace, and I am forever grateful. Unfortunately, I am still finding it!

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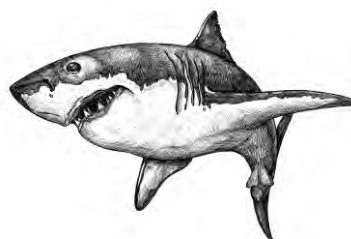
Luckily, I was able to assist two predecessors accomplish Master's projects during my time in Gansbaai. Not only was their guidance invaluable, but they were also the 'guinea pigs' to how this would all work. Thank you very much Alison and Oliver, I am so proud of what you have achieved. Especially to Alison, who had the most difficult task of clearing the path for all future DICT students to come.

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To Lalo Saily and Frank Pey, thank you for your invaluable data collection. I would not have the entire picture without your dedicated assistance and I hope you are as pleased with

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## Introduction

### General predator-prey theory

The risks that predators impose on prey have a major influence on spatiotemporal habitat use by prey species; these risks can be divided into effects which are lethal (i.e. the removal of animals from an ecosystem) (Taylor 1984), or non-lethal (i.e. anti-predator behaviour of animals) (Abrams 1984, Sih 1987, Kotler & Brown 1988). Non-lethal effects, including actual (Sinclair 1985) and perceived predation risk (Sih & Wooster 1994, Kats & Dill 1998, Lima 1998, Lima 2002), may be more influential to prey decision-making than direct mortality (Brown et al. 1999, Heithaus et al. 2008b). These decisions may affect group composition, group size, movement patterns, and habitat use (Bertram 1978, Schaik & Noordwijk 1985, Lima & Dill 1990, Heithaus et al. 2002, De Vos 2010), that in turn can trigger an ecological cascade of effects to linked species (Daborn et al. 1993, Moran et al. 1996), ultimately affecting ecosystem functionality.

A terrestrial example of this is Ripple and Beschta's (2004) study that uncovered the ecological cascade following the reintroduction of wolves (*Canis lupus*) into Yellowstone National Park after 70 years of top-predator absence. Wolves preferred the cover of forest edges to stalk their main prey, elk (*Cervus elaphus*). Consequently, the elk shifted to more open habitats with greater visibility in order to better detect approaching wolves. This shift in habitat use away from the forest fringe areas allowed for the rebound of slow-growth riparian cottonwood trees, a species which grows at forest fringe areas that had nearly been eradicated by the elk's unhindered browsing. In this example, the non-lethal effect of wolf presence in fringe forest habitats altered the forests' structure.

Many more terrestrial and aquatic examples highlight fear as an important driver of prey behaviour and the resultant structuring of those ecosystems (Werner & Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005, Verdolin 2006). Indeed much of our understanding of predator-prey relationships stems from studies of large terrestrial carnivores and their large prey (e.g. Mech 1966, Kruuk 1972, Schaller 1972, Bergerud 1988, Packer et al. 1990, Caro 1994). By contrast, little is known about the predator-prey relationships of large vertebrates in the marine environment (Le Boeuf 2004, Heithaus et al. 2006), and more specifically about how prey decisions are affected by their vertebrate predators (Dill et al. 2003, Wirsing et al. 2007).

Often, marine predators occupy large home ranges that occasionally overlap the equally large home ranges of their prey in small (tens of meters) patches (Heithaus & Dill 2006). Reliably predicting these small interaction patches within vast marine ecosystems can prove to be an improbable and expensive research endeavour. Thus, most marine predator/prey studies have been limited to coastal species at easily accessible areas with high predictability of both predator and prey presence (e.g. Martin et al. 2005, Heithaus et al. 2006, Heithaus & Dill 2006, LaRoche et al. 2008). It is in these areas where the mostly terrestrial-based theoretical hypotheses of predator prey interactions are applied and examined for divergence. One such hypothesis that has received much attention and will be examined in this thesis is the risk-allocation hypothesis, that attempts to predict how animals respond to the risk their predators impose over time (Lima & Bednekoff 1999).

### **The Risk Allocation hypothesis**

An evolutionarily stable strategy for prey individuals is to maintain a certain level of fear at all times, since few animals have perfect knowledge of their predator's whereabouts (Smith

1974, Brown et al. 1999). Yet, predator presence is rarely constant, and a persistent uniform level of fear can cost foraging opportunities (Sinclair 1985, Heithaus & Dill 2002), limit mate selection (Taylor 2005), or render the animal otherwise unfit (Heithaus et al. 2006, Ferrari et al. 2009). Therefore, selection favours the individual that can assess variation in predation risk and know when to pursue precarious life history traits (i.e. mating, foraging in food rich areas, thermoregulation) and when to wait for the risk to pass (Lima & Dill 1990, Lima & Bednekoff 1999, Heithaus et al. 2006, Mirza et al. 2006, Ferrari et al. 2009).

Although predation risk often varies temporally in a predictable manner (Laundre et al. 2010), i.e. across diurnal, lunar, or seasonal cycles, the effect that variation in risk plays on prey decision-making had been overlooked by behavioural ecologists until recently (Sih & McCarthy 2000, Ferrari et al. 2009). The most widely accepted hypothesis that synthesizes prey decision-making under varying levels of, and temporal variation in, risk is the risk-allocation hypothesis, developed by Lima & Bednekoff (1999). The risk-allocation hypothesis attempts to predict how prey species respond to varying levels of danger within the varying lengths of time that the danger exists. Three key predictions follow from the hypothesis, namely that: (1) prey that experience short periods of high risk among long periods of safety will halt feeding effort during that high risk period and return to normal levels of foraging once the danger has passed, (2) prey that endure long periods of high risk with interspersed short periods of safety increase foraging during the brief window of safety, and (3) prey that experience continual high risk or have no predictability of low risk will be compelled to forage during high-risk periods.

Even with wide appreciation, few empirical studies have tested this hypothesis in natural settings and laboratory tests yielded mixed results (Beauchamp & Ruxton 2011). This was

the case in a laboratory based study where marine snails (*Littorina* spp.) followed the predictions for high risk periods but not low-risk. More snails chose to forage as time at high perceived risk increased. However, at low-risk, there was no relationship between the number of snails foraging and time at high risk (Hamilton & Heithaus 2001). A laboratory test of freshwater physid snails (*Physa gyrina*) also had mixed results as snails exposed to high risk would respond with lower levels of activity, but snails under low risk exhibiting moderate activity did not significantly lower activity when exposed to a pulse of high risk (Sih & McCarthy 2002). Similarly, rainbow trout (*Oncorhynchus mykiss*) followed risk-allocation predictions by lowering activity during high risk, but did not increase activity during safe patches (Mirza et al. 2006).

Laboratory settings with tadpoles (*Rana lessonae*) and a field test with bank voles (*Clethrionomys glareolus*) did not follow any risk allocation predictions. When exposed to high risk pulses, tadpoles did not allocate more feeding to the low-risk times, and as tadpoles spent more time at risk, they did not increase feeding (Van Buskirk et al. 2002), whereas the field test with bank voles may have had experimental flaws (Sundell et al. 2004) and unfortunate intrinsic risk to laboratory settings. In support of the risk allocation hypothesis, juvenile convict cichlids (*Archocentrus nigrofasciatus*) did react as predicted to variable predation risk as fish that were exposed repeatedly to high risk showed moderate anti-predator behaviour and foraged significantly more during periods of safety compared to fish infrequently exposed to high risk (Foam et al. 2005).

Finally, and most appropriate to this dissertation, when the risk-allocation hypothesis was applied to the predator prey system of Cape fur seals (*Arctocephalus pusillus pusillus*) and white sharks (*Carcharodon carcharias*) at Seal Island, False Bay, Cape fur seals were shown

to limit their time in high predation risk areas (i.e., open water) and at peak predation periods (i.e., after sunrise) (De Vos 2010). Spatiotemporal shifts in habitat use in response to risk become critical to survival when prey species aggregate in finite areas that attract predators (Flaxman & Lou 2009, Valex et al. 2009). This is particularly relevant for Cape fur seal colonies within the home range of white sharks.

The Cape fur seal colony of Geysers Rock 100km to the east of Seal Island, False Bay, is an ideal setting in which to examine the theoretical concepts outlined above within a marine system, and to test the general findings of De Vos (2010). Seal Island hosts the same study species within the same Benguela upwelling ecosystem of Geysers Rock, yet the landscape of Geysers Rock varies significantly from that of Seal Island (Figure 1). The topography around Geysers Rock is more featured; the shallow (2m-15m) waters adjacent (<500m) to the colony include a variety of potential refugia, including; shallow rocky reefs, kelp forests, and rock pinnacles. In many cases, such habitat heterogeneity has been shown to render parts of other ecosystems more “escapable” than others (Wirsing et al. 2007, 2010). Therefore, the seals of Geysers Rock may have a higher ability to manipulate their predation risk by not only adjusting to temporal variation in high risk, but by being able to choose between areas that contain cover and areas that do not.

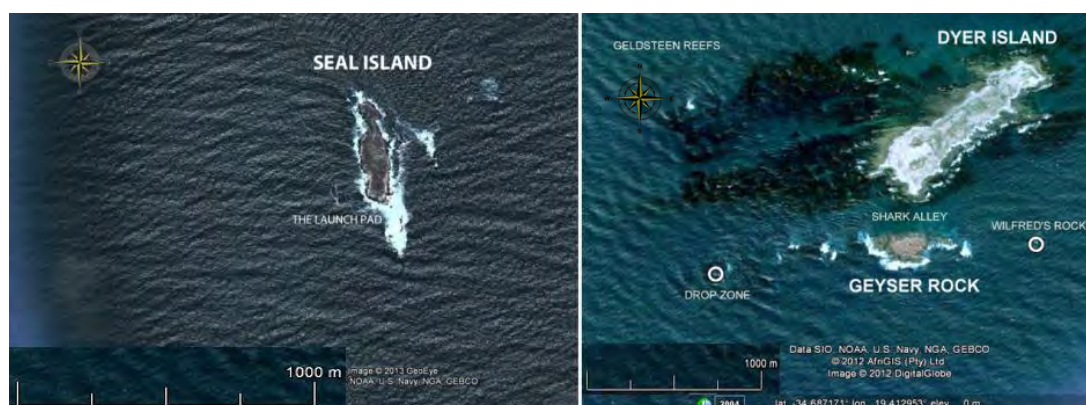


Figure 1: The mostly featureless system of Seal Island, False Bay (left) compared with the Geysers Rock system (right) characterised by extensive reef and kelp bed systems.

