Foraging Ecology of White Sharks
Carcharodon carcharias
at Dyer Island, South Africa

Oliver Jewell

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By Oliver J.D. Jewell

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Declaration

I, **Oliver J.D. Jewell**, declare this dissertation, which I hereby submit for the degree **MSc Zoology** at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signed:

Date:

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Summary

Title: Foraging Ecology of White Sharks *Carcharodon carcharias* at Dyer Island, South Africa

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Degree: MSc Zoology
Department: Zoology & Entomology, University of Pretoria

Abstract: Dyer Island is thought to host one of the most abundant populations of white sharks on the planet; this is often credited to the large (55 – 60,000) Cape fur seal colony at Geyser Rock. Yet relatively little work has ever been produced from the area. This may be attributed to the harshness in its location as a study site, exposed to wind and swell from west to east which limits research periods. This study accounts for over 220 hrs of manual tracking at Dyer Island with a further 68 added from the inshore shallow areas of the bay. Sharks focused their movements and habitat use to reefs or channels that allowed access to Cape fur seals. Movement-Based Kernel Estimates (MKDE) were used to compute home range estimates for shark movements through and around the heterogeneous structures of Dyer Island and Geyser Rock. Inshore two core areas were revealed, one being the major reef system at Joubertsdam and the other at a kelp reef where the tracked shark had fed on a Cape fur seal. At Dyer Island one core area was identified in a narrow channel, ‘Shark Alley’, here a second tracked shark foraged for entire days within meters of rafting Cape fur seals.

Rate of Movement (ROM) and Linearity (LI) of tracks were low during daytime and movements were focused around areas such as Shark Alley or other areas close to the seal colony before moving into deeper water or distant reefs with higher rates of ROM and LI at night. If moonlight was strong foraging would take place to the south of Geyser Rock but with higher ROM and LI than observed during the day. Foraging patterns in this study contrast studies from other sites in South Africa and home range and activity areas were comparatively much smaller than observed in Mossel Bay. It has been established that several known white sharks forage at Dyer Island and the other studied aggregation sites, such differences in foraging would suggest that they are able to adapt their foraging behaviour to suit the environment they are in; making them site specific in their foraging ecology.

Both satellite and acoustic telemetry are revealing aggregation hotspots of white sharks in South Africa. It is important that such information is used to assist the recovery of the species which has been protected since 1991, yet is rarely considered in planning of coastal developments.

Key Words: *Carcharodon carcharias*, Movement-based kernel density estimation, acoustic telemetry, swimming patterns, home range, activity area, rate of movement (ROM), linearity (LI), apex predator, heterogeneous structures, site specific foraging, Cape fur seal *Arctocephalus pusillus pusillus*, conservation hotspots

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Others are thanked within the chapter acknowledgments and Marthán Bester (supervisor), Alison Towner and Michelle Wcisel (scientific collaborators) are co-authors on the manuscripts produced from the chapters. For a full list of those who helped tracked (a vast number) please go to Appendixes I for track references and acknowledgments.

Thank you to you all, I am very relieved to have finally produced this dissertation from sketched ideas and rough plans to a final project and several manuscripts, thank you all for helping both myself and the project to grow.

Marine Dynamics; your choice makes a difference…

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Manuscripts

Chapters 2, 3 and Appendix II and III of this dissertation have been prepared and submitted for publication as manuscripts. As such a far degree of repetition takes place in method sections, which was unavoidable and for which I apologise. Chapters 2 and 3 were prepared for Aquatic Biology and Marine Ecology Progress Series respectively and as such the referencing for the entire thesis follows the guidelines of Inter Research for constancies sake. The appending chapters follow the referencing of the journals they have been submitted too.

Chapter 2: Defining home range of an apex predator within heterogeneous structures
Jewell OJD, Towner AV, Bester MN, Wcisel MA
In preparation
Journal of Oceans and Coastal Research

Chapter 3: Site specific foraging ecology of the South African white shark
Jewell et al.
In preparation
Aquatic Biology

Appendix II: Effect of Smart Position Only Tag (SPOT) deployment on white sharks in South Africa
Jewell OJD, Wcisel MA, Gennari E, Towner AV, Bester MN, Johnson RL, Singh S
Published Nov 2011
PLoS ONE 6(11): e27242
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Appendix III: Fine scale movements and activity areas of white sharks *Carcharodon carcharias* at Mossel Bay, South Africa
Jewell OJD, Johnson RL, Gennari E, Bester MN
2012
Environmental Biology of Fishes
DOI 10.1007/s10641-012-0084-4

Chapter 1: General Introduction

The plight of the shark

Sharks are thought to play a crucial role in almost all marine ecosystems (Simpfendorfer et al. 2001; Heithaus et al. 2002; Myers et al. 2007; Heithaus et al. 2008), however many aspects of their biology and life history remain unknown (Speed et al. 2010) and pressures of overfishing have forced most populations into steep decline (Baum et al. 2003; Baum et al. 2004; Myers et al. 2007). Unfortunately, of all the world’s charismatic animals, sharks are often seen as the one people fear the most (Magnuson 1987; Philpot 2002; Peschak 2006). Human-predator conflicts are often driven by fear and hinder conservation efforts (Zimmerman et al. 2001; Klatenborn et al. 2006). Sharks are often perceived as dangerous and aggressive regardless of species, size or diet; providing a huge challenge in efforts to conserve a single species (Techera & Klein 2011). Much of the negative perception of sharks comes from media sensationalism; Boyer (1987) wrote “The shark is a creature tailor made for media sensationalism. As typified by the great white, it’s a huge primitive carnivorous force who’s diet occasionally includes people, or at least that’s the popular view. The average journalist definition of news is: an event that concerns people, and is occurring now. Unfortunately, sharks generally become an event that concerns people only when a person is eaten by a shark.” Despite trends suggesting any increase in shark bites is due to a huge increase in recreational use of coastal waters across the world (Kock & Johnson 2006), any incidence of a shark bite instantly makes headlines across the globe (Woolgar et al. 2001).

People’s fear of sharks had led to numerous culling programmes across the world in response to attacks and in South Africa and Australia permanent establishments are in place using shark (gill) nets and drum lines to remove shark populations from popular swimming beaches (Dudley & Cliff 1992; Dudley & Simpfendorfer 2006). However, the most severe knock-on effect from the fear of sharks has been the unhindered growth of the shark fin soup fishing industry. People either did not know or did not care about the numbers of sharks being removed from the ocean for their fins alone until the turn of the century when an increase in documentaries and research articles began to spread a greater awareness of the plight of the shark (FAO 2000; Baum et al.

2003; Baum et al. 2004; Abercrombie et al. 2005; Shiviji et al. 2005; Myers et al. 2007). Today 20% of shark and ray species are characterised as being threatened by the World Conservation Union (IUCN) (Fergusson et al. 2006; Camhi et al. 2009; Gore et al. 2011). Ecotourism is also aiding conservation efforts by placing a greater value on live sharks, rather than dead sharks (Johnson & Kock 2006; Laroche et al. 2008; Gallagher & Hammerschlag 2011; Gore et al. 2011). Local initiatives such as the Shark Spotters programme in Cape Town, South Africa, are helping to find a balance between human/shark conflicts; spreading awareness and reducing encounter rates by monitoring beaches (Oelofse & Kamp 2006; Kock et al. 2012). However, the shark finning industry is already well established and shark stock declines are not showing any signs of slowing (Dulvy et al. 2008).

The White Shark

The white shark (*Carcharodon carcharias*) is considered the largest predatory fish in the ocean and of all species of shark receives the most attention from news headlines and media on account of its notoriety as a dangerous animal. This perception has been built up through years of Hollywood films and television documentaries (e.g. ‘Jaws’ or ‘Extreme Animal Attacks’ - Boyer 1987; Peschak 2006). It is considered vulnerable and is listed under Appendix II of the Convention on International Trade in Endangered Species (CITES) and the World Conservation Union (IUCN) (Ferguson et al. 2006; Dulvy et al. 2008). Trade in white shark products continues, particularly of those fished offshore in international waters for the shark finning industry (Shiviji et al. 2005). Within South African waters the species is protected (Compagno 1991), yet there are rumours that poaching for jaws and teeth still occur. Despite it being identified on news and online forums that deliberate targeting from recreational anglers has become a problem, at this time no one in South Africa has been charged with deliberate fishing of a white shark. Other serious threats to the population include habitat degradation in the form of coastal development (Jewell et al. 2012) and the shark nets deployed in the Kwa-Zulu Natal (KZN) region of the coastline (Dudley & Cliff 1992; Dudley & Simpfendorfer 2006).

The species is found in most of the world’s oceans and often aggregates close to the coastline (Compagno et al. 1997; Kock et al. 2012; Skomal et al. 2012). The species’ movements are characterised by patterns of site fidelity at aggregation sites followed by large scale migrations (both coastal and oceanic) (Bonfil et al. 2005; Weng et al. 2007a; Domeier & Nasby-Lucas 2012; Duffy et al. 2012). In South Africa several of these aggregation sites have been documented with most research coming from False Bay (e.g. Martin et al. 2005; Hammerschlag et al. 2006; Laroche et al. 2007; Laroche et al. 2008; Fallows et al. 2012; Kock et al. 2012), Mossel Bay (e.g. Johnson et al. 2009; Delaney et al. 2012; Jewell et al. 2012) or from catches in the KZN shark nets (Dudley & Cliff 1992; Dudley & Simpfendorfer 2006; Dudley 2012; Hussey et al. 2012; Smale & Cliff 2012). Historically there are few papers produced based on data from white sharks in the Gansbaai/Dyer Island region (Johnson 2003; Johnson & Kock 2006; Johnson et al. 2008), however, recent works are beginning to describe the region more thoroughly (Wcisel et al. 2010; Jewell et al. 2011; Towner et al. 2012; Towner 2012; Wcisel in prep; this dissertation).

The species' diet shifts from predominantly teleost, elasmobranch and cephalopod prey during the juvenile stage in life (< 280 – 300 cm Total Length, TL) to marine mammals in sub-adult and adult stages (Klimely 1985; Bruce 1992; Estrada et al. 2006; Hussey et al. 2011; Hussey et al. 2012; Smale & Cliff 2012) This has been attributed to jaw and tooth development that takes place around the time the shark reaches 300 cm in total length (TL), with the teeth growing more triangular and the jaw becoming stronger (Bruce 1992; Ferrara et al. 2011). However, a transitory stage may take place where juvenile white sharks will begin to learn to forage on marine mammals while still smaller than the 280 – 300 cm TL when they begin to specialise (Lowe et al. 2012). Likewise sharks over 300 cm TL will continue to prey on teleost and elasmobranch prey while not in the vicinity of abundant sources of marine mammal prey (Domeier 2012). Furthermore, recent evidence may suggest that large white sharks in the north-east Pacific feed on large mesopelagic squid during pelagic stages of their life-histories (Domeier 2012).

The effect of size also plays a major role in the movements of sharks; Weng et al. (2007a) found that juvenile white sharks in the north-east Pacific limited their movements to coastal regions whilst sub-adult and adult white sharks from the same region made oceanic migrations (Weng et al (2007b). On a finer scale both Goldman & Anderson (1999) and Jewell et al. (2012) found that larger white sharks had smaller activity areas and home ranges than smaller conspecifics at aggregation sites adjacent to pinniped colonies. Both studies suggested that it could be experience of the larger sharks which allowed them to limit their foraging to smaller areas, becoming more efficient in resource exploitation as a result. Smaller, younger individuals lacked this experience and would forage over larger areas. A second explanation could be that larger sharks dominate the best foraging areas, excluding smaller conspecifics (Goldman & Anderson 1999; Jewell et al. 2012).

Acoustic telemetry and tracking white sharks

The main challenge with tracking marine vertebrates is the ocean itself; satellite signals will not transmit through water and species such as sharks can make migrations into deep open water making physical tracking unfeasible (Block et al. 2011). Tracking devices for sharks were first developed during the 1980's when pioneer studies included Carrey et al. (1982); in which a white shark was fed a bait with an acoustic tag imbedded within it. The shark was tracked for 83 hrs using a boat based hydrophone and travelled 190 km. The tag's pings were coded to give temperature readings and for the first time internal temperatures of white sharks were documented. Technology has improved but the basic methods of active tracking are the same; a tag attached to a shark pings and is received by a boat based hydrophone and recording device (Voegeli et al. 2001). Active tracking studies have described the movements of many species of shark such as; grey reef *Carcharhinus amblyrhynchos* (McKibben & Nelson 1986), lemon *Negaprion brevirostris* (Gruber et al. 1988; Morrissey & Gruber 1993; Sundström et al. 2001), tiger *Galeocerdo cuvier* (Heithaus et al. 2002), sandbar *Carcharhinus plumbeus* (Rechisky & Weatherbee 2003), blacktip reef *Carcharhinus melanopterus* (Papastamatiou et al. 2009), bull *Carcharhinus leucas* (McCord & Lamberth 2009), thresher *Alopias vulpinus* (Cartamil et al. 2010), hammerhead *Sphyrna lewini* (Hearn et al. 2010) and white *Carcharodon carcharias* (Carey et al. 1982; Strong et al. 1992; Goldman & Anderson 1999; Johnson et al. 2009; Jewell et al. 2012). The methods are particularly useful for detecting fine scale movements, allowing rates of movement (ROM) and linearity (LI) of tracks to be calculated as well as activity areas and home ranges to be determined (Winter & Ross 1982; Morrissey & Gruber 1993; Rechisky & Weatherbee 2003; Johnson et al. 2009; Jewell et al. 2012).

The main weakness in active tracking is that it requires long hours at sea, good weather and often a lot of fuel. An alternative for longer acoustic monitoring uses listening stations placed at previous documented aggregation areas or in river mouths and estuaries (Voegeli et al. 2001; Heuple et al. 2004; Heuple et al. 2005; Simpfendorfer et al. 2010). Such passive monitoring allows for longer durations of tracking in all weather conditions, residency times to be estimated and through receivers placed elsewhere – the detection of large scale movements (Heuple et al. 2004; Johnson & Kock 2006; Delaney et al. 2012). The weakness with passive monitoring is that once out of the range of the receiver (typically 300 – 500 m; Voegeli et al. 2001) no data can be collected. Measuring fine scale movement patterns requires many receivers to be deployed (Simpfendorfer et al. 2010) and behaviours such as predation events cannot be observed (Klimely et al. 2001).

To track oceanic migrations away from coastlines satellite telemetry is required and in shark species pop-off archival (PAT) and smart position only (SPOT) tags are the most used (e.g. Bonfil et al. 2005; Weng et al. 2007a; Weng et al. 2007b; Domeier & Nasby-Lucas 2012; Duffy et al. 2012). However, these tags have too large degrees of error for fine scale movement detection (Teo et al. 2004; Weng et al. 2005; Jewell et al. 2011) and studies on high resolution localised movements, foraging and home ranges, require active acoustic telemetry.

Dyer Island - the world's best and worst study site

Figure 1. (above) working at Dyer Island during periods of moderate to heavy swell can be extremely challenging; a reef breaks to the North of Dyer Island (left) and a cage diving vessel working with white sharks in the Geldsteen (right).