## The importance of landscape structures in predator/prey scenarios

The way in which prey species generally utilize their spatial environment is thought to be determined by two polar facets; the attraction to resource patches and the avoidance of risky patches (Schoener 1971, Mangel & Clark 1986, Willems & Hill 2009). Additionally, the availability of structures within a landscape is a major determinant of the abundance and distribution of animals, both predator and prey, within marine and terrestrial environments (McCoy & Bell 1991). Predators are not efficient in every landscape type, thus predation risk often varies with habitat structures (Laundre et al. 2010). Equally, a prey's efficiency at avoiding detection by predators varies with landscape types, and habitat selection during times of risk is often based on optimizing the ability to avoid predator detection or heighten escape routes via areas of refuge (Taylor 1984). Prey animals choose complex habitats (i.e. the amount, density, and configuration of habitat structural elements) over spacious ones in response to risk, correlating with refuge availability, foraging opportunities, and the density of conspecifics (Crowder & Cooper 1982, Orth et al. 1984, Heck & Crowder 1991). The habitat preference of juvenile bluegill sunfish (*Lepomis macrochirus*) switched from highest prey abundance regardless of structural complexity during low risk, to high structural complexity during high risk (Gotceitas & Colgan, 1990). Grass shrimp (*Hippolyte californiensis*) preferred complex habitats in field studies, but in laboratory experiments, shrimp preferred whichever artificial habitat they first encountered (Tait & Hovel 2012). Similarly, the nutrient rich yet spacious algal patch use of juvenile black surfperch (*Embiotoca jacksoni*) was highly dependent on the relative risk of predators (Holbrook & Schmitt 1988). The above studies highlight how the effect of risk on a prey species' responses can be highly dependent on the context of the environment in which they occur.

Many studies have revealed seemingly contradictory systems where prey animals have

remained or even preferred areas where they are highly likely to encounter a predator (for a review, see Lima 1992). Often, these 'trade-offs' in animal safety are in relation to nutrient-rich foraging patches that overlap areas of predator presence (e.g. the habitat choices of desert baboons in Cowlshaw 1997). Yet, recent studies revealed systems where animals will choose high predator abundance yet nutrient-poor areas during times of high risk (Heithaus et al. 2008a, Wirsing et al. 2010). These seemingly detrimental choices in habitat use are governed by the species' optimal escape behaviour, coupled with the availability of 'escapable' habitat structures (Heithaus et al. 2008a, Wirsing et al. 2010). In addition to evaluating the likelihood of encountering a predator in an area, animals must also assess the probability that the encounter will be fatal (Lima 1992, Hugie & Dill 1994). Thus, growing evidence supports that the terrain of the landscape coupled with the prey-specific escape tactics and the predator-specific attack techniques are critical to the animal's evaluation of the latter.

In the marine realm specifically, tiger shark presence in Shark Bay, Australia affects bottlenose dolphin and dugong spatial patterns, which follows the general risk-allocation prediction that animals will alter their behaviour during times of risk. However, the 'edge microhabitats' (Heithaus et al. 2006) dugongs and dolphins chose during times of high risk coincided with high tiger shark abundance (Heithaus & Dill 2006, Wirsing et al. 2007, Heithaus et al. 2008b). These habitats are adjacent to deep water, which is required by both prey species to employ their primary escape tactic, namely fleeing and outmanoeuvring sharks (Heithaus et al. 2006, Heithaus et al. 2008b). While the risk of encountering tiger sharks increased in these areas (Heithaus et al. 2006), the probability of successfully escaping an encounter also increased (Wirsing et al. 2007), reducing the probability of fatal encounters overall. In this scenario, dolphins and dugongs prioritized habitat use during high risk by its

'escapability' characteristics, rather than a spatial patches' perceived risk of encountering a predator or resource richness. Other than Shark Bay, few systems have been identified where prey species select 'escapable' habitats that also coincide with high predator abundance but low predator mortality. Throughout the course of this study, it became evident that in certain spatial sectors, Cape fur seals of Geysers Rock displayed similar choices in habitat use by shifting their movement patterns to heterogeneous habitats. Thus, I was able to apply these relatively untested concepts to the predator-prey system of Geysers Rock.

## Overview

The examples above highlight the duplicity often seen between theory and empirical observations. Laboratory tests, while practical, can yield confounded results, thus predator-prey theoretical frameworks must ultimately be tested in empirical systems. This has proved to be especially difficult in marine environments with the exception of a handful of coastal areas that have predictable predator and prey occurrences essential for testing these concepts. Addressing this paucity of data, I examined the predator-prey system between white sharks and Cape fur seals at Geysers Rock within the theoretical frameworks of the risk-allocation hypothesis.

However, prey decision-making in risky situations may be affected by more than just temporal risk variables alone. Specifically, characteristics of the landscape, including the availability of habitat types and how those habitat types relate to the escape tactics of prey, seem to greatly influence a prey animal's evaluation of risk. By comparing the choices seals made in the featureless seascape of Seal Island, False Bay, to the choices seals make in the more complex habitat surrounding Geysers Rock, I hope to show how habitat complexity can influence habitat use by seals in a seasonally predator-abundant environment. Through this, I

am able to propose habitat-escape tactic relationships unidentified in previously studied white shark/pinniped systems.

### Study site:

This study was based at Geyser Rock of the Dyer Island system [-34.6875°S, 19.4152°E] which is located in the Western Cape of South Africa, 8km south of Kleinbaai harbour in Gansbaai (Figures 2-4). Dutch journals and ship records penned the area as “Branderbaai” or “Bay of Waves”, a tribute to its often stormy seas (Fourie 2002). The islands have little protection from either predominant winter westerly weather patterns or the predominant summer south-easterly winds. This exposure coupled with a dense maze of reefs made this area one of the more dangerous stretches along the “Cape of Storms” for early explorers, with 35 recorded shipwrecks in the area (Fourie 2002). In geological history, the islands were once joined to the mainland ca. 15,000 years ago forming a peninsula that wrapped around the Uilenkraal river estuary. The islands formed following the dramatic sea-level rise associated with the end of the Ice Age. The resultant bay is relatively shallow (majority of bay < 20m average depth), with a long reef stretching 3.5km from the mainland to the north-eastern corner of Dyer Island.

Geyser Rock is a small (20ha) rocky island lying approximately 200m south of Dyer Island. Penned as “The Island of Wild Animals” by the Portuguese, Geyser Rock supports an estimated 60,000 Cape fur seals throughout the year (Fourie 2002, Department of Environmental Affairs unpubl. data). Geyser Rock and Dyer Island are separated by a channel known as ‘Shark Alley’ (Johnson et al. 2009a), and the island system is characterized by a diversity of features, including reefs, ship wrecks, kelp (*Ecklonia maxima*), pinnacles, and relatively shallow (10–15m depth) waters. Notable features include ‘Shark Alley’, the

extensive ‘Geldsteen’ reefs, the rock pinnacle to the east called, ‘Wilfred’s Rock’, and the shallow stretch of rocky reefs/pinnacles/kelp to the west terminating at ‘The Drop Zone’ c. 800m from the main island (Figure 4).



Figure 2: The Western Cape province of South Africa showing the location of Geyser Rock in Gansbaai and Seal Island in False Bay.



Figure 3: A close up of Gansbaai showing the relative position of Kleinbaai harbour, Dyer Island and Geyser Rock.



Figure 4: An aerial perspective of the study site showing Dyer Island and Geyser Rock in addition to select prominent landmarks

The feature of 'Shark Alley', a 230m wide channel of relatively shallow (<6m) water immediately north of Geyser Rock, presented an ideal sector for fine scale analysis of spatial and behavioural adjustments in response to localized risk between age classes of seals (Figure 5). 'Shark Alley' is an area of high seal abundance of most age classes all year, and serves as a habitat where various behaviours are expressed, including; thermoregulation, socializing, swimming, and sub-adult mating (Johnson et al. 2009a, pers. obs). Additionally, 'Shark Alley' provides seals with better visibility and safety from sharks by virtue of being protected from wave action and being sufficiently shallow to allow for good visibility at all depths. Thus, it may provide young of year and juvenile seals with an area in which they may gain experience of white sharks without high predation risk. Prey animals are thought to learn about predators and predator avoidance via; direct predator encounters, observing a conspecific encounter a predator (Cook & Mineka 1990, Diaz-Uriarte 1999, Griffin & Evans 2003), or acquiring information via social learning (Johnsson & Sundström 2007, Brydges et al. 2008, Mazur & Seher 2008). Together these factors predisposed shark alley to a finer scale analysis of shark and seal interactions and consequently I present additional data for this sector within the main body of the results and discussion.



Figure 5: An aerial view of 'Shark Alley' between Dyer Island and Geyser Rock.

## Study species

### The Cape fur seal (*Arctocephalus pusillus pusillus*)

Cape fur seals are endemic to the South African/Namibian coastline, and the breeding colony of Geyser Rock is on the south-easterly boundary for the species (Kirkman 2010). Breeding colonies are largely restricted to areas with sufficient food availability, which is generally highest in the Benguela upwelling ecosystem where seals prey on a wide diversity of teleost fish and cephalopods (Rand 1959, David 1987, Lipinski & David 1990). A total population survey in 1993 revealed an estimate of 2 million individuals, showing recovery from prior indiscriminate seal culling in the 18 - 20<sup>th</sup> centuries that decimated many colonies (Kirkman et al. 2007, 2012).

Cape fur seals breed (pup and mate) from October–December, which is marked by the annual return of large bull seals who are absent for the rest of the year from the colonies (Rand 1967). During this time, seals become highly territorial both on land and nearby stretches of water (Bester 1990, Stewardson & Brett 2000, pers. obs). Bull seals experience elevated levels of androgens during breeding and their concurrent aggression triggers them to challenge anything that the bull perceives as a threat to its territory including humans, white sharks, conspecifics, or even seagulls (Stewardson & Brett 2000, Johnson 2009a, pers. obs). Because Seal Island and Geyser Rock are breeding colonies, all ages/sex class ranges of seals are represented at one point or another during the year (LaRoche et al. 2008, Kirkman et al. 2012). Adult females in particular must travel from the colony to forage offshore, returning to rest or to nurse their young (David 1987, LaRoche et al. 2008, pers. obs.). Besides traveling to and from offshore foraging grounds, seals enter the water for other purposes such as thermoregulation, and social play, or as a result of competition for space on the island (Rand 1967, Johnson et al. 2009a).

The prey of Cape fur seals is primarily schooling fish that seldom occur adjacent to seal colonies, thus seals must travel from their colonies to seek nutrient-rich patches. Seal movements to these areas are thought to be based on the diurnal movement patterns displayed by the fish-prey they seek (Gamel et al. 2005). De Vos (2010) showed that the majority of seal movements at Seal Island occurred at night, supporting this hypothesis. Geysers Rock seems to be no exception, because night-time trawling operations in the area record numerous seal encounters offshore (D. Chivell, pers. comm.). Thus, Cape fur seals are most exposed to risk when moving between these broad nutrient-rich patches and their island colony where white sharks focus their predatory efforts.

### **The white shark (*Carcharodon carcharias*)**

White sharks are pelagic apex predators found in all oceans except the extreme Arctic and Antarctic waters (Compagno et al. 1997). Despite this vast distribution, many white sharks display remarkable levels of site fidelity, and remain resident in small areas for many months with predictable seasonal arrivals and departure (Johnson & Kock 2006). White sharks are classified as vulnerable by the IUCN – Red data list and have been protected in South African waters since 1991 (Johnson & Kock 2006). Accurate estimates of white shark population sizes in South Africa are currently unknown. However, the Gansbaai-based MARK population estimates derived from a five-year white shark dorsal fin ID database gave a range of 808–1008 individuals (Towner et al. 2013), but this does not account for the known and unknown individuals that have been removed from the population via ‘bather protection’ nets in KwaZulu-Natal and fishing in international waters. The 4-year dorsal fin identification campaign in California, USA, a hot-spot for the species in the Eastern Pacific, revealed an estimate of 219 individuals (Chapple et al. 2011). Both studies suggest that population numbers may be smaller than previous estimates on which the IUCN classification is based.

White sharks consume a broad spectrum of prey species that vary with the age/size of the shark (Compagno et al. 1997). Juveniles feed primarily on other fish species with adults switching to marine mammals in coastal waters and cephalopods in deeper waters (Cliff et al. 1989, Compagno 2001, Smale & Cliff 2012). At Geyser Rock, white sharks are known to regularly predate on Cape fur seals during the winter months (Johnson et al. 2009a). One documented case of feeding on other marine mammals has been recorded in the area (Indo-Pacific humpback dolphin (*Sousa chinensis*), Weisel et al. 2010), and various seabirds (Marks et al. 1997, Johnson et al. 2006). Similar to the pattern established in False Bay (Kock et al. 2013), white sharks in Gansbaai exhibit a seasonal shift in activity patterns from Geyser Rock during the austral winter months to the shallower inshore waters of “Joubert's Dam” during the summer months (Towner 2012). The cause of this seasonal shift is unclear.

### **Summary of previous white shark/pinniped research**

Many marine predator-prey interactions fall outside the realm of human observation. This may explain why few marine predator-prey systems have been accurately quantified into 'landscapes of fear' - a landscape prey species navigate shaped by the variable risk of encountering predators (Laundre et al. 2001). However, white shark predatory effort is a notable exception as interaction patches are located within several hundred meters of seal colonies during seasonal peaks in foraging (Klimley et al. 2001, LaRoche et al. 2008), and many white shark strikes on pinnipeds occur at the surface (Compagno 2001), bringing the interaction into the human observer's range. Additionally, the occurrence of white shark predation events on prey is largely determined by environmental conditions (i.e. water clarity, ocean depth, tidal height, ambient light, current direction/speed) (Hammerschlag et al. 2006). White sharks take advantage of low light levels that do not penetrate the water column deep enough to reveal their position, yet do highlight prey at the surface (Strong et al. 1996),

which explains the morning pulses in predation observed at both the South Farallon Islands (Pyle et al. 1996) and Seal Island, False Bay (Martin et al. 2005, LaRoche et al. 2008, Martin & Hammerschlag 2012). All these elements combine to create predictable interaction patches, thus making white shark/seal predator-prey systems some of the best documented marine predator-prey systems in the world.

These interaction patches include the Cape fur seal colony of Seal Island, False Bay, South Africa (Martin et al. 2005, Hammerschlag et al. 2006, Johnson & Kock 2006, Martin et al. 2009, De Vos & O'Riain 2010, Fallows et al. 2012, Hammerschlag et al. 2012, Kock et al. 2013); the Cape fur seal colony of Seal Island, Mossel Bay, South Africa (Johnson et al. 2009b); the Australian fur seal (*Arctocephalus pusillus doriferus*) colony of Seal Rocks, Australia (Shaughnessy 2006); the New Zealand fur seal (*Arctocephalus forsteri*) colony of Kangaroo Island, Australia (Shaughnessy et al. 1994); the New Zealand fur seal colony of Neptune Islands, Australia (Shaughnessy & McKeown 2002); the Northern elephant seal (*Mirounga angustirostris*) colony of the Farallones Islands, USA (Ainley et al. 1981, Klimley et al. 1987, Klimley et al. 1992, Klimley 1994, Anderson et al. 1996, Klimley et al. 1996, Strong 1996); the Northern elephant seal colony of the Ano Nuevo Islands, USA (Le Boeuf & Crocker 1996, Klimley et al. 2001), the harbour seal (*Phoca vitulina*) colony of Sable island, Nova Scotia (Lucas & Stobo 2000); the growing harbour seal colonies along the Massachusetts sound (Skomal et al. 2012); and the multi-species pinniped colonies of Isla de Guadalupe, Mexico (Domeier 2009, Domeier et al. 2012) (Figure 6).



*Figure 6: A world distribution of areas (signified by fur seals) where white sharks are frequently documented preying on pinnipeds.*

The Cape fur seal colony of Geyser Rock is a commercially well-known white shark hotspot, yet until this study, white shark predatory effort around Geyser Rock had not been fully assessed. Geyser Rock is a notably difficult area for boating, because the exposed bay coupled with shallow reef systems adjacent to the island often result in dangerous conditions within the areas that white shark predations are known to occur (Ferreira & Ferreira 1996) (Figure 7). Only one communication detailing white shark and seal interactions at Geyser Rock exists, but these observations were limited to the sheltered area of ‘Shark Alley’ and were made while chumming was in progress (Johnson et al. 2009a), which may affect white shark and Cape fur seal natural behaviour. Additionally, predation events at Geyser Rock do not seem to occur in predictable spatiotemporal patterns as they do at Seal Island, False Bay, nor at the same frequency. Confirming this, Johnson et al. (2009a) observed a total of 14 white shark predations on seals after 135 days (4–6 hours/day) of effort only in Shark Alley, whereas, at Seal Island, more than 40 predations can be observed in a single morning (Hammerschlag et al. 2006). This combination of challenging boating conditions and less predictability may explain the lack of research on white sharks and seals at Geyser Rock in

what is otherwise a data-rich field.



*Figure 7: Aerial views of the Geysers Rock system taken during a 4.5m southwest swell, a regular sea condition during winter. Areas in white are breaking reefs (dangerous boating areas). Sharks signify areas where surface predation events have been previously documented by commercial operators.*

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## Aims and structure of dissertation

The aim of this dissertation was to establish the “landscape of fear” imposed by white sharks on Cape fur seals and to test whether seals adjust their temporal and spatial movement patterns in accordance with predation risk. More specifically I ask the following questions:

1. Does white shark presence and predation at Geyser Rock vary seasonally, spatially and temporally?
2. Do Cape fur seals adjust their movement patterns and behaviour in accordance with this risk?
3. Will Cape fur seals utilize areas of heterogeneous habitat (i.e. more refugia) when commuting to and from the colony during high risk?

I compare my results at Geyser Rock with previous studies of white shark/Cape fur seal interactions at Seal Island in False Bay in particular. In addition, I explore the generalities of the findings in the recent study by De Vos (2010) that revealed marked spatiotemporal variation in predation risk imposed by white sharks on Cape fur seals at Seal Island, False Bay, and showed that seals adjusted their movement patterns and behaviour in response to this risk. Specifically, I collected data that would allow me to test the following predictions based on the published research at Seal Island on white shark presence and predation (Martin et al. 2005, Hammerschlag et al. 2006, LaRoche et al. 2008, Martin et al. 2009, Fallowes et al. 2012, Martin & Hammerschlag 2012) and Cape fur seal spatiotemporal movement patterns (De Vos 2010) at Seal Island:

- White sharks aggregate at Geyser Rock during the austral winter season to target young of the year seals that are making their first exploratory forays into open water;
- White shark predation events will peak in frequency in the first two hours after sunrise when surface swimming seals have readily detectable silhouettes and low light

penetration provides concealment for sharks approaching from depth.

- White shark presence and the number of predation events will vary with relative seal abundance in open water habitat.
- Most seal movement will be to the South of Geysers Rock in the direction of the open sea (i.e. away from Dyer Island and the coastline) and their preferred feeding grounds.
- Seals will avoid high risk habitats (i.e. deep open water) during winter months (high risk).
- The median group size of seals leaving the island will be higher in the low risk time of year than the high risk, and leaving groups will be larger than returning groups.

## Methods

The Geysers Rock island system and surrounding waters were divided into six spatial sectors (Figure 8) each covering roughly  $600 \times 1000\text{m}$  area. The sectors were selected to ensure that all the major habitat types were included (i.e., reef, kelp, shallow open water and deep open water) in addition to compass bearings including north, northeast, northwest, southeast, southwest and south).



*Figure 8: The spatial sectors used to subdivide the study area into approximately equal sized sample areas, centred on Geysers Rock (on the dividing line between sectors 3 and 6).*

## White shark encounters and predations at Geyser Rock

During dedicated seal movement surveys (methods described below), I recorded GPS points of white shark predations on seals (sensu Martin 2005), that were categorized as follows: 1) white shark breach nearby surface swimming seals, 2) a sudden change in the travel behaviour of the seals with evidence of shark presence (i.e. dorsal and/or caudal fins disturb the water surface), or 3) the appearance of large surface patches of blood and seal entrails usually accompanied by seabirds. Once a predation had been detected, factors such as; time of day, age category of seal ([1] young of the year, [2] juvenile, [3] subadult/adult cows, [4] subadult/adult males), group size, direction of movement of the seal(s) (leaving or returning to the island), and whether the attack was successful or not were also recorded. Also, I recorded white shark encounters, which was when I observed a shark near the research vessel that was not associated with any predation activity.

## Seasonality of white shark presence at Geyser Rock: SPOT data

A collaborative satellite tagging project between the USA-based non-profit Ocearch and South African white shark researchers began in April 2012. A total of 35 white sharks were outfitted with Wildlife Computers Smart Position-Only Tag (SPOT) devices. SPOTs were outfitted to both sexes and most age classes of white sharks (excluding young-of-year) from 4 April–29 May 2012. The majority of sharks were tagged in Gansbaai in the month of April, as research permit controversies abated tagging efforts for the majority of May. White sharks were tagged at seven locations along the coastline of South Africa, including False Bay, Romaansbaai, Gansbaai, Struisbaai, De Hoop, Mossel Bay and Port Elizabeth (Figure 9). Baited barb-less circular hooks were used to catch white sharks. The hooked shark then had buoys clipped to the hook to keep the shark at the surface, and it was then led to the main

research vessel where sharks were directed onto a hydraulic platform to be lifted from the water. Shark gills were irrigated with two large hoses of oxygenated ocean water, and sharks received antibiotics and electrolyte injections to enhance recovery time. One of two types of SPOTs were then attached to the dorsal fins, smaller (2-year SPOT2) tags for juvenile (<3.0m) sharks and larger (5-year SPOT5) tags for adult (>3.0m) sharks.



*Figure 9: The seven tagging areas for the SPOT project along the South African coast.*

Data from the SPOTs were received via the ARGOS system, downloaded monthly into .kmz file types and distributed to the South African white shark researchers to be used for research projects accepted in January 2012. This aspect of my dissertation (establishing the seasonality of white shark presence at Geyser Rock) was an accepted project, so I was included in the monthly data distribution. I mapped the .kmz ARGOS data files using Google Earth and filtered tracks for surface signals and deleted predicted track lines. I then drew a 3km wide polygon around Geyser Rock and recorded the signals within the polygon as shark presence at the seal colony.