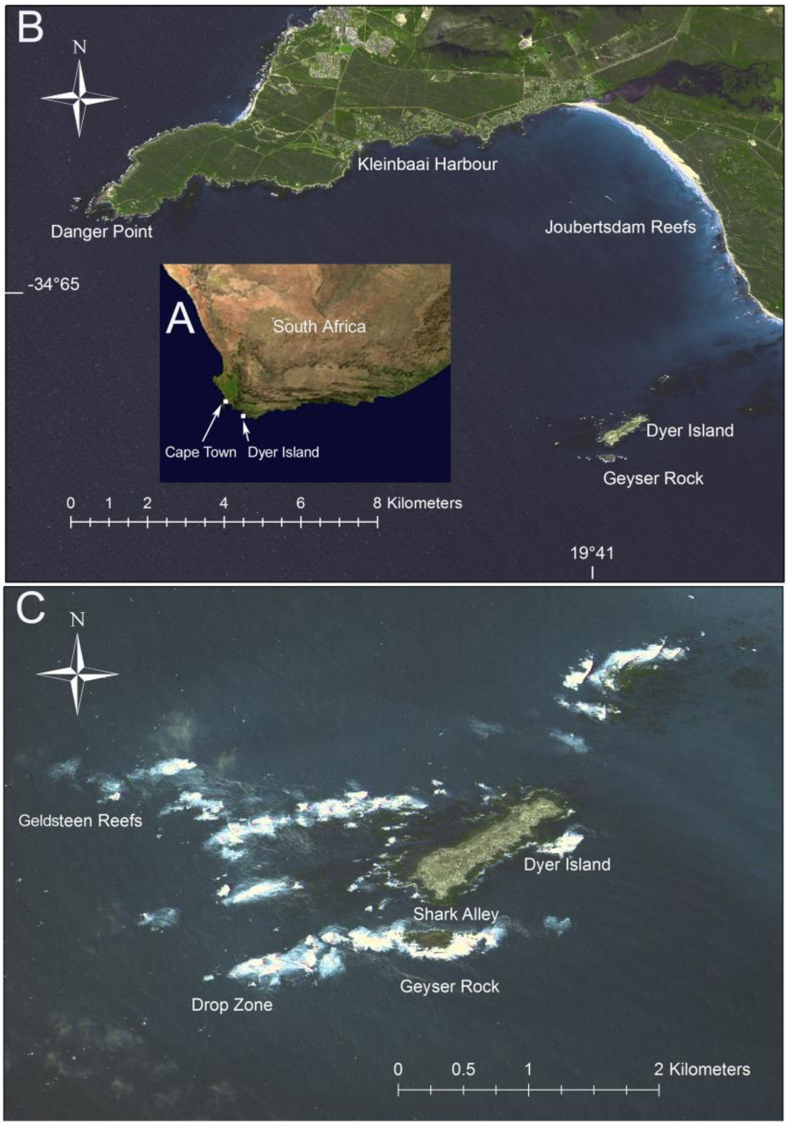

Figure 2. Study Site: Dyer Island and its situation on the South African coastline (A). Danger Point, Gansbaai, Joubertsdam and Dyer Island (B) and Geyser Rock and Shark Alley during heavy swell (C); note the breaking waves to the west of Geyser Rock, here a shallow ridge and thick kelp forest provide an extension of refuge for Cape fur seals (Wcisel pers. comm.).

Dyer Island is situated near the southern tip of Africa, approximately 60 km west of Cape Agulhas and 95 km east of Cape Point. It is famous for its wildlife and harsh weather and was first described to science in 1830 by A. Johnson Jardine who noted it’s dangers including the landing site that was ‘one of the most dangerous I have ever seen’ and ‘full of sharp rocks and kelp and waves break continually over the mouth of the cove’ (Fourie 2002). Dyer Island and Geyser Rock are exposed to sea conditions from both the west and the east and numerous shallow ridges and reefs make the site extremely challenging during periods of adverse weather (Figure 1; Figure 2). These challenges may account for the lack of published work from the area in comparison to other white shark hotspots (Dudley 2012), with only one study ever being completed on the local population of white sharks by Johnson (2003), with the results published in Johnson et al. (2006, 2008). Current studies indicate that the population of white sharks around Dyer Island may be the largest in Southern Africa (Dyer Island Conservation Trust unpublished data) and far larger than populations in other areas of the world such as California (Chapple et al. 2011) or Guadalupe Island (Nasby-Lucas & Domeier 2012). The abundance of white sharks in the area can be related to the food resources available from Geyser Rock, where 55 – 60,000 Cape fur seals reside (Dept. Environ. Affairs unpub. data) and the region is also a rich fishing ground for predatory fish and smaller species of shark. The highest abundance of white sharks at Dyer Island occur through winter (April – August) with a seasonal shift occurring and higher numbers sighted in inshore reefs (such as Joubertsdam) from late August/September – December (Johnson 2003; Towner 2012).

Over 220 hrs of tracking was accumulated at Dyer Island, including successful night tracks. An additional 68 hrs of inshore tracking is analysed in Chapter 2.

Structure of this dissertation

The overall aim of this dissertation is to examine the foraging and habitat use patterns of white sharks at Dyer Island. The first step (Chapter 2) is to test if white shark home range can be defined within the study site. The heterogeneous structures of Dyer Island and Geyser Rock provide a different challenge than faced in most other home range studies in that large areas (land, rock, shallow ridges and thick areas of kelp) are inaccessible for white shark foraging and should not be included in the home range estimate. Next (Chapter 3), white shark movement patterns are examined around Dyer Island in a bid to understand how white sharks exploit the food resources provided by the island and its seal colony. I further test if this foraging is similar or dissimilar to what has been reported elsewhere in South Africa. Finally (Chapter 4), I look at the potential for the data gathered in this study, and new data being collected from a collaborative national study, to provide better conservation measures for the species and help aid its recovery.

Aims & Research Questions

Chapter 2: Defining the home range of an apex predator within heterogeneous structures.

In this chapter I use a movement-based kernel estimate programme to define the home rage of two white sharks in the Gansbaai region. Specifically the following questions are addressed:

a) Are the activity areas of the white sharks aggregating in Gansbaai finite?
b) Can we observe core areas or hotspots within the activity area?
c) Can these core areas be projected into a home range unbiased by areas in which a white shark cannot forage?

Chapter 3: Site specific foraging ecology of the South African white shark.

In this chapter data collected from sub-adult and adult white sharks tagged and tracked specifically in the areas adjacent to Dyer Island are analysed. Using the Cape fur seal colony as the most obvious reference point to find mammalian prey, a direct comparison is made to previously published works from Mossel Bay and False Bay to answer the following questions:

a) What is the extent of effort devoted to hunting seals at Geyser Rock?
b) What patterns in foraging can be related to time of day/light levels?
c) What is the effect of body size on swimming patterns and activity areas?
d) Are these patterns in foraging unique to the local region or following a similar pattern to that reported in Mossel Bay and False Bay?

Chapter 4: General Conclusion

This chapter concludes the overall findings of the dissertation and the potential of future research projects devoted to studying the white shark.

Appendix I: The complete manually determined tracks of white sharks at Dyer Island.

Appendix II: Jewell et al. 2011, Effects of Smart Position Only Tag (SPOT) deployment on South African white sharks. Results of a study conducted alongside this dissertation.

Appendix III: Jewell et al. 2012, Fine scale movement patterns and activity areas of white sharks at Mossel Bay, South Africa. Results of a previous study similar in its methods to this dissertation but conducted in Mossel Bay.

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Chapter 2: Defining the Home Range of an Apex Predator within Heterogeneous Structures

Abstract

This chapter defines the home range of an apex predator, the white shark *Carcharodon carcharia*s, within heterogeneous structures at Dyer Island and the surrounding area in the Western Cape of South Africa. Utilization Distributions (UD) were projected using a Movement-based Kernel Density Estimation (MKDE) to consecutive active tracks from sharks tagged with acoustic transmitters. This method of kernel projection outperforms traditional methods by ignoring local movement information provided by the serial correlation between successive locations and incorporating the movement itself. It also lifts constraints to movement imposed by obvious boundaries which are prominent in the study area; where white sharks forage on Cape fur seals in a narrow channel between two islands. White sharks are seasonal and return visitors to this region allowing site specific home ranges to be estimated. This is the first study to apply MKDE UDs in the marine environment.

Key Words: Movement-based kernel density estimation, white shark, acoustic telemetry

Introduction

Studies observing movement patterns and site fidelity can provide vital information in order to aid the recovery and management of threatened species (Simpfendorfer et al. 2010). The concept of home range (Burt 1943; McNab 1963) is used to analyse movement patterns, to establish marine protected areas and assess their effectiveness (Meyer & Holland 2005; Hearn et al. 2010). Defining home ranges can be challenging in marine apex predators, which often make far and wide migrations into areas where observations are often unfeasible and fine scale tracking is naturally difficult (Block 2005; Block et al. 2011). At some sites, large marine apex predators make return migrations over a number of years, displaying site fidelity and spending a significant proportion of their life history in a limited area (Bonfil et al. 2005; Barnett et al. 2011; Jewell et al. 2012). Focusing on these areas, which can be referred to as site specific home ranges, can be considered crucial to conservation management strategies (Heupel et al. 2010).

Home ranges are traditionally estimated through the building up of the “Utilization Distribution” (UD); UDs are usually computed as smooth histograms using a location-based kernel density estimator (Worton 1989). However, it is possible to take advantage of the movement information provided by serially correlated locations to get UD estimates with an improved spatial resolution through Movement-based Kernel Density Estimates (MKDE; Benhamou & Cornélis 2010; Benhamou 2011; Benhamou & Riotte-Lamberth 2012). MKDEs consider activity times between serially correlated relocations rather than the spatial density of these relocations as if they were independent; this reduces the smoothing of the UD over areas which may never be used and reduces bias in space use and habitat selection estimates (Benhamou & Cornélis 2010). Furthermore, boundaries (such as river banks or mountains) can be taken into account in this framework (Benhamou & Cornélis 2010; Cornélis et al. 2011), making this approach particularly suitable for estimating UDs of marine animals and establishing their home ranges in a coastal environment. Previous studies into home ranges of fish or shark species have simply ignored the coastline when computing the UD, and then discarded the parts of the UD that lie beyond the coastline (e.g. Heupel et al. 2004; Weng et al. 2008; Domeier et al. 2012; Hammerschlag et al. 2012; Jewell et al. 2012). The issue is further complicated when coastal movements include navigations around island systems. Apex predators utilise waters adjacent to islands in order to exploit prey species present on the islands themselves (Laroche et al. 2008; De Vos & O'Riain 2010; Reisinger et al. 2011). A study looking to establish home range of a marine predator in the above circumstances should proceed with caution until the obvious boundaries have been considered.

In this chapter movement data collected from acoustically tagged white sharks *Carcharodon carcharias* in Gansbaai, South Africa. I selected sharks well documented as return visitors to the area and computed their UDs using movement-based kernel density estimators.

Study Area

Sharks were tagged and tracked in the Gansbaai/Dyer Island area (Fig. 1) where shark presence is well documented at two coastal sites (Towner 2012). The first is Dyer Island, which is a complex rocky island system consisting of one larger island approximately 15 ha in area with rocky outcrops, kelp forests and reefs surrounding it. The southern smaller island situated across a 200 m channel of water is Geyser Rock, which hosts a breeding Cape fur seal (*Arctocephalus pusillus pusillus*) colony of approximately 55 – 60,000 individuals (Dept. of Environmental Affairs, unpub. data). During austral winter months (May – August), sharks are observed feeding on the Cape fur seals in the channel between Geyser Rock and Dyer Island (Johnson et al. 2008). During spring and summers months, sharks are also found at Joubertsdam, a reef system to the Northeast of Dyer Island (Towner 2012). Such a complex system means shark movements are often shaped by the environment; patrolling through channels or on the edges of islands or kelp forest. As such the traditional kernel used to establish home range of white sharks in Mossel Bay (Jewell et al. 2012) may be considered unsuitable – in comparison we test the MKDE programme and its boundary option for the first time in the marine environment. Both sites are exposed to weather conditions; this limits research expeditions during periods of heavy wind of swell.

Methods

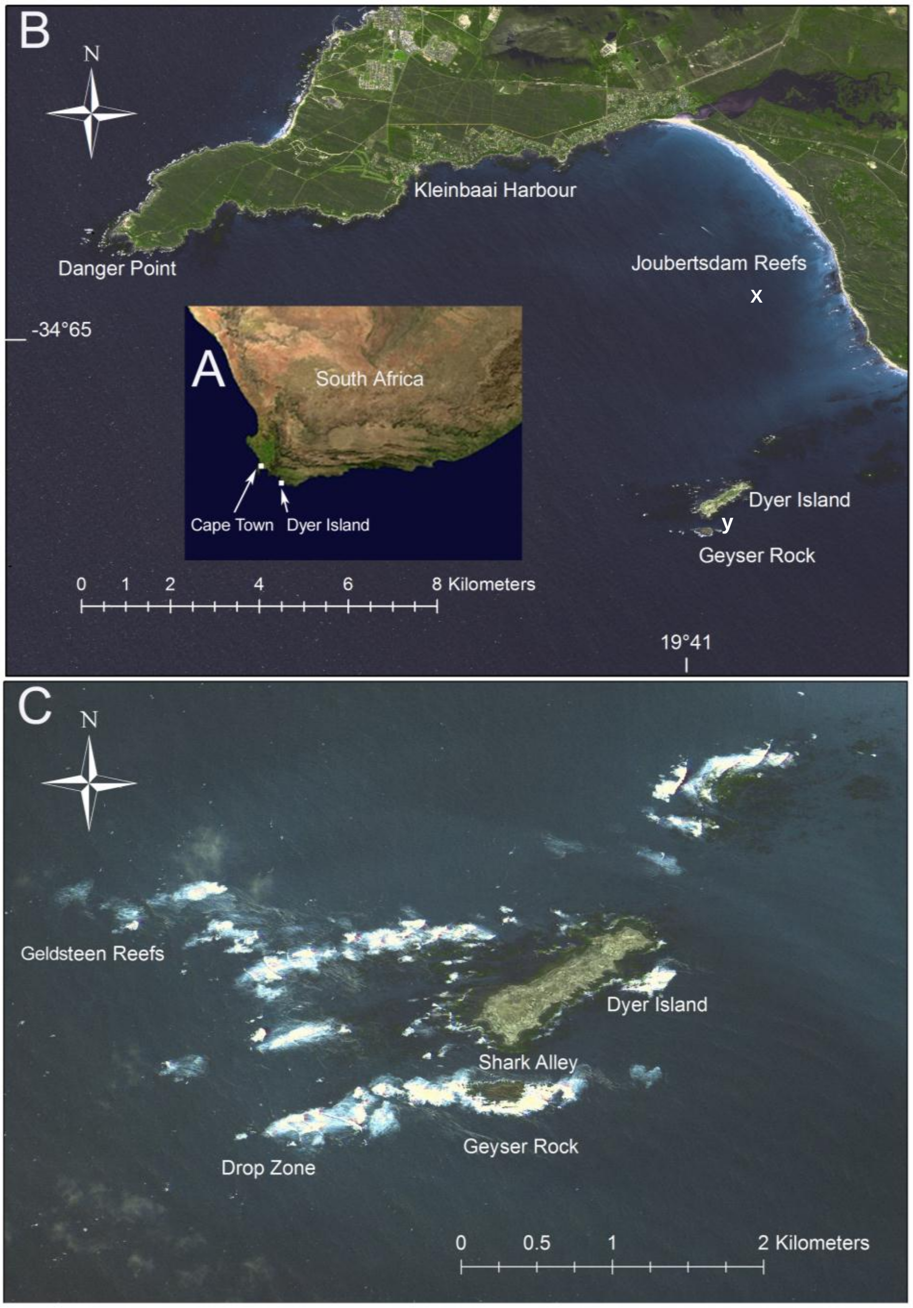

Figure 1. Study site: Position of Dyer Island and Gansbaai on the South African coastline (A). Dyer Island and the surrounding areas (B) Shark 1 was tagged in the Joubertsdam reef system (point x) and Shark 2 was tagged in Shark Alley between Geyser Rock and Dyer Island (point y). Higher resolution view of Dyer Island on a rough day, displaying ridges and island constraints on habitat use (C).

Sharks were attracted to a research vessel using a baited line and waste teleost products (chum) (see Strong et al. 1992). Once in the vicinity of the vessel sharks were sized based on comparison to known dimensions of the vessel. Photo ID of the sharks' first dorsal fin was used to identify the shark based on previous sightings from Marine Dynamics cage diving vessels (as in Chapple et al. 2011). Tags used were Vemco V-16 76.8 kHz (shark 1) and V-16TP (recording temperature (T) and depth (P)) 81 kHz (shark 2) ultrasonic continuous pingers (Voegeli et al. 2001). Tags were fitted with a brush-tip head to reduce shedding (Johnson unpublished data) which was attached to the main casing of the tag with a wire tether. Both tags and tethers were painted with anti-fouling paint to reduce algal growth, which can be excessive in Southern African waters and can interfere with tag performance and increase drag (Jewell et al. 2011). A tagging pole with a spear-tip head was used to place the tags at the base of the first dorsal fin. Once tags were placed tracking protocol was set up in a similar method to those used in Johnson et al. (2009) and Jewell et al. (2012). Sharks were tracked using a boat based VR100 with a VH110 (50 – 85 kHz) directional hydrophone. Sharks showed little reaction to tagging and after the initial time taken to prepare for tracking (± 10 minutes) movements had returned to normal (as defined by comparison to movements days, weeks and months after tagging). Sharks were tracked at a distance of approximately 20 – 40m (60-80 dbl; Johnson et al. 2009), an equipment failure meant positions could not be corrected further as in Heithaus et al. (2002) and tracking closer was deemed to interfere with sharks movements (Johnson et al. 2009).

Positions were recorded every 5 minutes, if the signal could not be received (for instance if there was an obstruction) recordings resumed upon reception of the next signal. At the start of a new tracking session a VH165 (50 – 85 kHz) omni-directional hydrophone was used to detect a shark’s transmitter; transects were run throughout the bay until such a signal was detected. Upon receiving these transmissions the omni-directional hydrophone would be switched for the directional hydrophone and tracking would resume. The methods of tagging and tracking were approved and permitted by the Department of Environmental Affairs, Oceans and Coasts.

Data Analysis

Traditional fixed-based kernel estimates were calculated with the animal movement tool on Arc 3.2 with smoothing parameter calculated using Least Squares Cross Validation (LSCV) (Jewell et al. 2012). Next the Pascal programme described in Benhamou & Cornélis (2010); Benhamou (2011) and Benhamou & Riotte-Lambert (2012) was used to compute MKDE UDs based on the tracks provided from the acoustic telemetry of two sharks. We first computed a diffusion coefficient (*D*) of roughly 1000 for each shark using the Biased Random Bridges (BRB) method in the programme (Benhamou 2011). H_{min} (minimum smoothing parameter in meters) was set to 100 (standard setting) and L_{min} 10 (the length threshold of movement in meters, i.e. any movement of less than this is considered to be resting). This is less than the standard setting (Cornélis et al. 2011 used an L_{min} of around 50m) as sharks were observed to make very limited movements whilst predating on Cape fur seals, particularly at two locations. I defined these movements as foraging rather than resting in contrast to Johnson et al. (2009); who defined limited movements in acoustically tracked white sharks as resting. When the boundaries of Dyer Island and Geyser Rock were added into the equation, the programme began to stall due to the minimum requirements of boundary lengths within the programme (boundary length cannot be in excess of $3^{x}H_{min}$, in this occasion 300m and angles between segments must not be sharper than 90°). This is an improvement on the original programme settings (Benhamou pers. comm.), yet still not of fine enough resolution to incorporate the boundary lines of Geyser Rock where Shark 2 had spent many hours in close proximity. As a result I used a lower H_{min} value of 50 giving boundary constraints of 150 m, enough to incorporate the boundary lines of Geyser Rock and the kelp ridge to its west without excluding any of the tracked movements of Shark 2. A second boundary was at Dyer Island and a third would have been used along the coastline had either shark's UD extended over it. Once MKDEs were projected they were imported into Arc GIS 10 for display and spatial analysis. Areas were calculated from the 95% and 50% isobars.

An activity area discovery curve was used to observe total activity area over time (e.g. Goldman & Anderson 1999). Minimum Convex Polygons (MCP) were computed for every cumulative hour of movement (i.e. 0-1, 0-2, 0-3 etc.) for each shark. Results were then incorporated into an observation-area curve as in Rechisky & Weatherbee (2003) and Jewell et al. (2012). A 5% change in activity area was used as the minimum tracking time before a UD was deemed a valid representation of home range (Rechisky & Weatherbee 2003). Minimum residencies were determined from first sighting until last detection.

Results

Shark 1 was tagged inshore on 03 September 2010 and identified as a female estimated to be 450 cm in length based on comparison to the 7.5 m research vessel. She had distinctive pigmentation on her dorsal fin and was matched to sightings from Marine Dynamics Shark Tours database in 2007 and 2008 (Fig. 2; Table 1). Shark 2 was tagged at Dyer Island on 11 April 2011 and identified as a male 420 cm in length. The shark is distinctive by pigment scaring on the dorsal fin and a large section of the upper caudal lobe missing. It was satellite tagged in 2004, was used in two previous studies (Bonfil et al. 2005; Jewell et al. 2011) and was also sighted several times at Dyer Island in 2010 and 2012 (Fig. 2).

Table 1. Shark sightings, hours tracked, minimum residency, area covered (MCP) and home range estimates based on MKDE projections.

Shark 1		
	Years Sighted	2007, 2008, 2010
	Hours Tracked	68
	Days Tracked	11
	Min Residency	33 days
	MKDE95 *Hmin* 100	7.91 km^2
	MKDE50 *Hmin* 100	0.99 km^2
	MKDE95 *Hmin* 50	6.66 km^2
	MKDE50 *Hmin* 50	0.77 km^2
	LSCV K95	7.07 km^2
	LSCV K50	0.72 km^2
	MCP	12.18 km^2

Shark 2		
	Years Sighted	2003*, 2009, 2010, 2011, 2012
	Hours Tracked	75.2
	Days Tracked	10
	Min Residency	76 days
	MKDE95 *Hmin* 100	4.93 km^2
	MKDE50 *Hmin* 100	0.27 km^2
	MKDE95 *Hmin* 50	2.48 km^2
	MKDE50 *Hmin* 50	0.10 km^2
	LSCV K95	1.09 km^2
	LSCV K50	0.19 km^2
	MCP	12.16 km^2

* = no data was available from 2004 – 2006

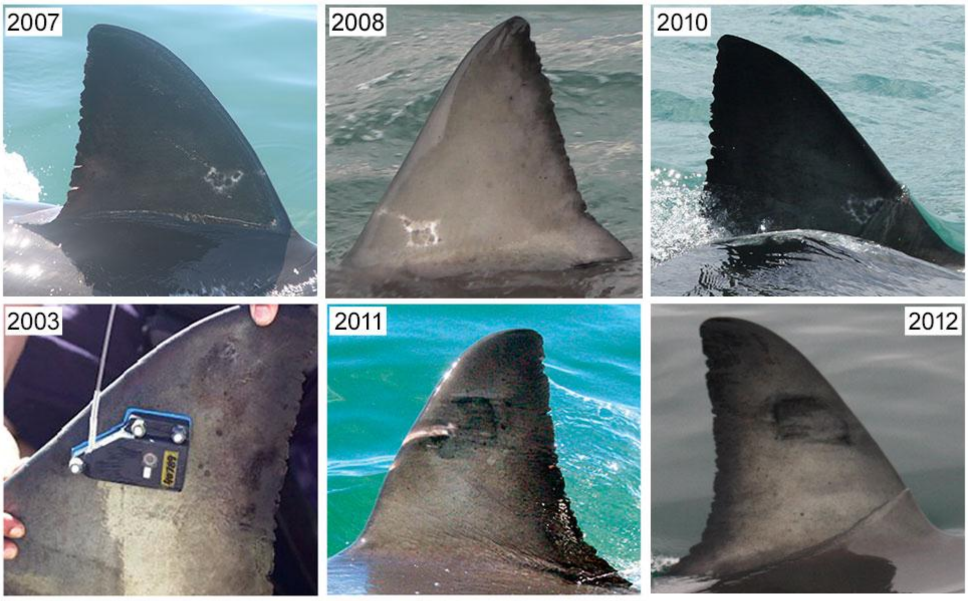

Figure 2. Dorsal fin IDs of both study animals. Both individuals also have distinctive features within the face of the fin which assists identification;
Shark 1 has natural pigmentation or a 'rosie' and Shark 2 has pigmentation scaring from a SPOT tag transmitted placed on its dorsal fin in 2004, it is also missing its upper caudal lobe.

Sharks were actively tracked for a total duration of 143 hours (68 and 75 hrs, respectively) over total areas (MCP) of 12.18 km^2 inshore (Shark 1) and 12.16 km^2 around Dyer Island (Shark 2). MKDEs were computed at both Hmin 100 (not incorporating boundaries) and H_{min} 50 (incorporating boundaries); with H_{min} set to 100, values of; 7.91 km^2 (95% isobar) and 0.99 km^2 (50% isobar) were produced for Shark 1 and 4.93 km^2 (95% isobar) and 0.77 km^2 (50% isobar) for Shark 2. With H_{min} set to 50; 6.66 km^2 (95% isobar) and 0.27 km^2 (50% isobar) Shark 1 and 2.48 km^2 (95% isobar) and 0.10 km^2 (50% isobar) for Shark 2 (Fig. 3 – 4). Location-based kernel estimates produced similar yet comparatively smaller UD estimates than MKDEs for Shark 1 at both 95 & 50% isobars and markedly smaller UD for Shark 2 for the 95% isobar (Fig.5). Both traditional estimates extended onto land and the entire area of Geyser Rock was covered by Shark 2's 95% isobar and encroached upon by the 50% isobar. The H_{min} 50 MKDE was the only UD produced for Shark 2 that did not cover any of Geyser Rock or Dyer Island.

Shark 1 intensively used two areas within its home range. One of these corresponded to the reef at Joubertsdam and the second was at a kelp reef east of this location, where the shark had successfully predated upon a Cape fur seal near the kelp line.

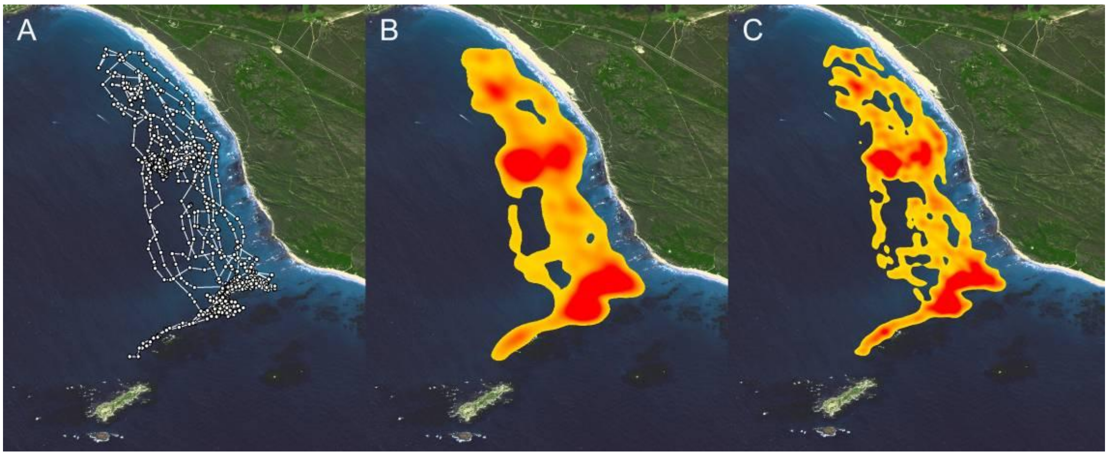

Figure 3. 68 hrs of active tracking movements of Shark 1 over a 2 month period (A). MKDE projection applied with H_{min}100 smoothing parameter (B). MKDE projection applied with H_{min}50 smoothing parameter (C).

Shark 2 extensively utilised the area of Shark Alley and was found or tracked into the channel on a total of 7 occasions during the 10 days of tracking. Within this area the shark was observed to successfully predate on a Cape fur seal and made several other unsuccessful attempts, all within close proximity to Geyser Rock.

Minimum residency of Shark 1 was 33 days based on first and last detections and 76 days for Shark 2 based on first photo ID and last detection. Discovery curves produced from MCP reached their highest levels at 55 hrs (Shark 1) and 62 hrs (Shark 2; Fig. 6A). The observation area curve reached a value of 5% change in MCP at 35 hrs (Fig.6B).

Discussion

The two sharks used markedly different home ranges. This may represent seasonal change in habitat use from winter, when the species utilise Cape fur seal colonies as a food resource, to summer when they utilise reef systems (Towner 2012). The first shark tracked utilised reef and kelp reef areas intensively. One feeding event was observed on a Cape fur seal at the kelp reefs to the eastern limit of its UD, it is also likely that other feeding events took place here subsurface with kelp forests known to harbour a host of teleost and elasmobranch species (Steneck et al. 2002).

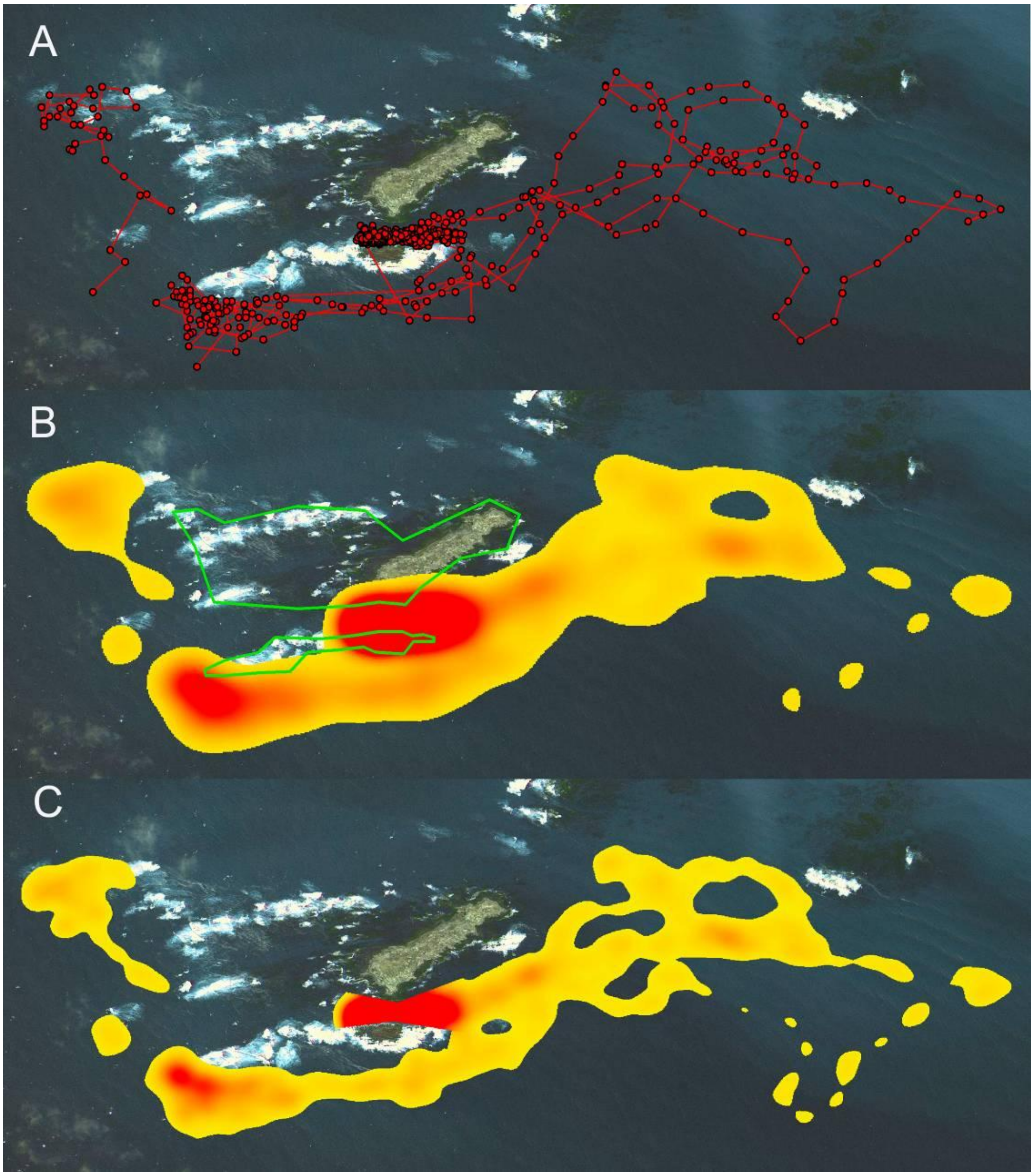

Figure 4. Active tracking movements of Shark 2 over 1 month and 75 hrs (A). MKDE projection applied with Hmin100 smoothing parameter with areas of rock, shallow ridge and kelp which are not useable by the shark highlighted (B). MKDE projection applied with Hmin50 smoothing parameter and boundaries successfully accounted for in projection (C).

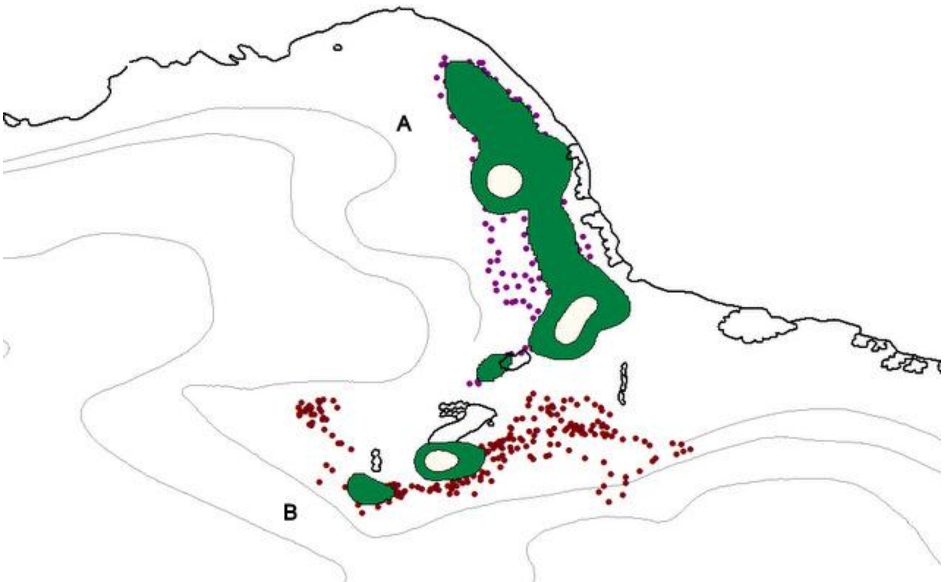

Figure 5. (above) Traditional location-based kernel estimates using LSCV smoothing parameters (Jewell et al. 2012) for Shark 1 (A) and Shark 2 (B).