## Cape fur seal habitat use at Geyser Rock

I followed the same seal movement survey methods of De Vos (2010), increasing the number of sectors to six (from four) due to greater habitat diversity at Geyser Rock compared to Seal Island. Observations were restricted to daylight hours and days with: no fog, average swell size  $<2.5\text{m}$ , and average wind speed  $<15$  knots. I performed 20-minute observation sessions while stationary on an 8.5m semi-rigid inflatable boat ('Calypso') in each of the six designated sectors around the island (Figure 8) from 1 January–15 November 2012. The choice of sector on a given day was randomized to prevent any sampling bias. Once I had completed the 20-minute observation session, I would then move to a new sector until all six sectors had been sampled once. If weather conditions permitted, I would continue sampling using the same randomised sector selection approach but for a maximum of four hours (two full 6-sector rotations). This method ensured that I standardised my effort equally across all sectors within each sampling day and across the entire study. By limiting sampling to a maximum of four hours per day, I avoided over-sampling on particular days. I attempted to remain at centrally located points within each sector using a boat-based GPS and by adjusting my position using the boats engines.

During each observation session, I recorded the following variables:

- 1) **Shark predation event:** (described above)
- 2) **Shark encounter:** (described above)
- 3) **Seal presence and activity:** the number and size category of seals in each group ( $n \leq 1$  counted as a group) and the direction of travel (to or from the island) were recorded. Geyser Rock is a popular area for commercial vessels and the seals appear to be habituated to the close presence of a boat. To minimize the potential impacts of boat presence, all seal follows were from  $>30\text{m}$  and aborted if seals

responded to the presence of the boat (i.e. swam towards boat).

- 4) **Water visibility:** vertical water visibility was determined on each day that environmental conditions allowed for behavioural observations. Visibility was determined for each sector across all time intervals using a standard secchi disk.

### Seal and shark activity within 'Shark Alley' – a fine scale assessment of habitat use and risk at Geyser Rock

To further explore how seal behaviour and space use is affected by shark presence; I sampled seal presence within 'Shark Alley', the sector at Geyser Rock with the highest year-round density of seals. Two habitat types were sampled by driving the boat at a 'no-wake' speed along pre-determined parallel GPS transects (Figure 10), one in deep (4-6m) and one in shallow (<1m depth) open water habitats. Data were recorded on a GoPro HD-Hero digital camera (set to f4: wide angle HD video) that was mounted on a 5m aluminium mast attached perpendicularly to the boat deck. The GoPro was always pointed in the direction of Geyser Rock and the transect was driven from right to left. Video data were subsequently downloaded and viewed in QuickTime to record the total number of seals and sharks along each transect and the age classes of seals present.



*Figure 10: The deep and shallow open water transects sampled within Shark Alley; -34.687 = deep transect and -34.688 = shallow transect*

## Mapping the major habitat types around Geyser Rock

The habitat map of the Geyser Rock complex was established using a combination of aerial and satellite imagery. First, I collected Google Maps information of the area in 2004, 2006 and 2010 that together allowed for reliable mapping of the four broad scale habitat types identified above. I then used aerial photos taken during a fixed-wing flight at 1000m elevation using a 50–200mm lens on a Canon 550D. These photographs were taken on a low-swell day with good water visibility to allow for fine-scale mapping of the different habitat types. Aerial photos taken during a large swell day were used to confirm the presence of shallow (5-10m) reef areas via reverse topography. The final habitat maps were subjected to ground-truthing using direct observations in addition to a boat mounted GPS on calm days with good visibility.

Final images were overlaid in Google Earth satellite imagery and polygon layers were drawn to denote each of the four broad scale habitat types identified from the aerial photographs including:

1. Island – rocky substrate that remain above sea level during spring high tide
2. Reef – rocky substrate characterized by strong wave action with water depth varying between 5 and 10m
3. Kelp – dense patches of kelp (*Ecklonia maxima*) in water varying in depth between 1 and 10m.
4. Open water – all other habitat including deep ( $\geq 10\text{m}$ ) and shallow water with no wave action and a mixture of sand, boulder and rocky substrates

I then applied a grid with a cell size of  $150 \times 150\text{m}$  over the study area so that each spatial sector was comprised of 100 equal sized cells. Each grid cell was assigned a habitat based on

which of the four types comprised more than 50% of that particular grid cell.

## Data analyses

Exploratory data analyses highlighted limitations in the data set for parametric statistical analyses. Thus, I used non-parametric statistical tests for most analyses. I used the non-parametric Wilcoxon rank sum tests with continuity correction for two-factor comparisons of median values (i.e. one factor between both seasons) (Wilcoxon et al. 1970). Likewise, to test multiple null hypotheses of constant medians in more than two non-normal populations, I used the Kruskal-Wallis test (Kruskal & Wallis 1952). I created predicted value charts using the observed data and then applied chi-squared comparison of proportions tests or tests of independence to determine significant differences between my observed and the predicted values (Townend 2002). The expected values were calculated under the null hypothesis of uniform distributions over time or space. For temporal analyses of seal movement at the colony, I used the same uneven time intervals [7:00-8:29, 8:30-9:59, 10:00-14:29, 14:30-16:59, 17:00-19:30] following De Vos (2012) to enable a direct comparison with the data collected at Seal Island. Observations were converted to an hourly rate to allow for comparisons with published results for Seal Island and to allow for comparisons across time intervals of differing duration sensu De Vos (2010). Individual sharks surfaced multiple times near Geysers Rock on the same day, so SPOT tag data were filtered to provide the single strongest signal of the day for each individual. I then used these data to calculate a monthly average of unique tags, corresponding to individual sharks, detected within the 3km zone around the island. Secchi disc data were averaged across all sectors and all sampling days to provide an average for each time interval around Geysers Rock

## Results

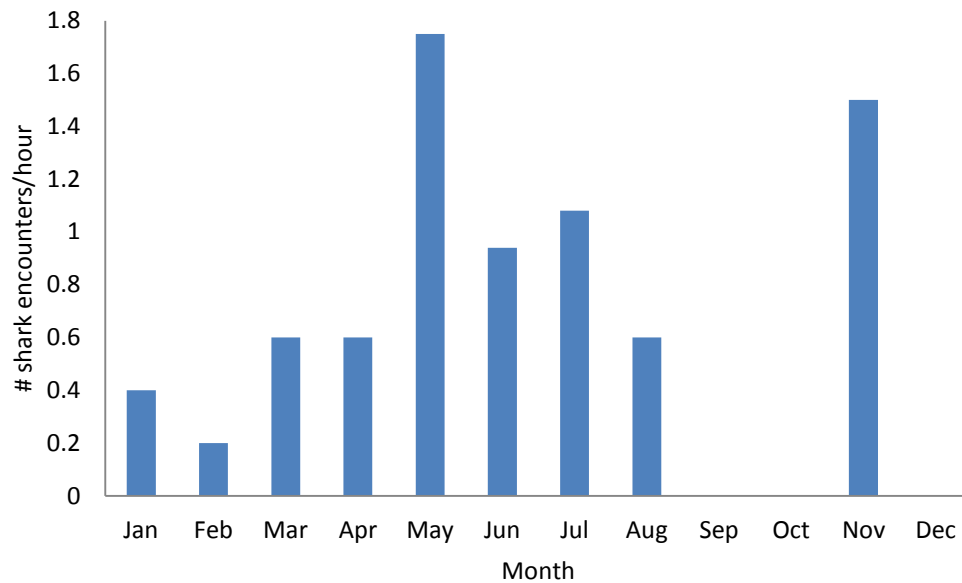
### The 'landscape of fear' at Geyser Rock

I was able to conduct seal movement surveys on 33 out of 319 days resulting in a total of 62.3 hours observation time (Table 1). These were evenly distributed across sectors but differed with respect to season, month and time intervals as indicated below.

*Table 1: The number of observation hours collected at Geyser Rock over the 2012 study period split by month, sector, daily time intervals, and season.*

Effort by month		Effort by sector		Effort by time intervals		Effort by season	
Month	Hours	Sector	Hours	Time intervals	Hours	Season	Hours
Jan	5	1	9.7	7:00 - 8:29	4.7	Summer	25.6
Feb	15	2	9.3	8:30 - 9:59	11.3	Winter	36
Mar	6.7	3	11	10:00 - 14:29	33.3		
Apr	9	4	10	14:30 - 16:59	8.7		
May	4	5	8.3	17:00 - 19:30	3.3		
Jun	6.3	6	13				
Jul	8.3						
Aug	1.7						
Sep	3						
Oct	2						
Nov	0.67						

In total, 39 white shark encounters were recorded across all sectors during the study period, with a peak in July (nine encounters or 23.1% of total), and zero presence in September, October and December (Figure 11). The hourly median number of white shark encounters between the winter months of March and August was 0.8 (n=33, range 1–9) and 0.1 between summer months of September and February (n=6, range 0–3); this difference was significant (Wilcoxon W=5, p=0.04).



*Figure 11: The number of white shark encounters per hour of observation for each month at Geysers Rock in 2012.*

### Smart position-only tag (SPOT) data

A total of 172 SPOT signals were recorded at Geysers Rock from May – December 2012 from 25 individual sharks. The number of signals peaked in August ( $n=43$ ) with only one signal recorded in December (Figure 12-13). The median number of SPOT signals was 40.5 from March – August ( $n=161$ , IQR=39-41.5), and 2.5 from September – December ( $n=11$ , IQR=1.7-3.5); this difference was significant (Wilcoxon  $W=16$ ,  $p=0.02$ ). April was excluded from the analysis as the majority of tags were not deployed until the end of the month.

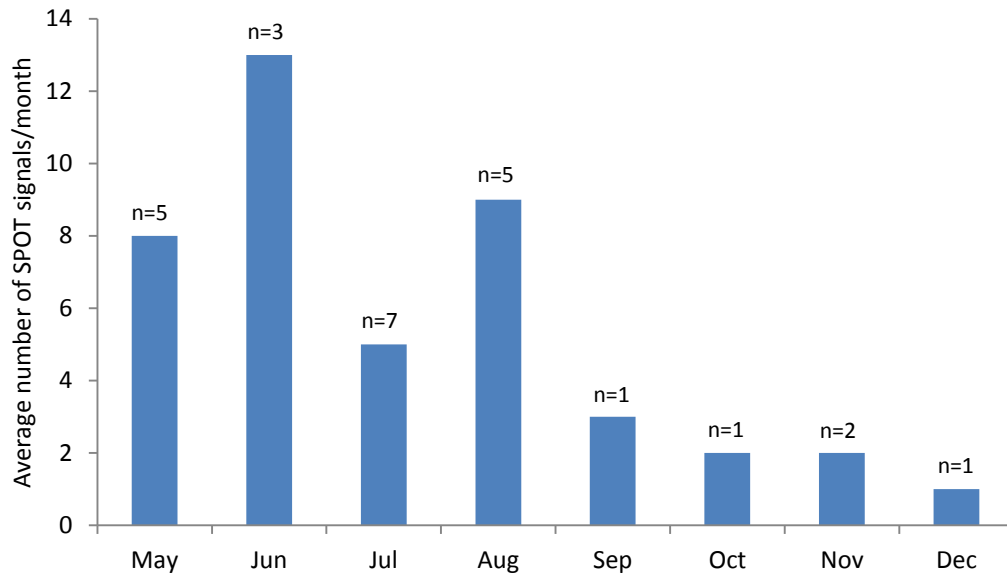


Figure 12: The average number of SPOT signals recorded per month (May to December 2012) for the 25 tagged white sharks that were detected within 3km of Geyser Rock. The n-value indicates the number of unique sharks that contributed SPOT transmissions during each month.