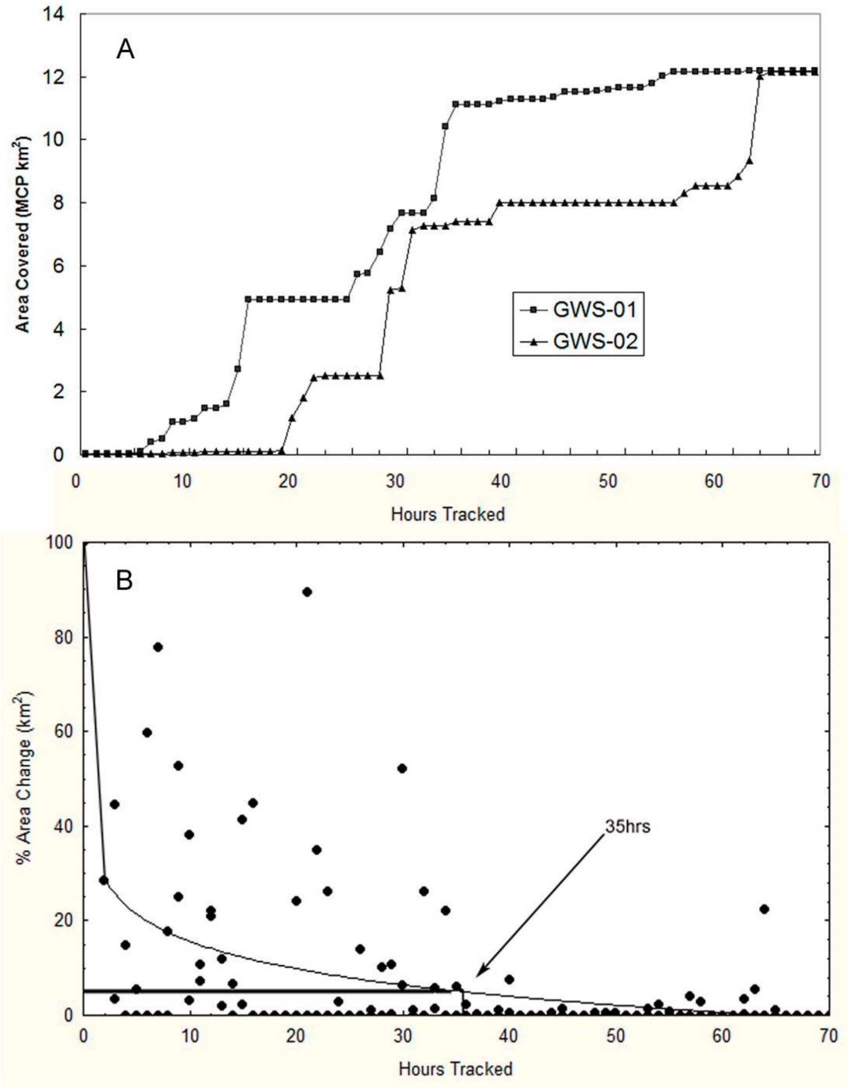

Figure 6. (left) Discovery curves of both Shark 1 and Shark 2 (A) when comparing activity area (MCP) over time. Observation area curve based on 5% change (B), the result suggests the minimum tracking time to estimate home range in the Dyer Island area is 35 hrs.

The second of the two sharks was tracked during winter, and its home range included the seal colony at Geyser Rock. The most intensively utilised area was the narrow channel between the two islands, where the shark would patrol for many hours in small area moving close to the rafting groups of seals and make repeated predation attempts. Other areas of the home range less intensively used included the area known as the Drop Zone where seals swim from a shallow ridge covered in kelp at Dyer Island into deeper water on their way to forage offshore (Wcisel pers. comm.) and the Geldsteen reef (Fig. 4). At night the shark migrated to the east to utilise a reef system or moved further offshore into deeper waters. This behaviour may be related to light levels with movement patterns observed in other sharks suggesting that when light levels are too low white sharks utilise other resources and return to forage on seals when light levels improve (Johnson et al. 2009; Chapter 3).

The differences between the MKDE and traditional kernel estimates are apparent when compared. In Shark 1's UDs the location-based kernel stretched onto land and also extended into the kelp forest to the west, the MKDE of the same tracking data did not. The location-based kernel also became more clumped over the spots the sharks patrolled and areas of tracks only migrated through were not covered by the UD (Fig.5B). Despite giving smaller values, more of the estimate extended over land in all cases, most notably in Shark 2's K95% estimate. Providing the boundary lines of the coast are within the $3^{x}H_{min}$, constraints of the programme and less than 90º in angle, the MKDE method will outperform the traditional kernel estimates in any coastal UD estimates. The island system proved too complex for the programme to compute with Hmin set to 100, however, lowering the smoothing parameter allowed the finer scaled boundaries to be incorporated into the computation without compromising or biasing areas which were intensively exploited by the sharks (this study). If the programmes constraints could be lifted further (i.e. smaller minimum segments and smaller angles) any study limited by heterogeneous structures such as islands (which will often have angles less than 90º) would be able to use the method to account for movements around structures.

The activity area curve and photo ID resightings of the individuals over several years suggest that the UDs given in this investigation are a valid representation of both sharks' temporary and seasonal home ranges within waters adjacent to Dyer Island. At night it appears that shark 2 was using larger areas than during the day and it is possible that there may have been movements outside of the home range during this time. However, within daylight hours the shark was successfully located at every attempt in areas within the home range and was also detected in the channel post-tracking for a time while another shark was being tracked (pers. observation). The main weakness with active tracking is the limitations of weather patterns and the effort required to build up long tracks. Given that the area is exposed to the open ocean and weather in the Western Cape is often harsh; efforts of manual tracking are unlikely to exceed durations attained in the present study; for longer tracking passive acoustic telemetry is preferable. The two methods could be employed side by side in the same manor of Simpfendorfer et al. (2010) or Johnson et al. (2009) with receivers placed within the home ranges highlighted in this, and likely future studies, to better quantify whether patterns in shark movements and home range are more individualistic or follow a general pattern.

No habitat map exists for the area as no bathymetric survey has ever taken place there. Reefs were mapped from satellite imagery, kelp reefs defined as the habitat adjacent to kelp forest, and kelp as the areas which are covered by kelp forest. Further and deeper offshore areas are as yet undocumented but may be covered by surveys at a later date. Once a more detailed map is available the Biased Random Bridges (BRB) habitat use analysis used by Benhamou (2011) and Cornélis et al. (2011) could be applied to further this study.

The results from in this study provide a tried and tested method of home range analysis, previously used on terrestrial animal movements, and now successfully applied to the marine environment. The MKDE method is preferable in coastal or complex marine systems, computing unbiased UDs, despite obstruction from island systems and highlighting areas either used intensively or not used by the animal in a more accurate way than traditional home range methods. Such improvements aid the understanding of predators' movements in complex coastal locations which in turn can aid policy makers' decisions regarding the conservation of such species.

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Chapter 3: Site Specific Foraging Ecology of the South African White Shark

Abstract

White shark (*Carcharodon carcharias*) foraging at Cape fur seal (*A. pusillus pusillus*) colonies is well documented at two sites in South Africa; Mossel Bay and False Bay. Acoustic telemetry of sharks tagged and tracked at a third location, Dyer Island, Gansbaai, revealed novel foraging patterns, distinct from the previously documented areas. White sharks at Dyer Island utilised small areas within a shallow channel next to the seal colony or close to kelp forest adjacent to it (day time activity areas = 0.67 km^2 ± 0.38). Foraging close to the seal colony did not peak at dawn and dusk as observed in Mossel Bay and False Bay. Instead foraging took place during times of high ambient light (i.e. daylight or moonlight). When moonlight levels decreased, sharks moved into deeper water or patrolled distant reefs before returning to forage close to the seal colony during the day. Linearity (LI) and Rate of Movement (ROM) were lower during daytime than night (LI = 0.72 day, 0.96 night, ROM = 0.28 m/s^{-1} day, 0.75 m/s^{-1} night), and showed either no significance (ROM = 0.31 adult, 0.30 sub-adult $P = 0.9$) or little variance when compared to body size (LI = 0.73 adult, 0.80 sub-adult). Home range and activity areas were smaller than found in Mossel Bay and also independent of shark body size. The target prey is the same at all three locations, and a significant number of known sharks forage in at least two or all three of the locations, including one of the sharks tagged in this study. This suggests that white sharks are able to adapt their foraging behaviour to suit the environment they are in, in order to utilize prey resources efficiently.

Key Words

Carcharodon carcharias, swimming patterns, home range, activity area, Dyer Island

Introduction

As top predators; understanding the patterns of habitat use and foraging behaviour of sharks is crucial in order to gain insight into ecosystem dynamics (Heithaus et al. 2002). The global decline in shark populations is of concern as their role as ecosystem moderators is assumed but not fully understood (Dulvy et al. 2008; Myers et al. 2007; Barnet et al. 2010; Simpfendorfer et al. 2010; Speed et al. 2010). The white shark (*Carcharodon carcharias*) is globally threatened and despite receiving protection in most of the world's oceans trade has continued in its fins, teeth and jaws (Fergusson et al. 2005; Shiviji et al. 2005). South Africa is thought to host one of the most abundant populations of the species and distributions are often found close to Cape fur seal (*Arctocephalus pusillus pusillus*) colonies (Compagno 1991).

The presence of white sharks at aggregation sites near pinniped colonies has been the focus of many studies which account for a large portion of our knowledge on the species (e.g. Bruce 1992; Strong et al. 1992; Klimely et al. 2001; Bruce et al. 2005; Martin et al. 2005; Domeier & Nasby Lucas 2007; Chapple et al. 2011; Anderson et al. 2011; Domeier et al. 2012; Domeier 2012). Colonies are often either shore based or on rookeries close to the shoreline and interactions between white sharks and pinniped species often take place at the sea surface (Klimely et al. 1992; Martin et al. 2005; De Vos & O'Riain 2010). At these rookeries distinct patterns in white shark foraging coincide with optimum periods of predation (Klimely et al. 2001; Laroche et al. 2008; Johnson et al. 2009). Active tracking of sharks within these sites allow a unique insight into their spatial dynamics, foraging effort and habitat use (Strong et al. 1992; Goldman & Anderson 1999; Johnson et al. 2009).

Much work has been published on foraging of white sharks in False Bay (Martin et al. 2005; Hammerschlag et al. 2006; Laroche et al. 2008) and Mossel Bay (Johnson et al. 2009; Jewell et al. 2012) yet relatively little has been produced for the Gansbaai Dyer Island system. Sharks were found to increase foraging effort at dawn in False Bay (Hammerschlag et al. 2006; Laroche et al. 2008) and both dawn and dusk at Mossel Bay (Johnson et al. 2009). The current study generates manual tracking data to quantify whether such foraging ecology is similar in the Dyer Island system which varies greatly in topography from both Mossel Bay and False Bay.

Study Site

The presence of two islands with surrounding kelp forest, reef systems and rocky outcrops make the Dyer Island system unique when compared to other white shark aggregation areas described in South Africa. The larger of the two islands, Dyer Island, is approximately 15 ha in area and a protected sanctuary for African penguin and four species of cormorant (Dept. of Environmental Affairs, unpublished data). The smaller island, Geyser Rock, is home to a colony of approximately 55 – 60,000 Cape fur seals (Dept. of Environmental Affairs, unpublished data) and the two islands are separated by a narrow channel of water approximately 200 m across with 6 – 7 m maximum depth. This channel is locally known as ‘Shark Alley’ (Figure 1). During austral winter (April – August) sharks are observed in this channel feeding on Cape fur seals (Johnson et al. 2008). Major reef systems are found to the west (Geldsteen) and east of the islands, whilst to the south of Geyser Rock the bottom drops to 20 – 30 m. A ridge runs from Geyser Rock west to the Geldsteen/Drop Zone area, which is covered in kelp. Direct comparisons are made between foraging at this location and previously published works from Mossel Bay using similar methods of active tracking (Johnson et al. 2009; Jewell et al. 2012) and from False Bay using passive monitoring (Laroche et al. 2008). Mossel Bay is home to a colony of approximately 5,500 Cape fur seals (Dept. of Environmental Affairs, unpub. data) but has no kelp forest or rocky outcrops nearby, and False Bay host a colony of approximately 77,000 Cape fur seals without heterogeneous structures or kelp forests nearby.

Methods

Shark Tagging and Tracking

Sharks were attracted to a research vessel using a baited line and waste teleost products (chum) (see Strong et al. 1992). Once in the vicinity of the vessel sharks were sized based on comparison to known dimensions of the vessel. Photo ID of the sharks’ first dorsal fin was used to identify the shark based on previous sightings from Marine Dynamics cage diving vessels (as in Chapple et al. 2011). Tags used were Vemco V-16TP (recording temperature (T) and depth (P)) 51 – 82 kHz ultrasonic

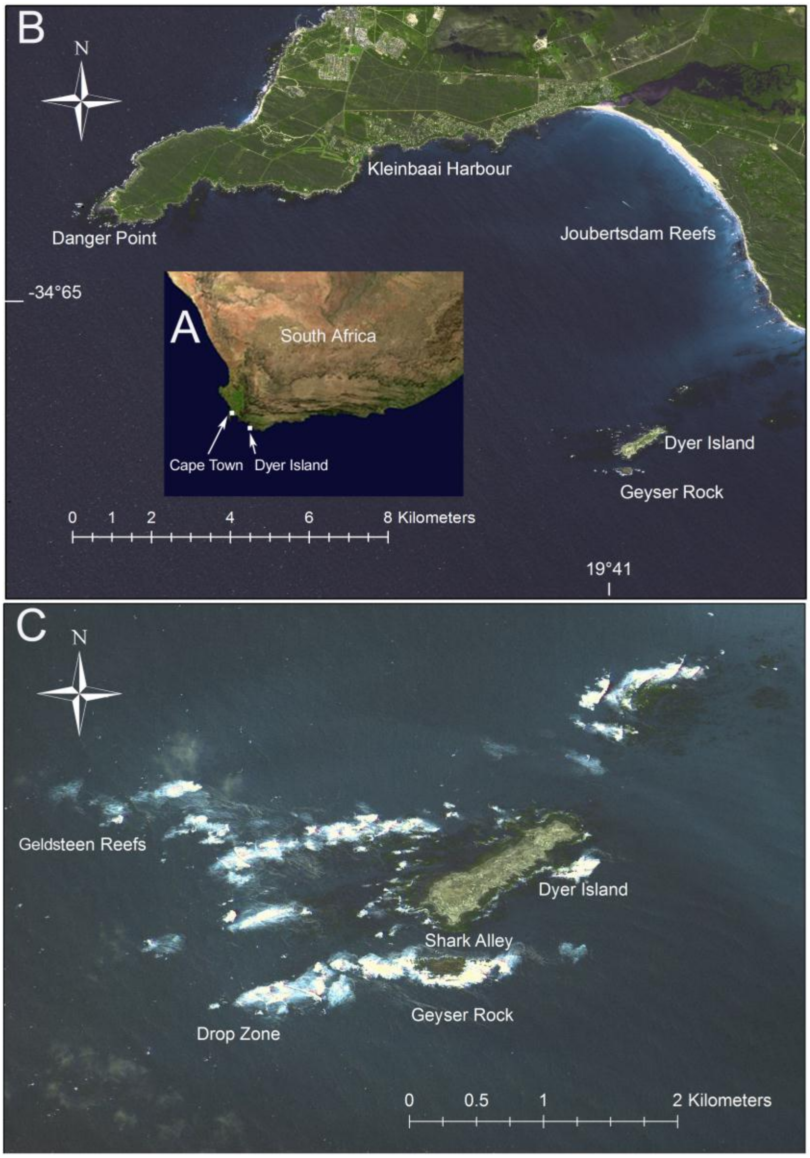


Figure 1. Study Site: Dyer Island is located at approximately 34º68’S, 19º41’E, 200 km south-east of Cape Town and 9 km from Kleinbaai Harbour (A, B). Adjacent to the main island is a large rocky outcrop known as Geyser Rock which hosts a colony of 55 – 60,000 Cape fur seals. There are also several other smaller rocky outcrops, submerged ridges and kelp forest. White water (C) indicates shallow reefs, ridges and kelp forest hazardous for boating.

continuous pingers (Voegeli et al. 2001). Tags were fitted with a brush-tip head to reduce shedding (Johnson unpublished data) which was attached to the main casing of the tag with a wire tether. To reduce algal growth both tags and tethers were painted with anti-fouling paint; such growth can be excessive in Southern African waters and can interfere with tag performance and increase drag (Jewell et al. 2011). A tagging pole with a spear-tip head was used to place the tags at the base of the dorsal fin. Once tags were placed tracking protocol was set up in a similar method to those used in Johnson et al. (2009) and Jewell et al. (2012). Sharks were tracked using a boat based VR100 with a VH110 (50 – 85 kHz) directional hydrophone. Sharks showed little reaction to tagging and after the initial time taken to prepare for tracking (± 10 minutes) movements had returned to normal. Sharks were tracked at a distance of approximately 20 – 40m (60-80 dbl, VR100 set to manual gain 0 – 24; Johnson et al.

2009), an equipment failure meant positions could not be corrected further as in Heithaus et al. (2002) and tracking closer was deemed to interfere with sharks movements (Johnson et al. 2009).

Positions were recorded every 5 minutes, if the signal could not be received (for instance if there was an obstruction) recordings resumed upon reception of the next signal. At the start of a new tracking session a VH165 (50 – 85 kHz) omni-directional hydrophone was used to detect a shark's transmitter; transects were run throughout the bay until such a signal was detected. Upon receiving these transmissions the omni-directional hydrophone would be switched for the directional hydrophone and tracking would resume. The methods of tagging and tracking were approved and permitted by the Department of Environmental Affairs, Oceans and Coasts.

Data analysis

Rate of Movement

Spatial data was analysed using ArcMap 10 and the Animal Movement extension of ArcView 3.2. Rate of Movement (ROM) in meters per second (m/s^{-1}) was determined by calculating the distance between consecutive positions and dividing by time elapsed (Strong et al. 1992; Johnson et al. 2009). ROM cannot be considered a swimming speed because it does not incorporate error, vertical changes or currents and assumes that the movement has been in a straight line from point to point (Sundström et al. 2001).

Swimming linearity

Linearity of sharks' individual tracks was determined using the Linearity Index (LI) of Bell & Kramer (1979) and used by Sundström et al. (2001), Johnson et al. (2009) and Jewell et al. (2012):

$$LI = (F_n - F_1)/D$$

Where $F_n - F_1$ is the distance between first and third position taken for the shark and D is the total distance travelled by the shark. A linearity of 1 indicates linear movement (i.e. straight line travel). A LI near zero indicates little movement from the area with a great deal of overlap and reuse of the activity space.

Distance from Geyser Rock

Swimming distance from the seal colony was used to asses if certain times of the day are more devoted to foraging on seals than others. The distance was measured from position (at 5 min intervals) to the nearest point of Geyser Rock using the measuring tool from ArcMap 10. Seals use the shallow ridge and kelp to the east of Geyser Rock as a refuge (Wcisel pers. comm.); as such the kelp ridge was included as an extension of Geyser Rock. Similarly the thick areas of kelp at the Geldsteen reefs were also included as an extension of refuge.

Activity areas and home range

Activity areas were determined for each of the shark tracks using Minimum Convex Polygon (MCP Goldman & Anderson 1999; Jewell et al. 2012). A discovery curve was used to observe total activity area over time. MCPs were computed for every accumulated hour of movement (i.e. 0-1, 0-2, 0-3 etc.) for each shark. Results were then incorporated into an observation-area curve to determine optimum tracking time for white sharks at Dyer Island (Rechisky & Weatherbee 2003; Jewell et al. 2012).

Utilisation Distribution (UD) was measured using the Movement-based Kernel Density Estimate (MKDE) programme (Benhamou & Cornélis 2010). This method of kernel projection outperforms traditional methods by ignoring local movement information provided by the serial correlation between successive locations and incorporating the movement itself (Benhamou & Cornélis 2010). The method also incorporates the boundaries of Dyer Island, Geyser Rock and the denser areas of kelp and ridge.

Index of Reuse

The day to day usage was compared using an Index of Reuse (IOR) as in Jewell et al. (2012) using one days/nights activity area to the next:

$$IOR = [OV(A1 + A2)]/(A1 + A2)$$

Where [OV(A1+A2)] is the area of overlap between two activity areas and (A1 + A2) is the total area of both activity areas (Morrissey & Gruber (1993) modified from Cooper (1978) and McKibben & Nelson (1986)).

Results

Individual Tracks

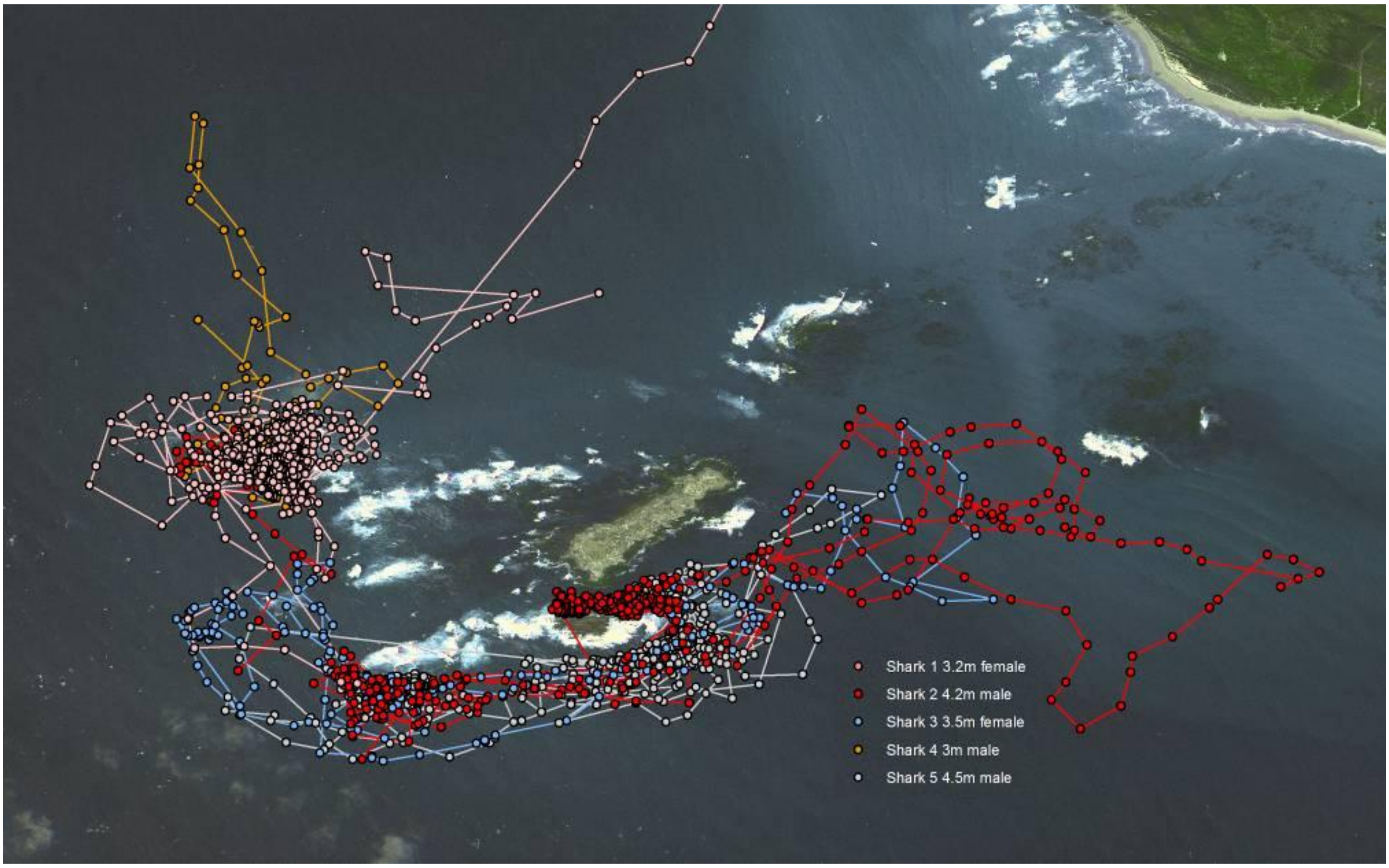
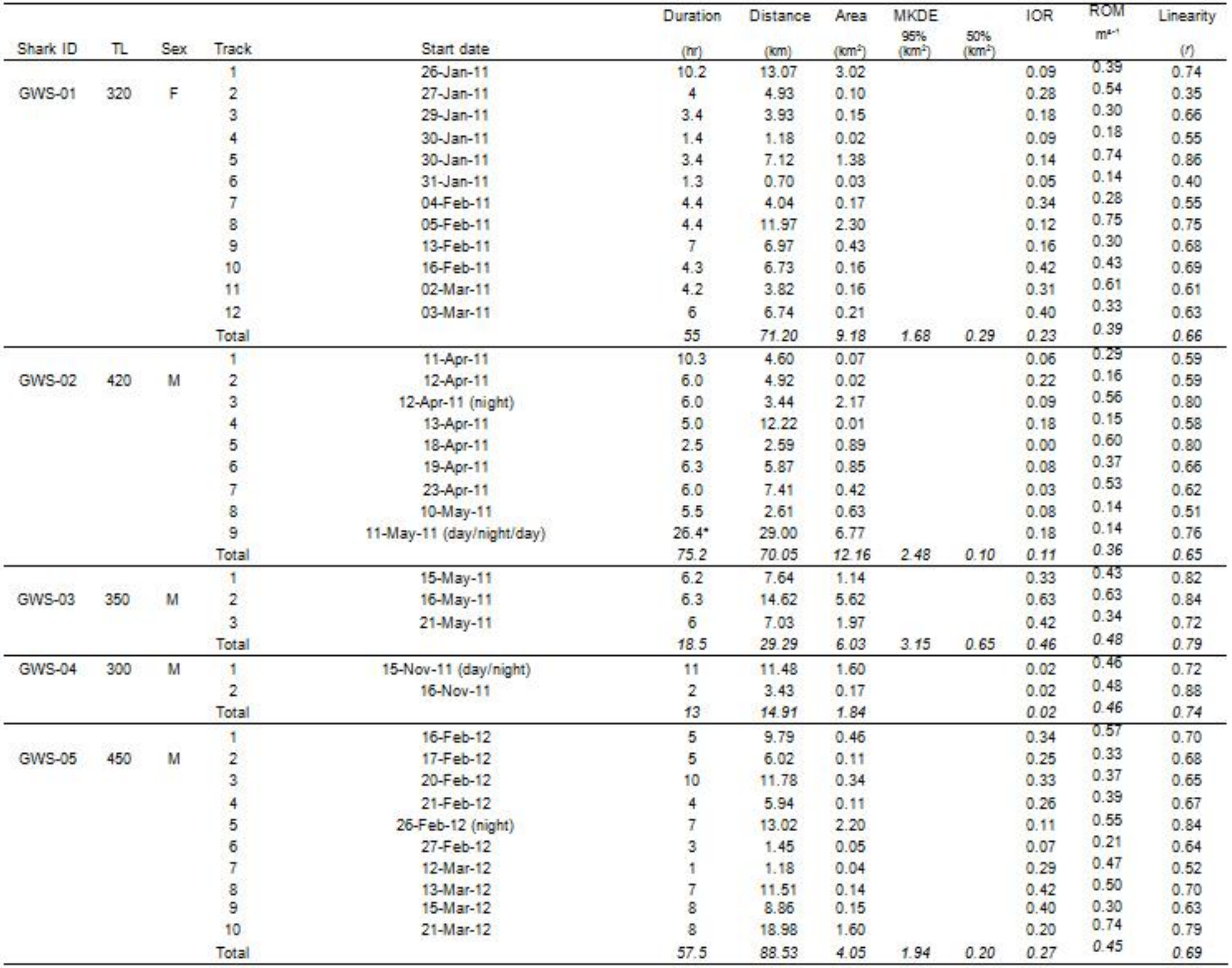


Figure 2. Total tracking effort around Dyer Island; Shark 1 was tagged in the inshore reefs at Joubertsdam and moved to the Geldsteen where it remained for the duration of its track. Sharks 2, 3, 4 and 5 were all tagged at Dyer Island in Shark Alley (Sharks 2 and 5), the Drop Zone (Shark 3) or the Geldsteen reefs (Shark 4).

Total tracking exceeded 220 hrs with a majority of the tracking taking place at the Geldsteen reefs, Drop Zone, areas south of Geyser Rock, Shark Alley and reefs to the east of Dyer Island (Table 1; Figure 2). Shark 1, a 3.2m sub-adult female, was tagged in the Joubertsdam reefs and tracked for 55 hrs over 36 days from 26th Jan 2011 – 03rd March 2011. It reached the Geldsteen reefs within 4 hrs of being tagged 5.8 km away and stayed within this vicinity, or close by, for the remainder of tracking. During this period heavy fog was prominent on most wind free days which limited tracking to daylight hours only. Linearity (LI) values per track ranged from 0.35 – 0.75, with an overall average of 0.66 (95% Confidence 0.03). Rate of Movement (ROM) averaged 0.39 m/sec^{-1} (95% Confidence 0.03). The combined track covered a distance of 71.20

Table 1. Details of 36 manual tracks of 5 white sharks at Dyer Island, totalling over 220 hrs of data. Values of ROM, LI, IOR, activity areas and MKDE are included.