Figure 13: SPOT signals from tagged white sharks around Geyser Rock from May – August (left) and September – December (right) 2012.

## Predation events

I observed seven predations on seals during 62.3 hours of observations, which is an average of 0.1/hour. The rate of predation events was similar in winter and summer (Figure 14) and occurred in all sectors but sector two (Figure 15).

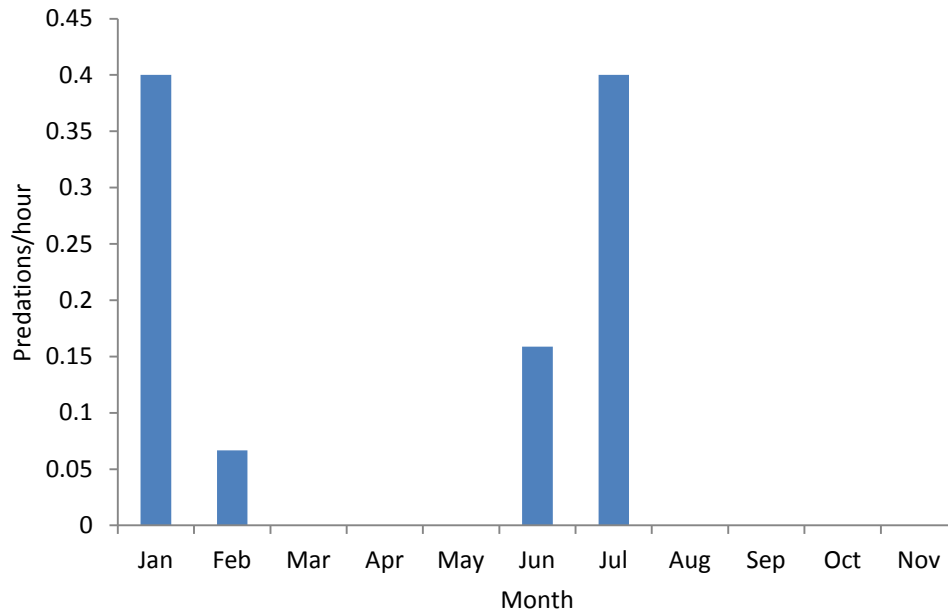


Figure 14: White shark predation rates around Geyser Rock over the eleven month study period in 2012.

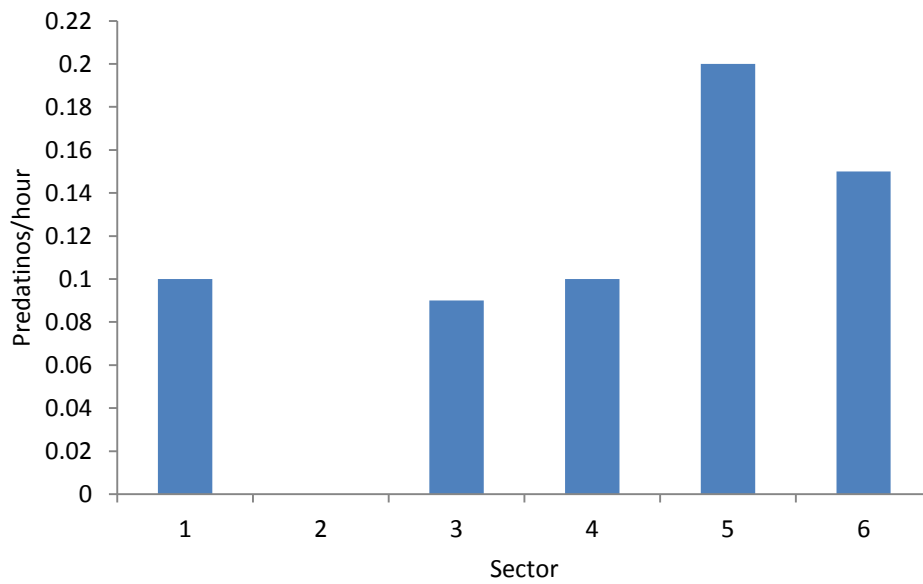


Figure 15: White shark predation events for each sector around Geyser Rock across all months in 2012.

## Cape fur seal habitat use at Geyser Rock

### Risk effects on seal group size

The median group size of all seal groups leaving and returning to the island was four in winter (n=106, range=1-25) and five in summer (n=100, range=1-30); this difference was not significant (Wilcoxon W = 4869.5, p=0.3). The median group size of departing seals in all months was seven (n=133, range = 1-30) compared to two (n=49, range 1-10) for returning groups; this difference was significant (Wilcoxon W = 1057, p< 0.001) (Figure 16).

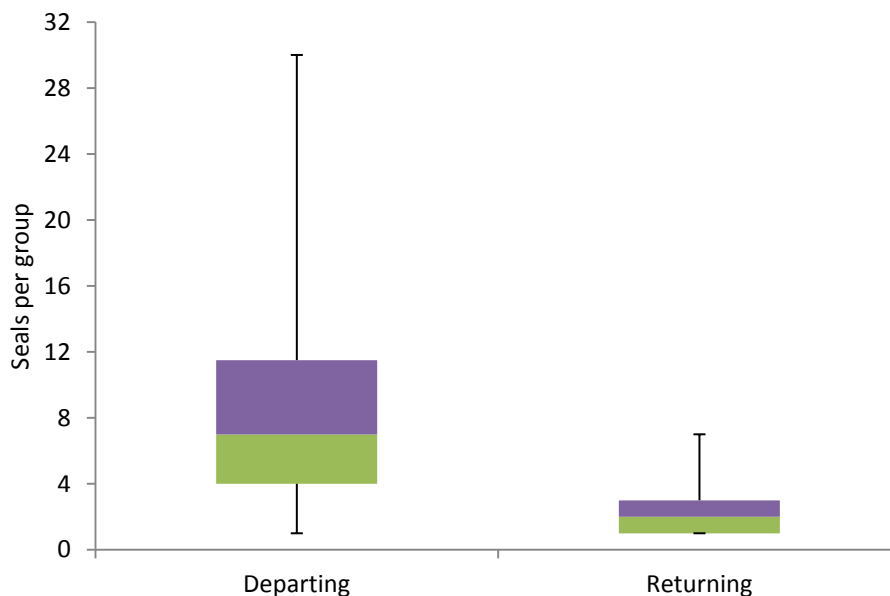


Figure 16: A box and whisker plot of median group size for departing and returning Cape fur seals at Geyser Rock. Green = 1<sup>st</sup> quartile, boundary between colours = median, and purple = 3<sup>rd</sup> quartile.

### Spatial patterns of departing and returning seals

Sectors six, 'Shark Alley' was excluded from this analysis as movement to or from the foraging grounds from this sector was not possible without traversing another sector. In summer, the majority of seal groups (54%) departed from and returned to the island from

sector three. Observed spatial use of departing seal groups differed significantly between seasons (Kruskal-Wallis chi-squared = 11.76,  $df = 3$ ,  $p = 0.008$ ) (Figure 17).

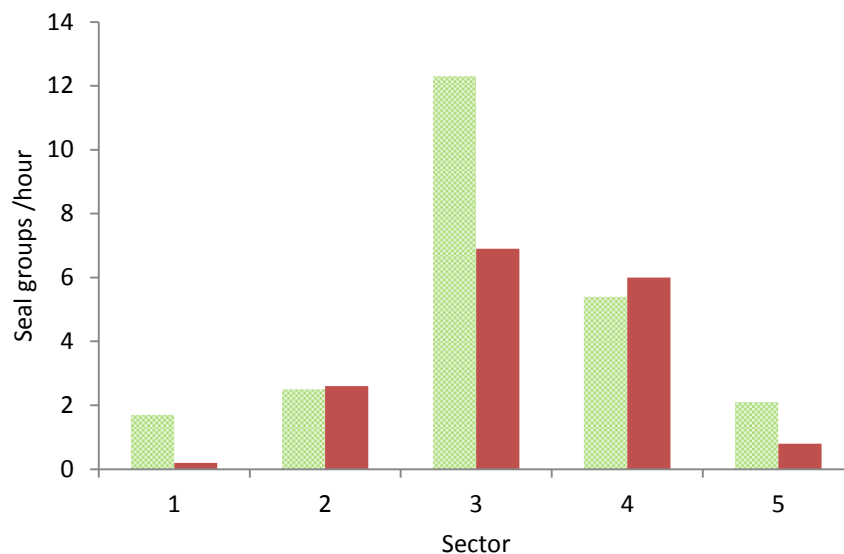


Figure 17: The number of departing seal groups for each spatial sector of Geysers Rock in 2012, with Green = summer and Red = winter.

### Habitat use within 'Shark Alley'

The proportion of seals in the deep transect was substantially higher in summer (82%) than in winter (18%), whereas the proportions were very similar across season in the shallow transect (Figure 18). The median number of seals observed along the deep transect during winter was zero ( $n = 84$ , range = 0-18) and 4.5 ( $n = 72$ , range = 0-42) in summer; this result was significantly different (Wilcoxon rank sum test with continuity correction  $W = 286$ ,  $p$ -value = 0.03).

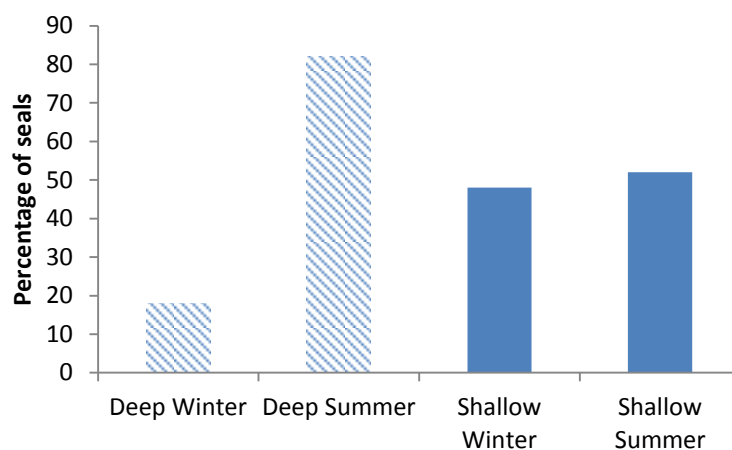
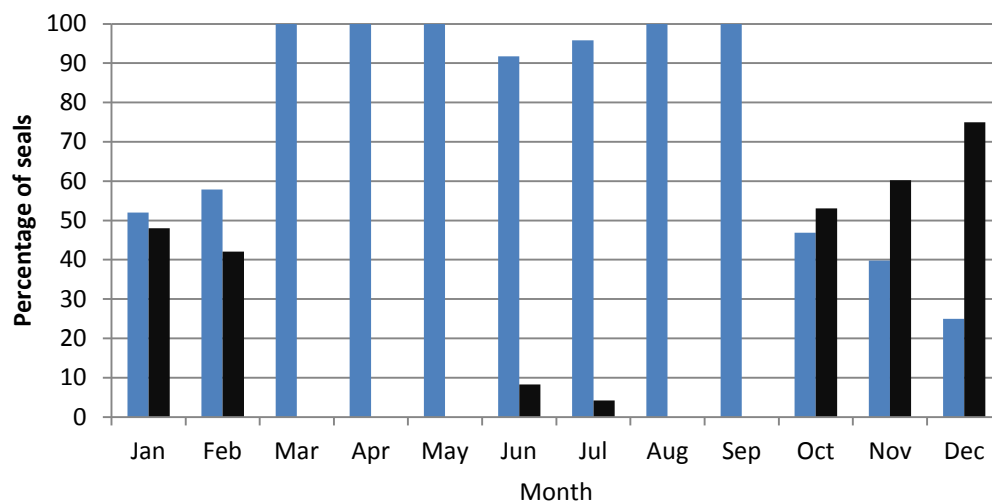


Figure 18: The percentage of all Cape fur seals observed within the shallow (solid blue) and deep (dashed) waters in Shark Alley in summer and winter.

The majority (72.8%) of seals observed in the deep transect during winter were ‘young-of-year’ (Figure 19), with fewer juveniles/subadults and few adults. This result was significantly different (Chi-square test of independence,  $df=2$ ,  $p<0.001$ ) (Table 2).

*Table 2: Observed proportions of seals in the deep transect of Shark Alley during winter compared to the expected proportions created by the null hypothesis that all seal age classes have equal chance of being observed in the deep transect.*

Age class of seal	Obs (Exp)	Test statistic	df	p
YOY	72.9 (33.3)	78.95	2	<0.001
JUV	25.4 (33.3)			
ADU	1.7 (33.3)			



*Figure 19: The percentage of young-of-year/juveniles (blue) to adults/ bulls (black) present in the deep water transect of Shark Alley in all months of 2012.*

‘Young-of-year’ and juvenile seal presence within the deep transect was highest from March to September (i.e., throughout winter) and lowest in October to November (i.e. into summer). By contrast adult seals were rarely detected in the deep transect through the winter and exhibited a marked proportional increase from October to February (Figure 19).

## Temporal variation in movement through danger zone

There was marked variation in seal movement between time intervals in both winter ( $\chi^2=41.07$ ,  $df=4$ ,  $p<0.001$ ) and summer ( $\chi^2=4.65$ ,  $df=4$ ,  $p<0.001$ ). In winter, seal movement increased from expected values during the 7:00-8:29 time period and decreased during the 8:30-9:59 time period expected values, which were significant changes ( $\chi^2=30.73$ ,  $df=4$ ,  $p<0.001$ ) (Table 3). The number of seal groups per hour increased during the 7:00-8:29 time interval from 3sg/h in summer to 5.4sg/h in winter (Figure 20).

Table 3: Chi-squared table of temporal variation of Cape fur seal movement across spatial sectors during winter at Geysers Rock. The expected values were calculated under the null hypothesis time of movement was uniform through the day, and take account of the uneven time periods.

Time interval	Winter Obs (Exp)	Summer Obs (Exp)	Test statistic	p
7:00-8:29	19 (10.8)	1 (9.16)	30.73	<0.001
8:30-9:59	13 (23.8)	31 (20.2)		
10:00-14:29	56 (53.7)	43 (45.3)		
14:30-16:59	7 (4.3)	1 (3.7)		
17:00-19:29	2 (4.3)	6 (3.7)		

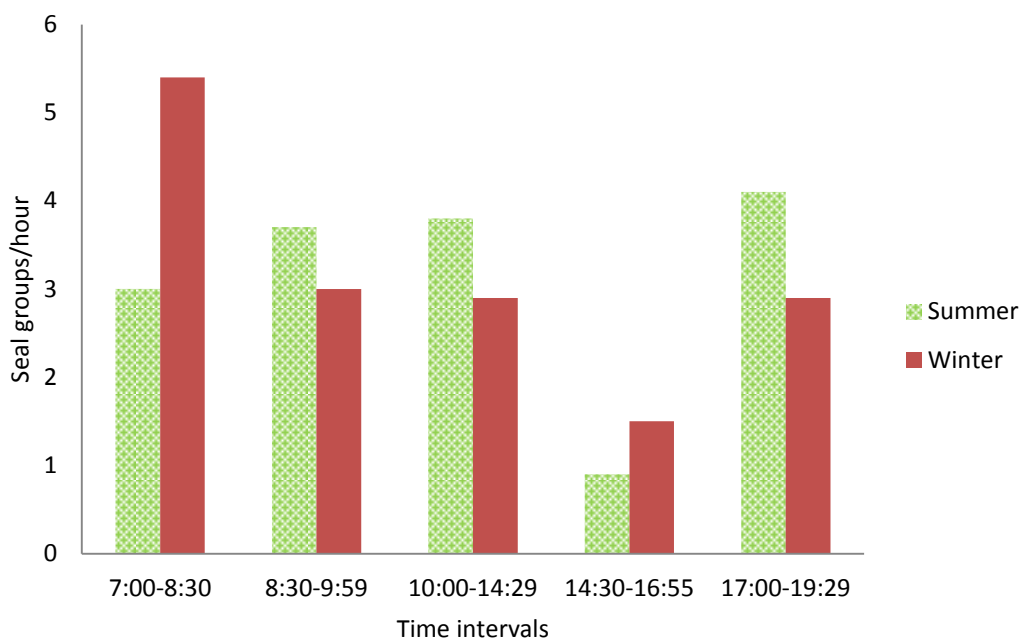


Figure 20: Cape fur seal groups/hour of observation time commuting to and from Geysers Rock in summer (green) and winter (red).

## The habitat types and visibility around Geyser Rock

The most abundant habitat type within the study area was ‘open water’ (77.8%) with ‘kelp’ (11.78%) ‘reef’ (6.02%) and ‘island’ (4.4%) together comprising the remaining 22.2%. Sectors five and six had the largest proportions of kelp and reef and kelp and island respectively (Figure 21). Sector two was the most homogenous comprised of 99% open water and 1% reef, whereas all other sectors had at least three of the four habitat types present (Table 4).

Table 4: The distribution of habitat types per sector around Geyser Rock.

Sector	Habitat Type			
	Kelp	Rock	Reef	Open Water
1	4%	2%	3%	91%
2	0%	0%	1%	99%
3	4%	2%	7%	87%
4	9%	0%	8%	83%
5	21%	0%	17%	62%
6	13%	22.5%	0%	45%

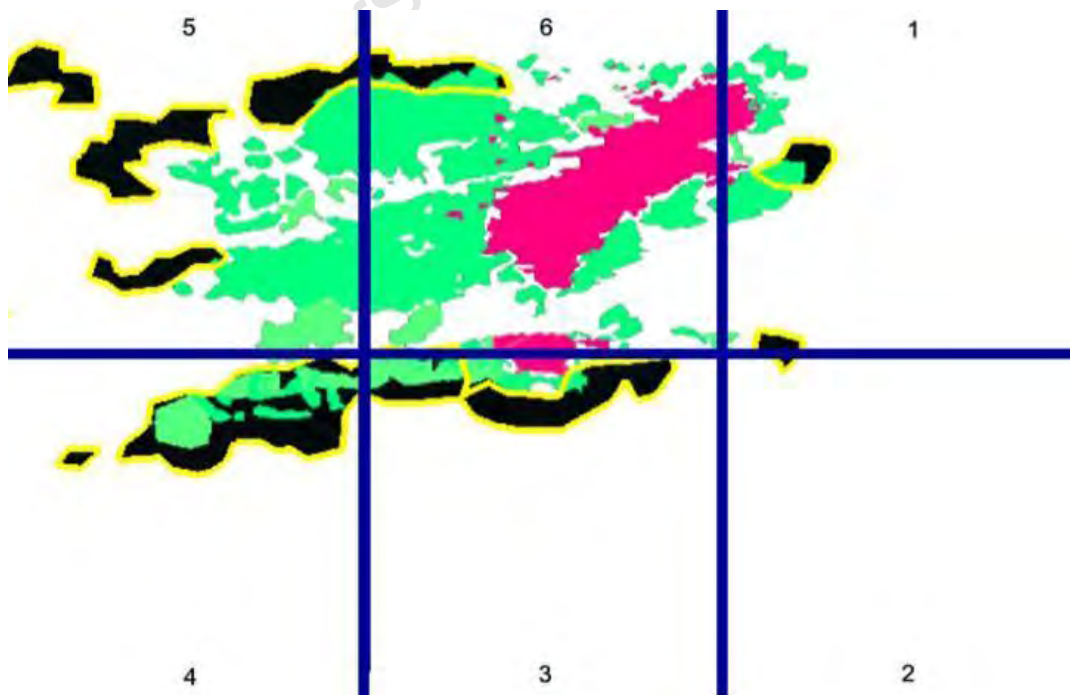
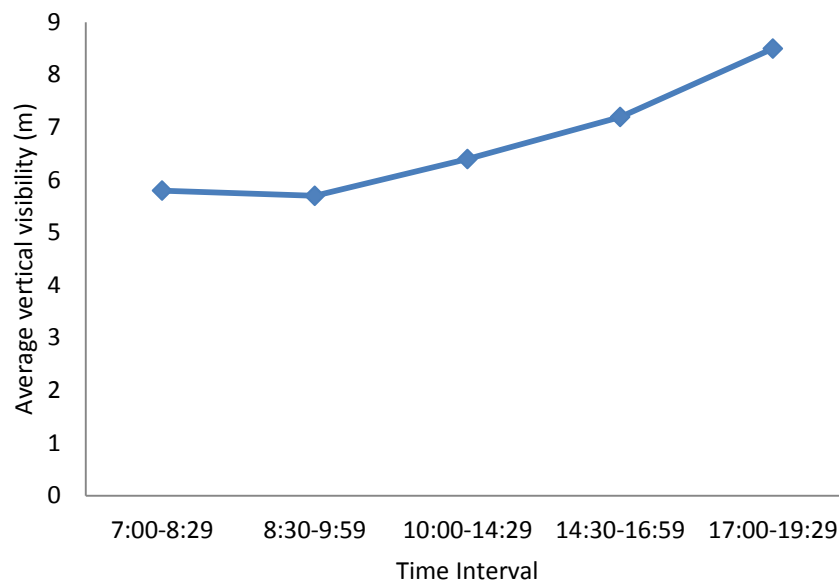


Figure 21: The habitat map for each of the six spatial sectors around Geyser Rock; Pink = rock, Green = kelp, Yellow outline with Black centre = reef, White = open water.

## Secchi disk measurements over time

Visibility average across all sectors increased throughout the day, with the lowest mean level (5.7m) occurring at 8:30 – 9:59 (Figure 22). Average visibility reached a maximum of 8.5m by the 17:00 – 19:29 time interval.