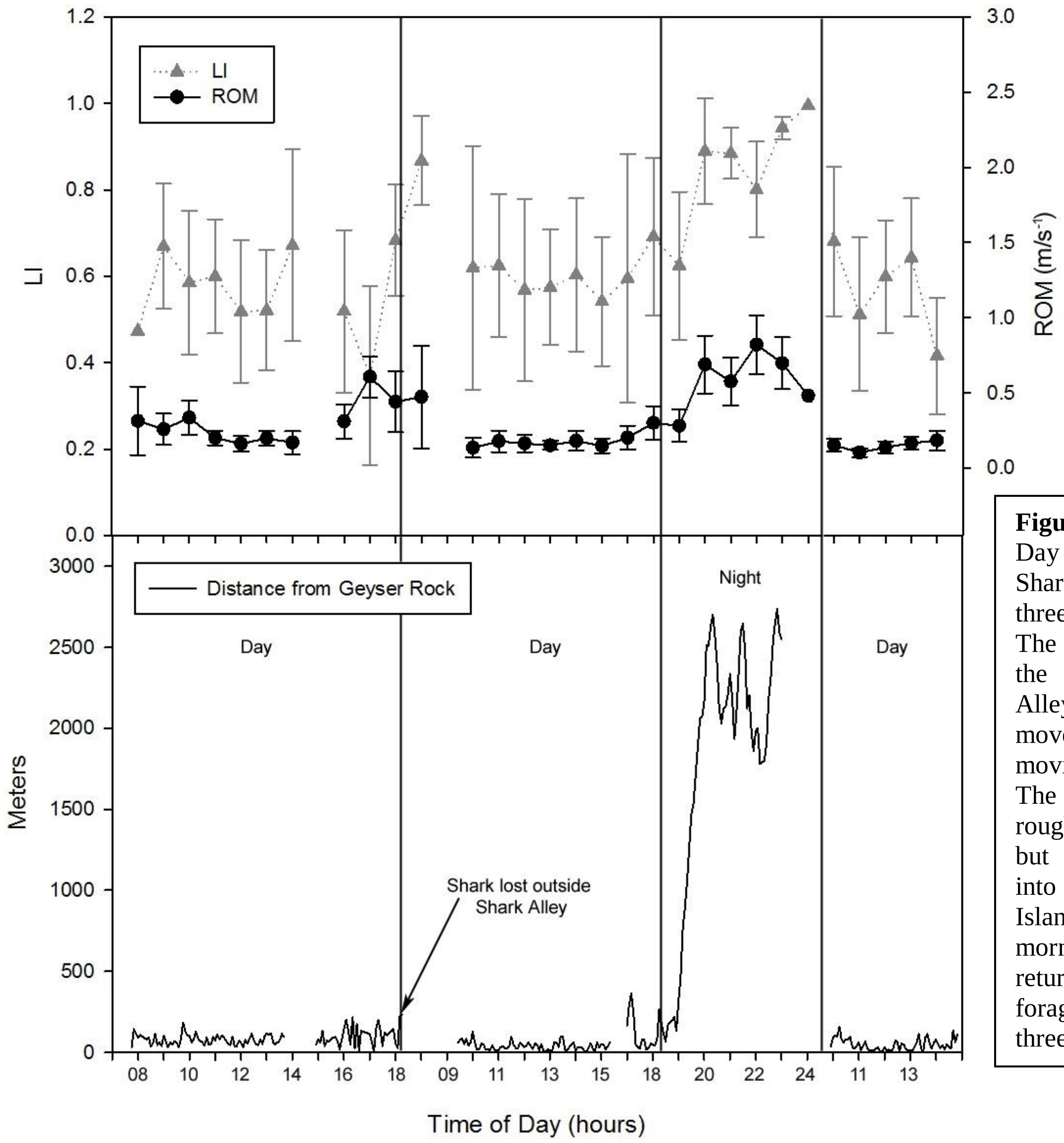


Shark ID	TL	Sex	Track	Start date	Duration (hr)	Distance (km)	Area (km^2)	MKDE 95% (km^2)	50% (km^2)	IOR	ROM m^{a-1}	Linearity (r)
GWS-01	320	F	1	26-Jan-11	10.2	13.07	3.02			0.09	0.39	0.74
			2	27-Jan-11	4	4.93	0.10			0.28	0.54	0.35
			3	29-Jan-11	3.4	3.93	0.15			0.18	0.30	0.66
			4	30-Jan-11	1.4	1.18	0.02			0.09	0.18	0.55
			5	30-Jan-11	3.4	7.12	1.38			0.14	0.74	0.86
			6	31-Jan-11	1.3	0.70	0.03			0.05	0.14	0.40
			7	04-Feb-11	4.4	4.04	0.17			0.34	0.28	0.55
			8	05-Feb-11	4.4	11.97	2.30			0.12	0.75	0.75
			9	13-Feb-11	7	6.97	0.43			0.16	0.30	0.68
			10	16-Feb-11	4.3	6.73	0.16			0.42	0.43	0.69
			11	02-Mar-11	4.2	3.82	0.16			0.31	0.61	0.61
			12	03-Mar-11	6	6.74	0.21			0.40	0.33	0.63
			Total		*55*	*71.20*	*9.18*	*1.68*	*0.29*	*0.23*	*0.39*	*0.66*
GWS-02	420	M	1	11-Apr-11	10.3	4.60	0.07			0.06	0.29	0.59
			2	12-Apr-11	6.0	4.92	0.02			0.22	0.16	0.59
			3	12-Apr-11 (night)	6.0	3.44	2.17			0.09	0.56	0.80
			4	13-Apr-11	5.0	12.22	0.01			0.18	0.15	0.58
			5	18-Apr-11	2.5	2.59	0.89			0.00	0.60	0.80
			6	19-Apr-11	6.3	5.87	0.85			0.08	0.37	0.66
			7	23-Apr-11	6.0	7.41	0.42			0.03	0.53	0.62
			8	10-May-11	5.5	2.61	0.63			0.08	0.14	0.51
			9	11-May-11 (day/night/day)	26.4*	29.00	6.77			0.18	0.14	0.76
			Total		*75.2*	*70.05*	*12.16*	*2.48*	*0.10*	*0.11*	*0.36*	*0.65*
GWS-03	350	M	1	15-May-11	6.2	7.64	1.14			0.33	0.43	0.82
			2	16-May-11	6.3	14.62	5.62			0.63	0.63	0.84
			3	21-May-11	6	7.03	1.97			0.42	0.34	0.72
			Total		*18.5*	*29.29*	*6.03*	*3.15*	*0.65*	*0.46*	*0.48*	*0.79*
GWS-04	300	M	1	15-Nov-11 (day/night)	11	11.48	1.60			0.02	0.46	0.72
			2	16-Nov-11	2	3.43	0.17			0.02	0.48	0.88
			Total		*13*	*14.91*	*1.84*			*0.02*	*0.46*	*0.74*
GWS-05	450	M	1	16-Feb-12	5	9.79	0.46			0.34	0.57	0.70
			2	17-Feb-12	5	6.02	0.11			0.25	0.33	0.68
			3	20-Feb-12	10	11.78	0.34			0.33	0.37	0.65
			4	21-Feb-12	4	5.94	0.11			0.26	0.39	0.67
			5	26-Feb-12 (night)	7	13.02	2.20			0.11	0.55	0.84
			6	27-Feb-12	3	1.45	0.05			0.07	0.21	0.64
			7	12-Mar-12	1	1.18	0.04			0.29	0.47	0.52
			8	13-Mar-12	7	11.51	0.14			0.42	0.50	0.70
			9	15-Mar-12	8	8.86	0.15			0.40	0.30	0.63
			10	21-Mar-12	8	18.98	1.60			0.20	0.74	0.79
			Total		*57.5*	*88.53*	*4.05*	*1.94*	*0.20*	*0.27*	*0.45*	*0.69*

km within an area (Minimum Convex Polygon, MCP) of 9.02 km^2. One attempted predation was observed during track 8; a sub-adult Cape fur seal was chased but not captured north-west of Dyer Island.

Shark 2, a 4.2m adult male, was tagged in the mouth of Shark Alley and tracked for 75.2 hrs from April 11th – May 12th 2011. Daytime movements were often limited to the vicinity of Shark Alley or the Drop Zone with the occasional movement recorded between the two and one track recorded in the Geldsteen reefs. On day one the shark limited its movements to an area of 0.07 km^2 within Shark Alley (Figure 3A) where it remained until nightfall, it then moved out of the channel and was lost in heavy swells. The next morning the shark was found in Shark Alley and limited its day movements to an area of 0.2 km^2 before moving away at nightfall to a reef east of Dyer Island. LI rose from 0.59 during the day to 0.80 at night and ROM from 0.16 to 0.56 from day to night. The following morning the shark was found back in the same area as on the previous day where it remained for the duration of the track. Index of Reuse (IOR) between day 2 and 3 was 0.71, the second highest recorded in this study. Between the 11th and 12th of May a 27 hr continuous track was interrupted only by changeovers of crew (Figure 3B). The shark limited its day movements to Shark Alley before being lost through a narrow channel between kelp and rock at west end of Geyser Rock. At this point a crew change over was made and the shark was found after nightfall patrolling to the South of Geyser Rock. Seals were seen and heard moving through this area although exact numbers and movement direction were not quantified. After moonset the shark moved away from Geyser Rock into deeper waters reaching a maximum distance of 3.9 km from the seal colony before turning back and entering Shark Alley at dawn. During this traverse the average LI was 0.91, average ROM 0.80 and average swimming depth 11.25 m. There were a total of 6 predation events during tracking with 1 successful kill in Shark Alley and 5 unsuccessful attempts close to the rocks where the seals rafted. Other sharks were also observed predating on seals in this area.

Shark 3, a 3.5 m sub-adult male, was tagged in the Drop Zone and tracked for 19 hrs from 15th – 21st May 2011. Its movements extended from south of the Geldsteen reefs to east of Dyer Island. A technical error with tracking equipment lead to the first night



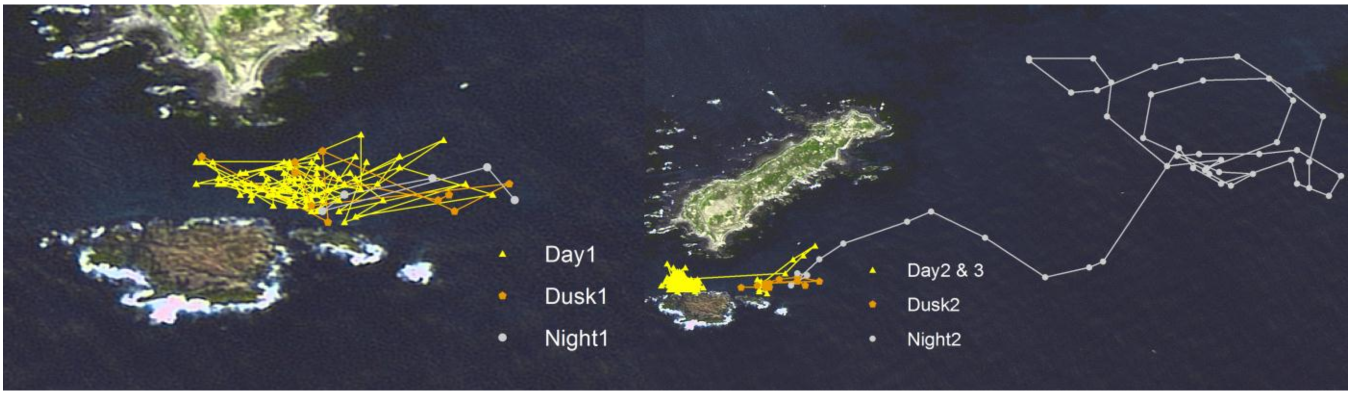


Figure 3A.
Day and night tracks of Shark 2 from the first three days of tracking. The shark stayed within the vicinity of Shark Alley for day time movements before moving away at night. The shark was lost in rough seas the first night but successfully tracked into a reef east of Dyer Island in the second. By morning the shark had returned to Shark Alley foraging in each of the three day tracks.

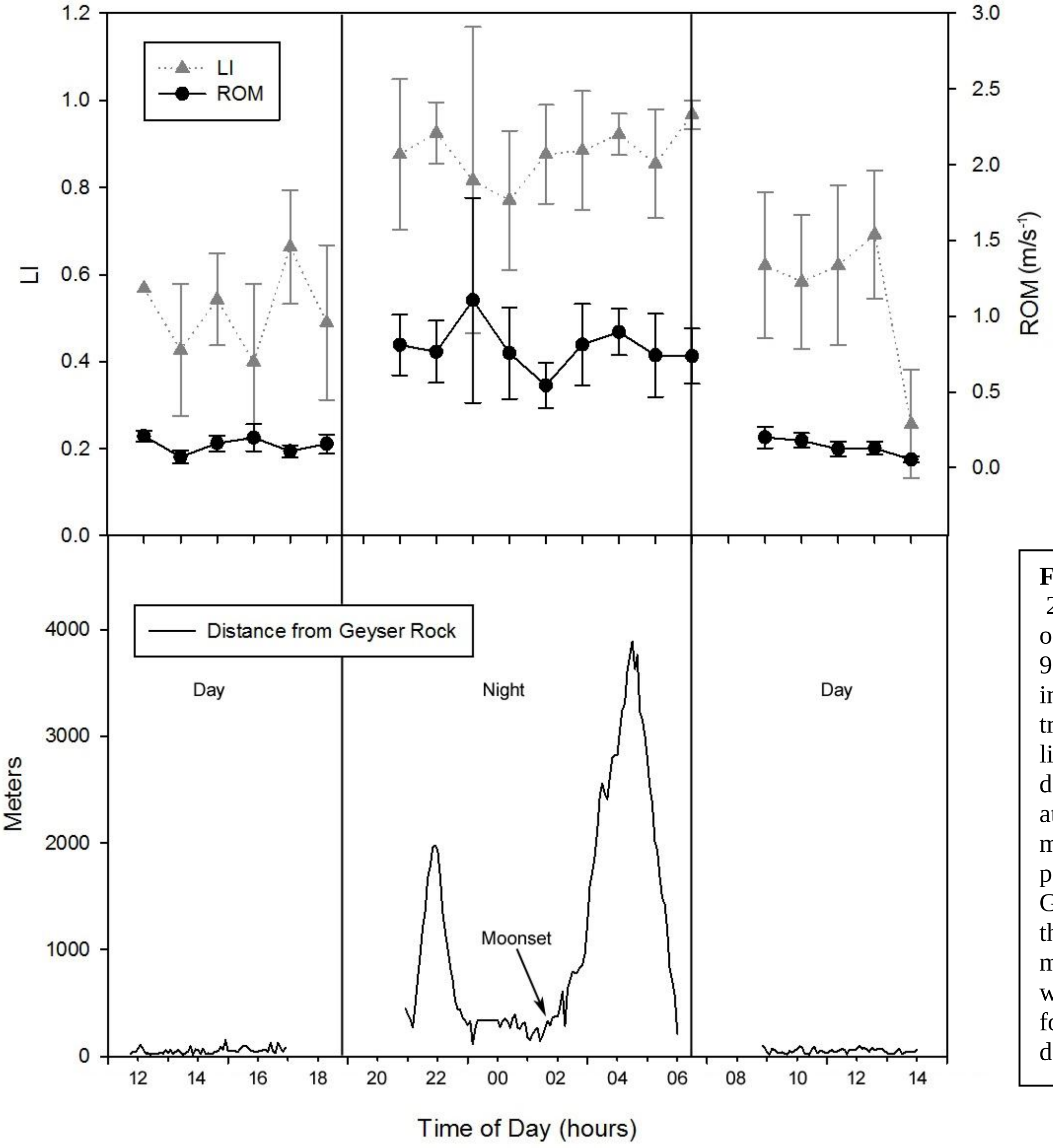
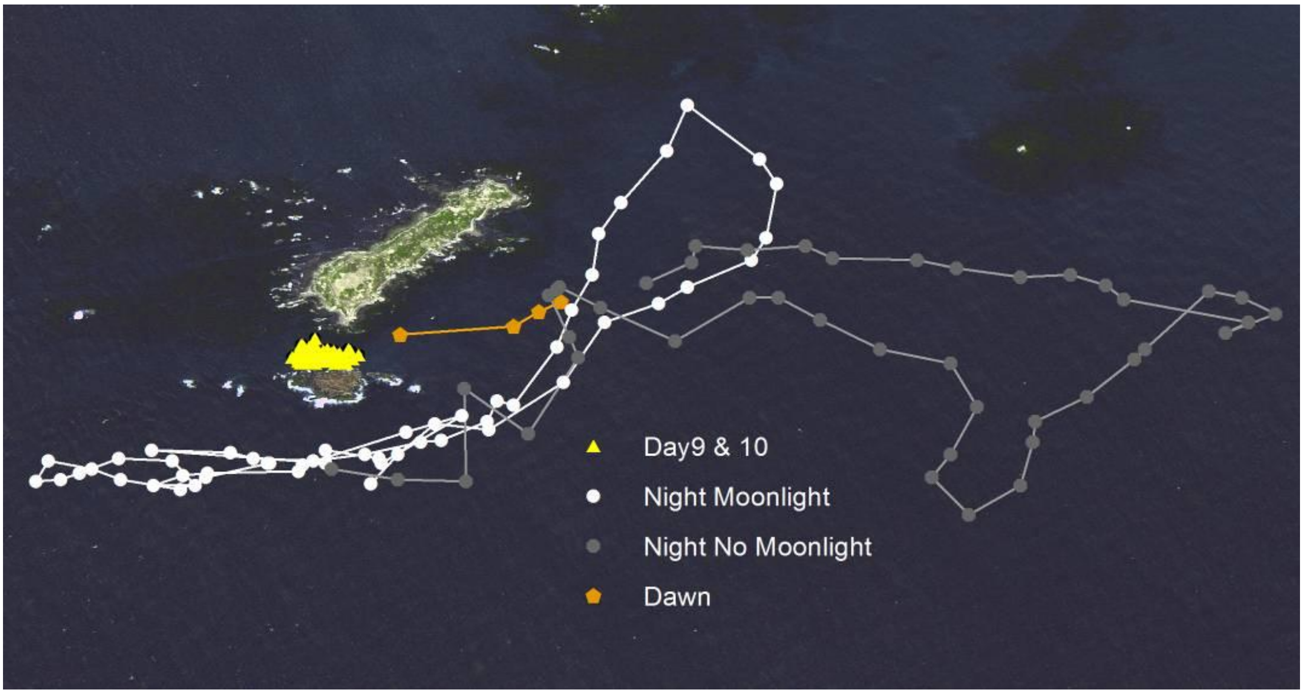


Figure 3B.
27 hr continuous track of Shark 2 between days 9 and 10 of tracking. As in previous day time tracks movement was limited to Shark Alley by day and further offshore at night. Under strong moonlight the shark patrolled the South of Geyser Rock and after the moonset the shark moved east into deeper water before returning to forage in Shark Alley at dawn.