*Figure 22: Average vertical visibility across all sectors and all sampling days at different times of the day.*

## Discussion

### A comparison of seasonal patterns between Seal Island & Geyser Rock

Similar to results published for Seal Island, False Bay (Martin et al. 2005, Hammerschlag et al. 2006, LaRoche et al. 2008, De Vos 2010, Fallows et al. 2012, Kock et al. 2013), white sharks aggregated around the Cape fur seal rookery of Geyser rock during winter (Figure 13). At Seal Island, this aggregation is characterised by a clear spatio-temporal pattern of seal predation, with frequent (1.24/hr, Kock in prep) events during winter on the southern side of the island at sunrise (Hammerschlag et al. 2006). By contrast, I rarely observed predation events (0.1/hr) and thus it was not possible to determine any clear spatial or temporal patterns of predation around Geyser Rock. While this confounded my original aim of quantifying seal movement patterns and behaviour in response to specific spatiotemporal patterns of predation at Geyser Rock (sensu De Vos 2010), it does open an interesting debate as to what factor(s) drive these differences, especially given that the same white sharks visit both rookeries, but the behaviour of sharks in relation to seals differs markedly between the two systems. Similar to Seal Island, SPOT data revealed very clear temporal patterns in white shark presence at Geyser Rock, with significantly higher average levels of detection during winter than summer (Figures 12-13). Thus, the risk of predation would appear to peak during the winter months when white shark presence was highest.

### Spatial patterns of habitat use by seals within the context of predation risk

Seals at Seal Island avoided deep open water near the island during the high predation risk season of winter (De Vos 2010). Similarly, seals within 'Shark Alley' at Geyser Rock were significantly less likely to be in the deep transect during winter (high risk) compared to summer. Importantly, this pattern was age-class dependent, with adult seals being

significantly less likely to be present in the deep transect during winter relative to summer (Figure 19). This was not a function of reduced adults being present in ‘Shark Alley’ during winter as the median number of adult seals within ‘Shark Alley’ was similar between seasons (Wilcoxon rank sum test;  $W = 376.5$ ,  $p\text{-value} = 0.9$ ), suggesting that adults actively avoid the dangerous open water habitat during the high risk winter months. Thus, the presence of shark-naïve seals frequenting habitat that suits white shark predatory tactics may be driving the marked seasonal presence of sharks at Geysers Rock as it does at Seal Island. ‘Shark Alley’ may provide an ideal study area to test hypotheses on how young animals learn about predators within a marine environment, and underwater observational equipment, which is becoming more affordable and accessible, may soon enable this work to progress.

Important differences between Geysers Rock and Seal Island are both the spatial distribution of seal movement to and from the respective colonies and the spatial distribution of predation events. At Seal Island, seals leave almost exclusively from the south west sector, in the direction of their foraging grounds. Not surprisingly, the majority of predation events were recorded in this sector (Martin et al. 2005, Hammerschlag et al. 2006, LaRoche et al. 2008, De Vos & O’Riain 2010, Fallows et al. 2012) suggesting that white sharks match areas of high seal concentration (De Vos 2010). By comparison, seal movement at Geysers Rock is more spatially dispersed in winter than in summer (Figure 17) when sharks are largely absent. Although my sample size of predation events was low, they did not occur with any spatial predictability (Figure 15) and anecdotal data from commercial operators support this. Operators record attempted predation events on decoys in all sectors of the island, with the majority occurring in sectors 3 and 5. While commercial boat observations were not standardised for effort it is expected that operators will over-disperse in areas where they are most likely to be rewarded with an attempted predation event, given they wish to reward

paying clientele with such events.

In summer, seals primarily commuted to and from Geysers Rock in sector three, and in the absence of predators, this would appear to be a simple ergonomic decision as this sector leads in the direction of the primary foraging areas. Additionally, I detected a “dive-zone” within sectors two and three between 400 and 450m south of Geysers Rock. During both seasons, departing seals would not appear at the surface before this zone and returning seals would dive at this point. I only observed one group of returning juvenile seals (n=3) who remained at the surface past the dive zone, and they were subsequently attacked. The presence of a dive zone is not unique, as other white shark/pinniped studies have found that seals will dive to darker waters at the bottom in order to limit their detection by sharks (Pyle et al. 1996, Goldman & Anderson 1999, LaRoche et al. 2008). The seals at Geysers Rock provide another example of such anti-predator tactics but it is very difficult to systematically record the distribution of such dive zones given the limitations on below surface observations of seal movement.

With the onset of winter and the arrival of more white sharks, seals at Geysers Rock decreased their use of sector three and increased their use of sector four that is characterised by increased habitat complexity (i.e. the presence kelp and reefs) relative to the largely open water of sector three. On the contrary, seals at Seal Island do not change their spatial habitat use between seasons (De Vos 2010) presumably because the waters around the island lack the structural complexity that would provide commuting seals with suitable refugia.

## Refuge use

The aquatic habitat around Seal Island is fairly homogenous with few nearby sub-surface structures (Figure 1), such as shallow reefs and kelp beds that may provide refuge for seals commuting to and from the island (De Vos 2010). In the absence of such refugia, there are few incentives for seals to adjust their spatial movements when commuting through high predation risk areas. Rather the best anti-predator strategy for seals traversing the danger zone is to firstly travel in groups (De Vos & O’Riain 2010) and secondly to avoid brief periods of high predation risk (i.e. post sunrise). In this study, the median size of seal groups leaving Geyser Rock was greater than for returning groups but there was no difference in the size of seal groups in winter (high risk) versus summer, suggesting that grouping is not as important an anti-predator strategy as it is at Seal Island (De Vos 2010). Neither grouping nor avoiding temporal peaks in predation risk would benefit from any spatial bias and seals are predicted to commute primarily in the direction of their preferred feeding areas viz., to the south west of the island. This in turn may explain the high concentration of surface predations in this sector of the water around Seal Island. By contrast, Geyser Rock offers a much greater diversity of subsurface habitats, particularly in sectors four and five, which allows seals to choose habitats that provide concealment en route to and from the island and the opportunity to pause in safe areas and visually assess risk before traversing open water.

In support of refuge hypotheses, seals at Geyser Rock showed an aversion to homogenous deep open water habitats (sectors one and two) in winter, and a preference for the structurally more complex habitat of sector four characterized by a long and shallow reef (in essence a submerged peninsula) covered with kelp that extends from Geyser Rock in a south westerly direction. Thus, this ‘Seal Alley’ feature appears to offer seals an extensive front of refuge habitat through which they can commute and from, and that they can safely gather

information on predator presence to adjust their departure from the refuge to areas of reduced predator presence (Figure 23). This appears to result in seal departure from Geyser Rock being considerably less predictable in space and time relative to Seal Island (De Vos 2010).

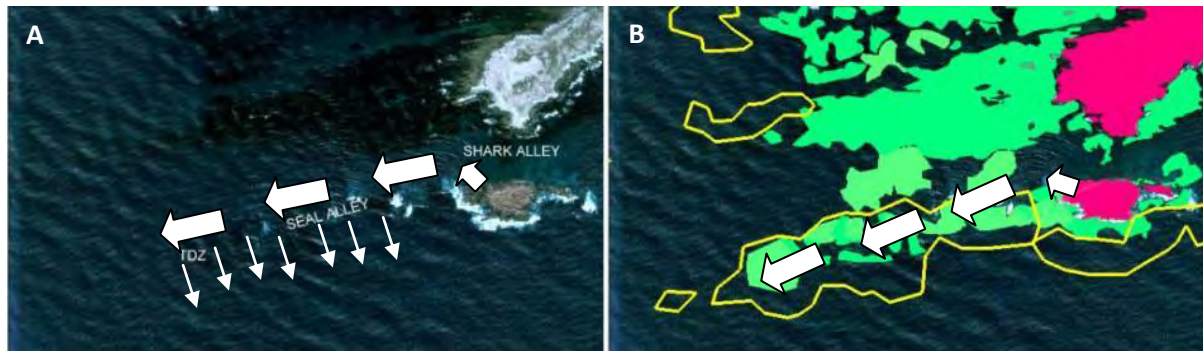


Figure 23: a) A graphical depiction of seal movement patterns observed within sector four through 'Seal Alley'. The large white arrows show the general movement patterns away from Geyser Rock with the smaller white arrows highlighting the extent of the possible exit points for travelling to the foraging grounds. b) Habitat type superimposed on the general movement patterns away from Geyser Rock. Pink = rock, Green = kelp and Yellow = shallow reef outline

The low number of predations I observed could not be explained by an absence of sharks in these near-colony areas, as acoustic tracking data from Jewell (2012) revealed that the kelp fringes of sector four, as well as sectors five and six, are areas of high white shark presence (Figure 24). Similar positive correlations between predator and prey spatial presence have been recorded at Shark Bay, Australia, where dugongs and bottlenose dolphins preferred predator abundant areas during times of high risk (Heithaus et al. 2008a, Wirsing et al. 2010). In these areas, the chance of encountering a tiger shark was high, but the chance of that encounter being lethal was comparatively lower than other areas (Heithaus et al. 2006, Wirsing et al. 2007). Considering the high densities of both seals and white sharks in sector four, encounter rates between the two may be high but the abundant refugia offered by the kelp cover may lower the risk of a lethal encounter, thus making this area more 'escapable' than others (e.g. Heithaus et al. 2008a, Wirsing et al. 2007, Wirsing et al. 2010).

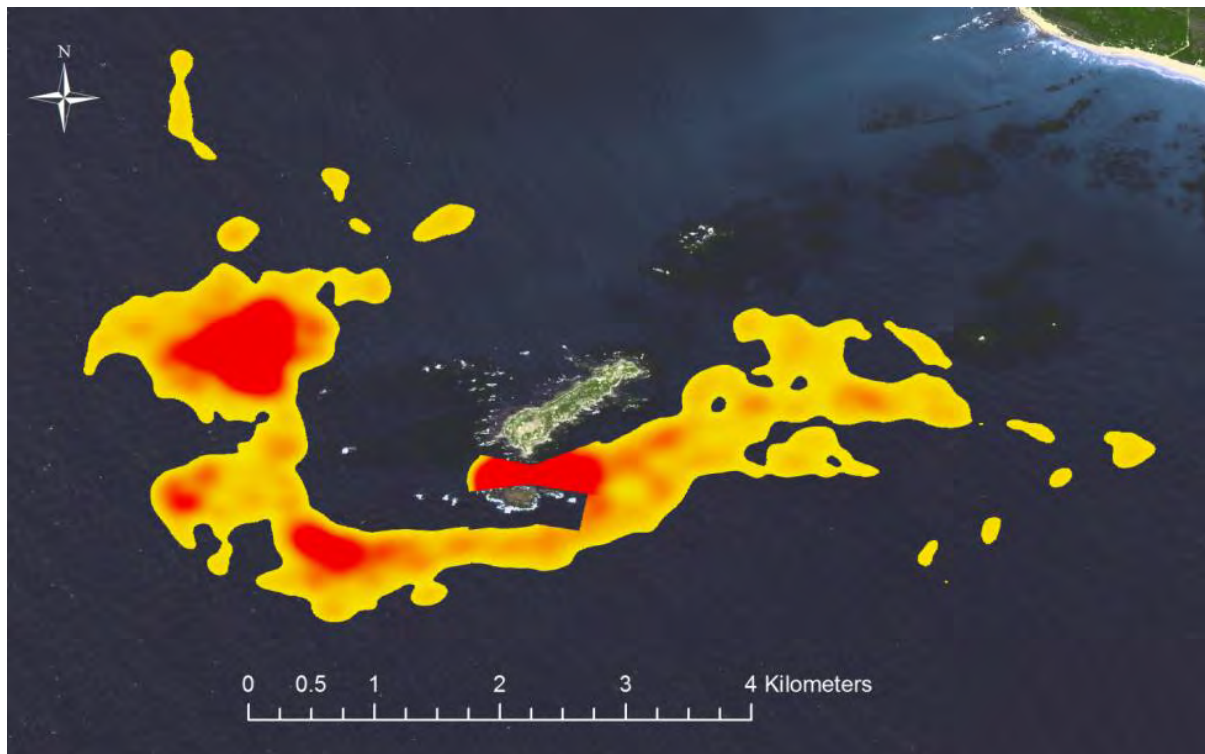


Figure 24: A Movement-based Kernel Density Estimation (MKDE) of spatial use from five white shark tracks at Geysers Rock. Yellow areas represent the majority of use (95% of tracks) with Red representing the core (50% of tracks) use (Jewell 2012).