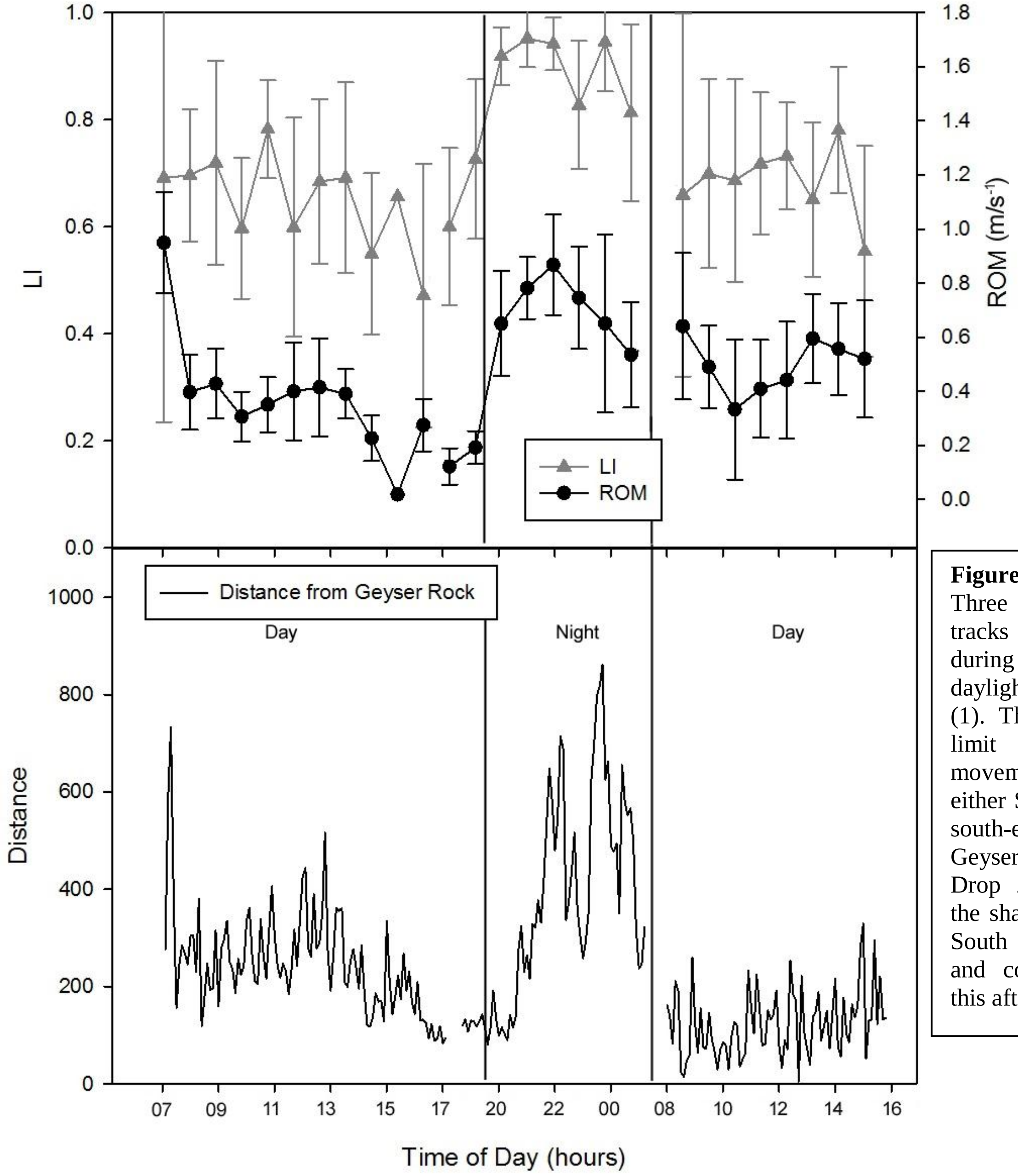
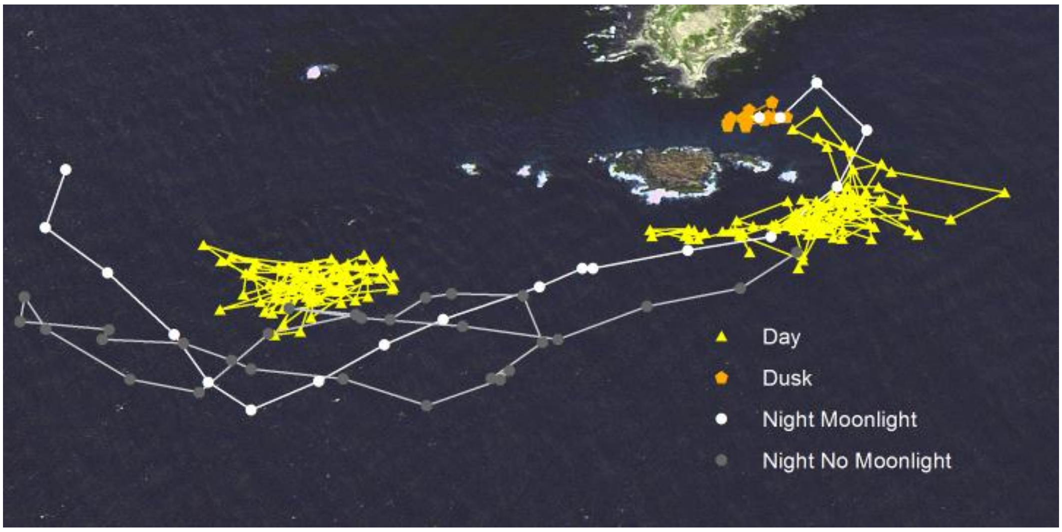


Figure 3C. Three non continuous tracks of Shark 5 during hours of daylight (2) and night (1). The shark would limit its daytime movements to areas at either Shark Alley, the south-eastern corner of Geyser Rock or the Drop Zone. At night the shark patrolled the South of Geyser Rock and continued to do this after moonset.



of tracking to be called off as the shark moved east and a crew injury meant the second night was also abandoned. Adverse weather conditions prevented any further night tracking limiting this shark's movements to day analysis only. The day movements extended over greater activity areas and with higher rates of LI and ROM than for the other sharks tracked (MCP 29.29, LI 0.65, ROM 0.36).

Shark 4, a 3 m sub-adult male, was only tracked on two occasions; day movements were limited to the Geldsteen reefs with the shark moving to deeper water during the night. LI and ROM averaged 0.74 and 0.38 respectively during daylight and 0.89 and 0.86 during night time (no moon). Three predation events observed on track one were close by but did not involve the tracked shark.

Shark 5, a 4.5 m adult male, was tracked for 57.5 hrs from 16th Feb – 21st March 2012. It displayed similar patterns of habitat use to Shark 2; with daytime movements limited to small areas around the mouth of Shark Alley, south-east corner of Geyser Rock or the Drop Zone. Night movements included patrolling to the south of Geyser Rock under moonlit conditions (Figure 3C), but the shark did not move into deeper water when the moon set, continuing to patrol the same area at a high rate of LI and ROM (0.84 and 0.55 respectively). One predation event (successful) was observed in Shark Alley during track 6 and a potential predation event was observed at the Drop Zone on track 9; the shark breached but thick fog prevented tracking crew from determining if a seal had been killed.

Swimming Patterns

Both LI and ROM were significantly higher during night hours than day (Figure 4A; t-test LI, T = 319461, n = 207, 1905, P = < 0.001; t-test ROM, T = 338569, n = 207, 1941, P = < 0.001). Both were found to be a factor of Distance from Geyser Rock (Figure 4B; Kruskal-Wallis one way ANOVA, n = 2213, H = 4733.99, P = < 0.001) with higher rates taking place the further the movement was from Geyser Rock. Depth of swimming and activity area also showed variance between day and night. Night

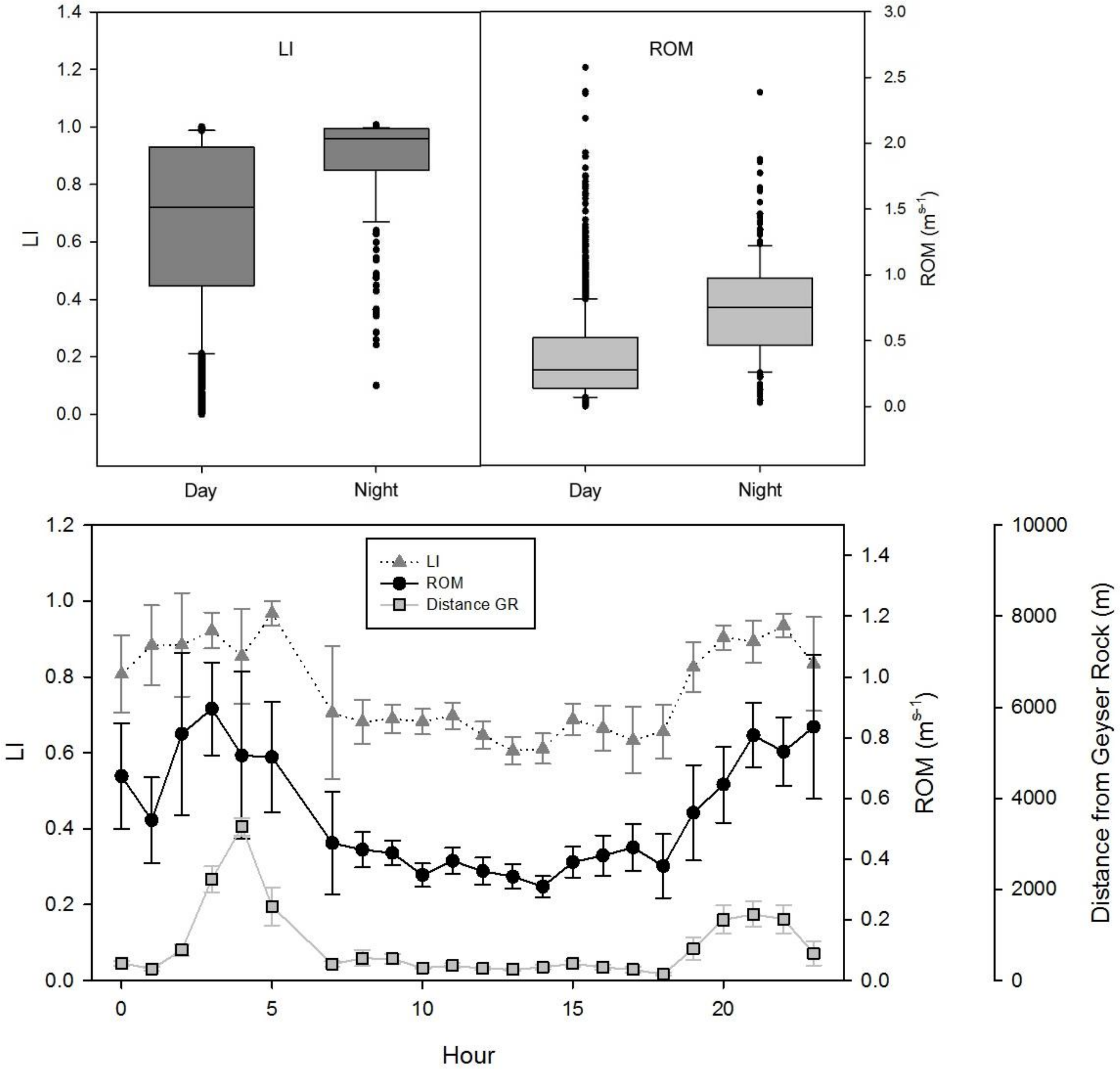


Figure 4. Rates of Movement and Linearity were significantly higher during night than daylight. Patterns followed movements close to Geyser Rock or kelp forest during daytime before moving further away with higher rates of movements and linearity during night.

swimming depths averaged 11.51 m and were significantly deeper than the day's 8.81 m (t-test T = 55276, n = 153, 798, P = < 0.001). Activity areas were not significantly different but displayed a large variance between day and night (Figure 5; 0.67 km^2 day, 2.93 km^2 night).

Effect of Size

There was no significant difference between adult and sub-adult ROM (Figure 6; adult = 0.31, sub-adult = 0.30, T = 903550, n = 830, 1342 P = 0.902). There was a significant difference in LI (adult = 0.73, sub-adult = 0.80, T = 922999.5, n = 847, 1366, P = < 0.001) with variance lower than observed between day and night. IOR showed no relation to size (Figure 7A; t-test, T = 525, P = 1.00) but the highest average was found for the largest shark (S5; 0.27, 95% Con 0.07, n = 10) and the lowest for the smallest (S4; 0.02, n = 2), which had little overlap between its first and second day tracks or night time activity area.

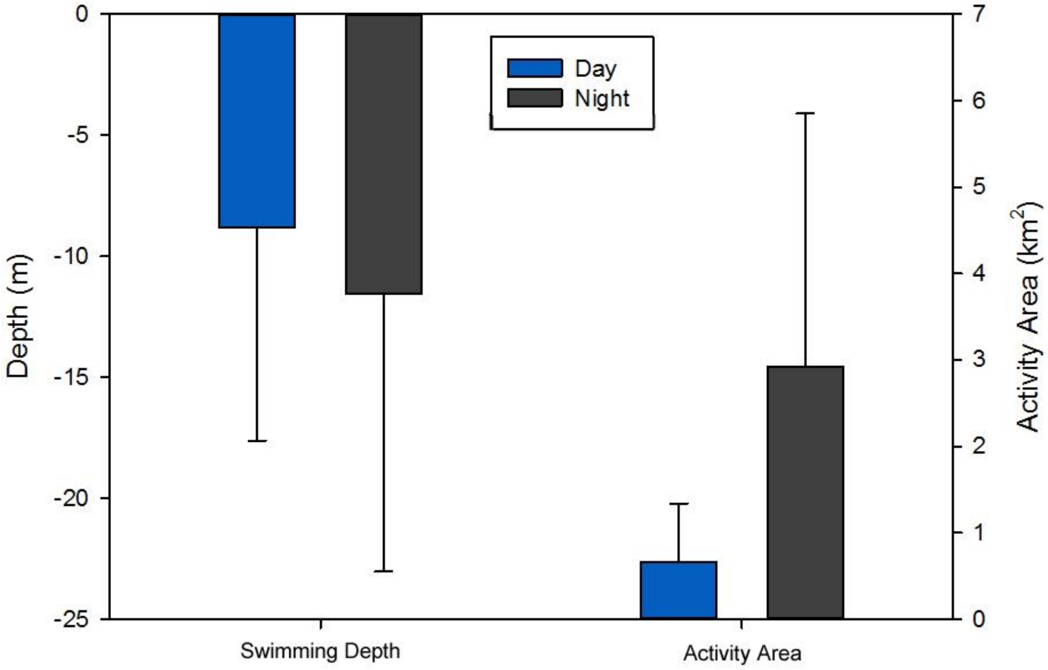


Figure 5. Swimming depths were significantly deeper during night and activity areas were greater during the night than the day.

Activity areas also showed no relation to size (Figure 7B; t-test, T = 375.5, n = 17, 21, P = 0.212), the largest average was for Shark 3 (2.91 km^2, 95% Con 2.38, n = 3) and the smallest for Shark 2 (0.68 km^2, 95% Con 0.57, n = 11).

Home Ranges

Plateaus on the discovery curve indicate that adequate hours of tracking allowed for home range analysis on 4 of the 5 shark tracks (Figure 8A). The steep rise between 60 and 63 hrs in Shark 2’s activity area (MCP) is during the night traverse east of Dyer Island, the steep rise in the middle of both Shark 2 and Shark 5’s activity areas are

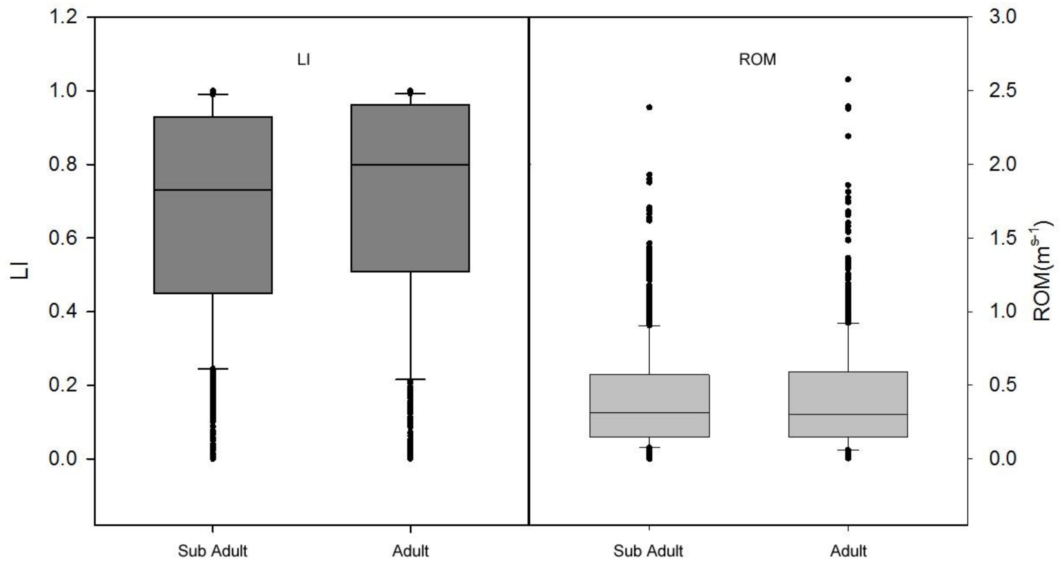


Figure 6. Rate of Movement (ROM) shows no significant different between adults and sub adults. There was a significant difference between Linearity in adults and sub-adults, however the variance was lower than observed between day and night.