The pattern of seal movement in sector five highlighted the importance of both reef and kelp systems as refugia. Few seals were observed commuting through sector five, yet predations were observed during my study in this sector, and anecdotally, this sector is one of the primary areas to elicit white shark predations on seal decoys. Additionally, there was no surface seal movement prior to the predation I observed, which suggests that seals may traverse this sector below water. This may be linked to both bathymetry and habitat type as shallow reefs may offer seals abundant subsurface refugia (Figure 25). As telemetry products become more accurate in fine-scale positioning, future seal-based telemetry would improve our understanding of subsurface movement patterns and how this varies with season and age class of seals. Akin to this, manual tracking of acoustically tagged sharks in sector five revealed a possible ‘sit and wait’ strategy in water channels between reefs (Jewell et al. *in prep*), suggesting that sharks may have adjusted their predatory behaviour in response to the use of reef refugia by seals.

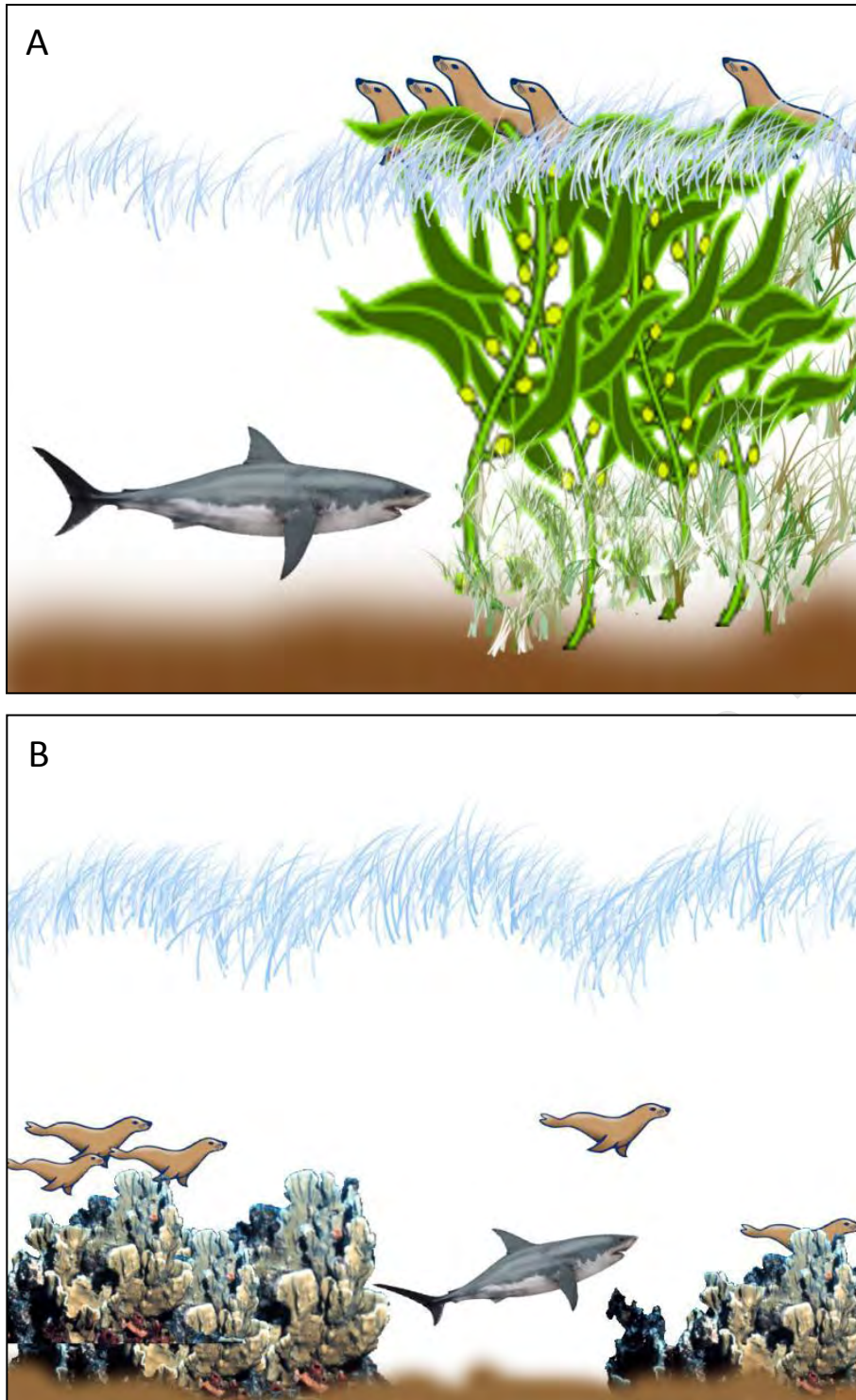


Figure 25: Schematics of the possible benefits of kelp use (A) and reef use (B) by Cape fur seals at Geysers Rock. Kelp could provide surface cover as white sharks searching for surface prey from below would not detect seal silhouettes amongst the kelp. The shallow reefs systems adjacent to Geysers Rock could provide cover from both above and below while 'hugging' the reef, only exposing seals to white shark detection between reef patches.

## Conclusions

I set out to test the following predictions based on research findings from the nearby Seal Island shark-seal system, and here I present the results based on the research completed in this dissertation.

**Prediction: White sharks aggregate at Geyser Rock during the austral winter season to target young of the year seals that are making their first exploratory forays into open water;**

Result: White sharks did aggregate at Geyser Rock during the austral winter season (Figure 13), providing support for the first part of this prediction. I was not able to confirm whether shark arrival at the rookery was to target young of the year seals, as surface predation events were rare, and precluded an analysis of dietary preference with age class of seals.

**Prediction: White shark predation events will peak in frequency in the first two hours after sunrise when surface swimming seals have readily detectable silhouettes and low light penetration provides concealment for sharks approaching from depth;**

Result: The limited sample size of predation events precluded my testing of this prediction. However, anecdotal observations from commercial operators suggest that the peak time for predations at Geyser Rock is later (8:00am – 9:00am). This delay may be related to the poor visibility (Figure 22) at Geyser Rock during the morning hours, as surface swimming seals would not have detectable silhouettes until the sun was higher, allowing light to penetrate deeper through the murky water. Additionally, seals increased movement to and from the colony during the hours after dawn (7:00-8:30) and decreased movement later in the morning (Figure 20), which is very much to the contrary of seal movement at Seal Island (De Vos 2010). This also supports a delayed peak in predation effort by sharks around the colony.

**Prediction: Most seal movement will be to the South of Geyser Rock in the direction of the open sea (i.e. away from Dyer Island and the coastline) and their preferred feeding grounds;**

Result: This prediction was supported, as most seal movement was to the south and southwest of the island through sectors three and four, which is in the direction of the open sea and the seals' feeding grounds (Figure 14).

**Prediction: Seals will avoid high risk habitats (i.e., deep open water) during periods of high predation risk;**

Result: This prediction was supported, as seals at Geyser Rock avoided sectors one and two that are characterized by deep open water during both season. Seals also reduced their use of sector three during winter when shark presence was highest and increased their use of sector four that has more refugia (Figure 14).

**Prediction: The median group size of seals leaving the island will be larger in summer when shark presence is low, and leaving groups will be larger than returning groups;**

Result: There was no significant difference in the mean group size of seal groups leaving the island in winter or summer but leaving groups were on average larger than returning groups (Figure 16).

In conclusion, the exceptionally low frequency of predation events around Geyser Rock precluded a rigorous analysis of Cape fur seal movement patterns and habitat in relation to fine-scale spatiotemporal patterns of predation. However, the lack of observed predations at Geyser Rock is a major finding of this dissertation, and it suggests a dramatically different anti-predator strategy by seals when faced with the same predator at two different island

rookeries (Table 5). Seals shifted their movement to heterogeneous habitats during winter when white shark presence is highest and hence predation risk is assumed to peak. The presence of shallow reefs and kelp in the channel, dubbed ‘Seal Alley’ provides seals with protection from surface scanning white sharks and may allow seals to assess risk from the relative safety of a refuge. The abundance of refugia at Geysers Rock and the preference for sectors with such refugia by seals may explain both the reduced levels of overall surface predation at Geysers Rock relative to Seal Island and the more dispersed nature of surface predation events at Geysers Rock as seals use a diverse number of safer routes when commuting to and from the island.

*Table 5: A summary of various white shark and Cape fur seal patterns in comparison to those established at Seal Island and tested at Geysers Rock*

<b>Pattern</b>	<b>Seal Island</b>	<b>Geysers Rock</b>
White sharks aggregate at the seal colony in winter months, followed by a marked absence in summer	Yes	Yes
The majority of white shark predations occur just after dawn	Yes	<b>Could not be determined – unlikely</b>
White shark predation frequency is higher during winter	Yes	<b>Could not be determined - likely</b>
The majority of white shark predations occur in one area to the south of the island	Yes	<b>No</b>
Adult Cape fur seals avoid areas of open water during winter	Yes	Yes
Cape fur seals form groups to reduce the probability of predation (selfish herd hypothesis) when leaving the rookery	Yes	<b>No</b>
Cape fur seals alter their temporal patterns to avoid time periods of high predation risk	Yes	<b>Could not be determined – likely</b>
Cape fur seal alter their spatial use during winter	<b>No</b>	Yes
The seascape surrounding the colony has potential refugia	<b>No</b>	Yes

Overall, the major limitation to this and many other marine-based behavioural studies was the absence of below surface observations and the paucity of calm sea conditions to allow more

observation time. Technological advances in remote camera equipment may provide a future solution to these challenges, but funding and insuring such equipment in areas of high predator abundance are likely to be persistent challenges. I feel this dissertation highlights how there is still much to be learned from individual marine predator-prey systems, and that it is not possible to extrapolate from nearby similar systems when inferring predator-prey interactions. Although Seal Island and Geyser Rock host the same predator-prey species and occur within the same Benguela upwelling ecosystem, the spatiotemporal patterns of both white sharks and Cape fur seals differed in structurally dependent ways.

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