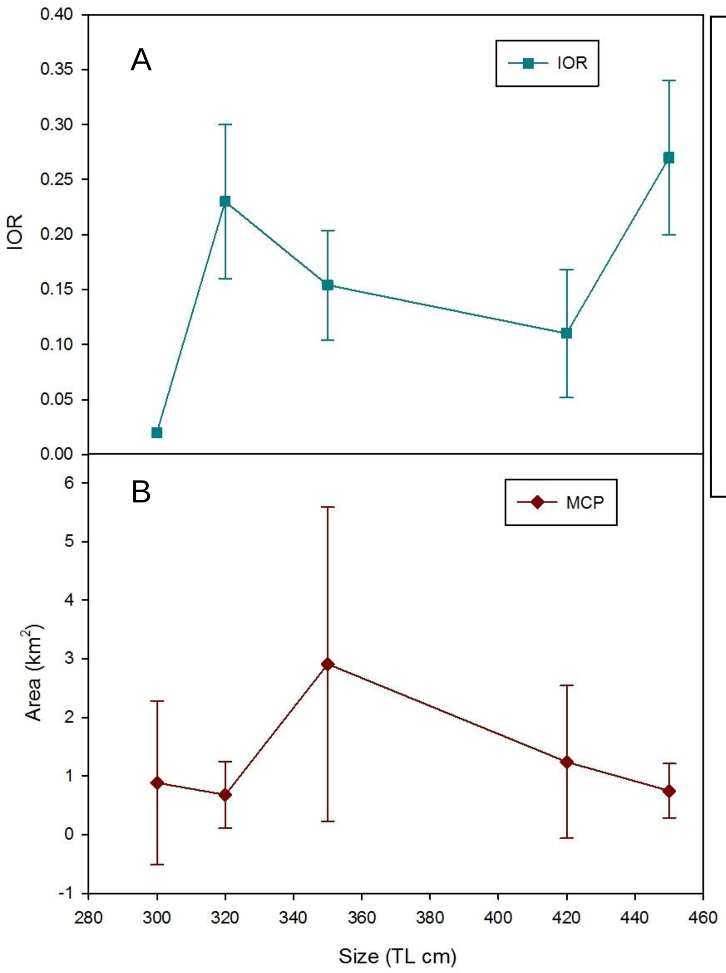
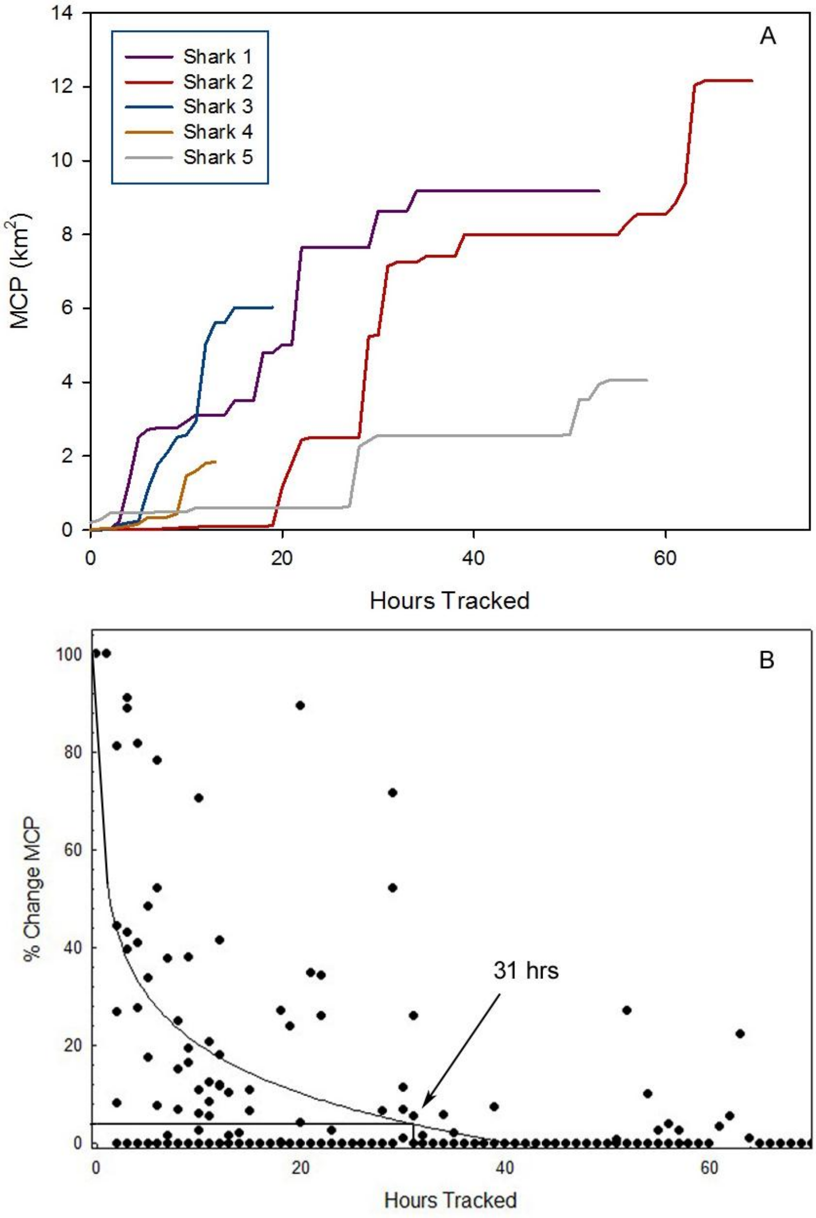


Figure 7. (Left) Index of Reuse (IOR) compared to size (TL) of individual sharks (A); IOR was not found to be a function of size (t-test, P = 1.0) however the largest value corresponded to the largest shark (0.27, 450 cm TL) and the smallest value to the smallest shark (0.02, 300 cm TL). Activity area compared to size (TL) (B); activity area was not found to be a function of size to size (TL) (t-test, P = 0.212) with the largest activity area a 350 cm individual (2.91 km^2).

also from night movements. Shark 1 and 3 both have steep rises in MCP during the first 10 – 20 hrs of tracking before beginning to stabilize. The observation area curve

(Figure 8B) indicated that the optimum tracking duration was 31 hrs based on 5% activity area change per hour of tracking.



Movement-based Kernel Density Estimates (MKDEs) revealed the extent of home range within activity areas based on 95% isobars and showed core areas of habitat use using 50% isobars. Shark 1's home range encompassed the entire Geldsteen reef system (Figure 9A), covering 1.68 km^2; the core area within this range was 0.29 km^2 and located close to the kelp forest boundary. Shark 2's home range included part of the Geldsteen reef and connected between the Drop Zone and the reefs east of Dyer Island, covering an area of 2.48 km^2 (Figure 9B). The core area was the smallest recorded at just 0.10 km^2 in Shark Alley where the successful seal predation took place. Shark 3's home range covered much of the same area as Shark 2 with the

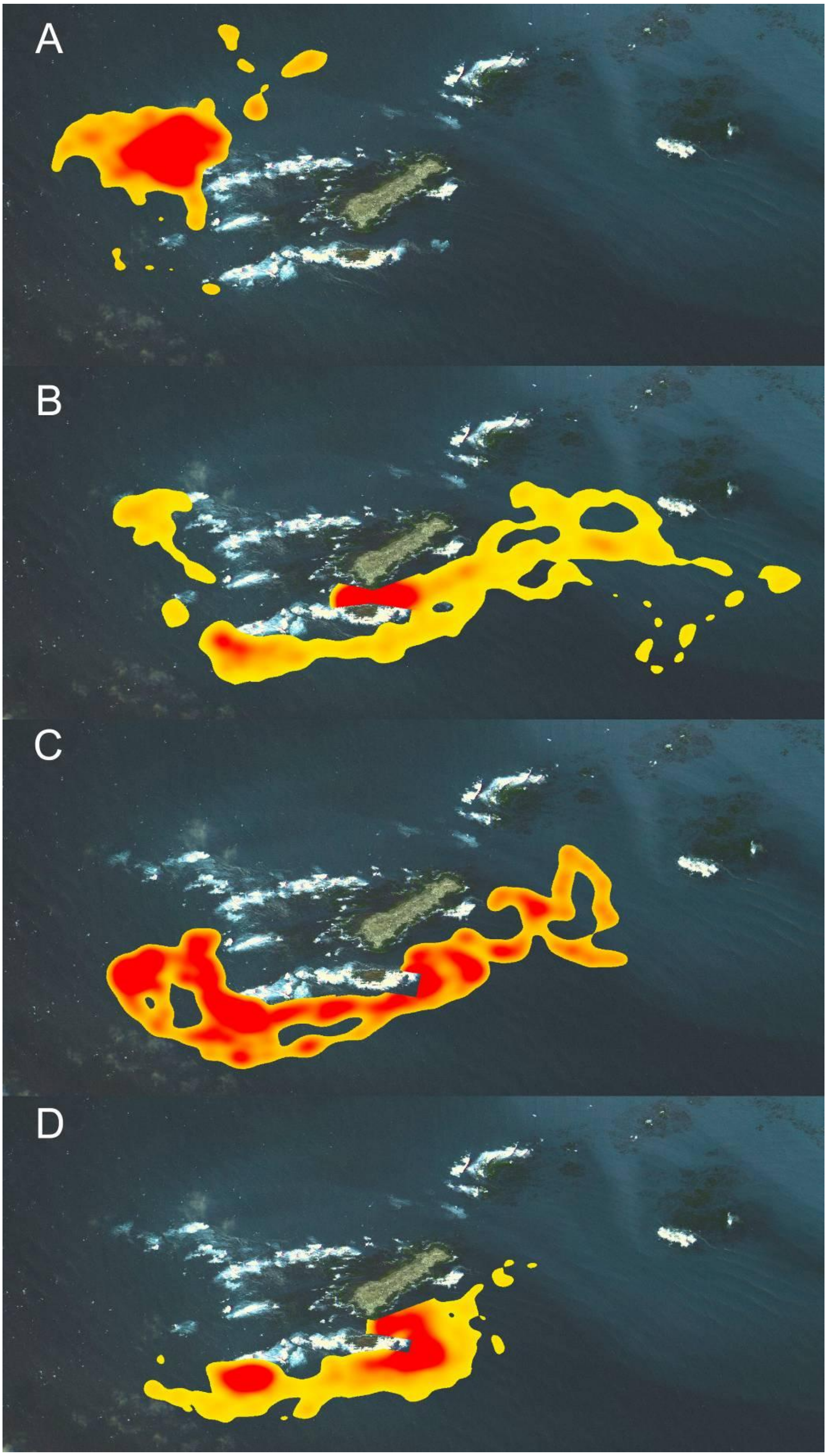


Figure 9. Home ranges as determined by MKDE of 4 white sharks at Dyer Island: a3.2 m sub-adult female with a home range (95% isobar) of 1.68 km^2 and a core area (50% isobar) of 0.29 km^2(A). A 4.2m adult male with a home range of 2.48 km^2 and core area of 0.10 km^2 (B). A 3.5m sub-adult male with a home range of 3.15 km^2 and a core area of 0.65 km^2 (C). A 4.5m adult male with a home range of 1.94 km^2 and a core area of 0.20 km^2 (D).

exception of Shark Alley which this shark did not enter (Figure 9C). It covered an area of 3.15 km² with 2 core areas at the Drop Zone and the south-east corner of Geyser Rock with a combined area of 0.65 km². Shark 5's home range covered a similar area as Shark 3 but was more focused around the south-east corner of Geyser Rock and the mouth of Shark Alley. It covered an area of 1.94 km² with 2 core areas with a combined value of 0.20 km². Activity areas and home range were not related to size (TL) or tracking duration (Figure 10). Higher activity area was not an indicator of larger home range; once within an activity area when sharks limited movements to a small areas, home range estimates decreased. This is indicated in Shark 1 and Shark 3's home range estimates.

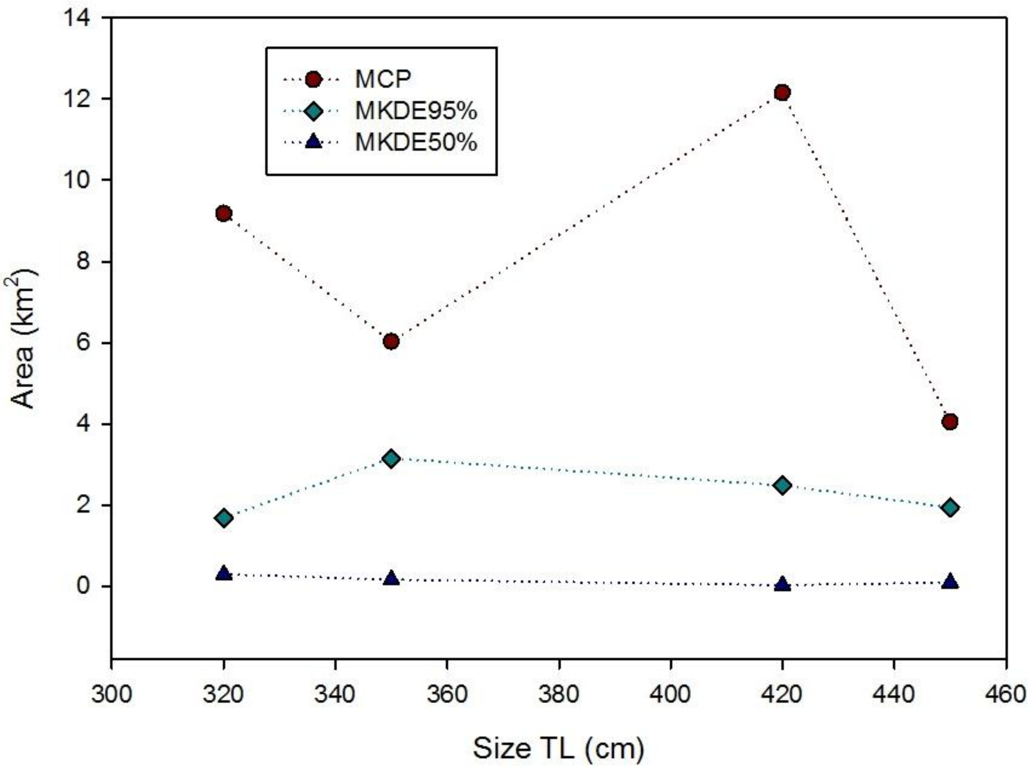


Figure 10. Activity area (MCP), home range (MKDE 95% isobar) and core area use (MKDE 50% isobar) of 4 white sharks from Dyer Island. Size of area was not a function of size but larger activity areas do not necessarily correspond to larger home range or core area use as indicated by Shark 1 (320 cm female) and Shark 2 (420 cm male).

Discussion

Predatory behaviour and the effect of light levels

The results show very different patterns of foraging by white sharks to those reported elsewhere at seal colonies in South Africa. Laroche et al. (2008) found white sharks would swim in close proximity to Seal Island, False Bay, at dawn and to a lesser extent dusk in order to predate on Cape fur seals residing there. Johnson et al. (2009) manually tracked white sharks away from the seal colony at Mossel Bay and found that a large majority of time was spent resting and patrolling in reef systems away from the seals. Only during periods of dawn and dusk would sharks regularly move close to the seal colony to feed on Cape fur seals. Laroche et al. (2008) suggested that during these crepuscular periods sharks could swim higher in the water column whilst undetected by seals; leading to a higher predatory success. In contrast, all sharks tracked in the present study spent a considerable amount of the daytime patrolling in close proximity to the seal colony at Geyser Rock or the kelp forests connected to Geyser Rock and Dyer Island (Figures 3A, B and C). Predation events were recorded by 4 of the 5 shark's tracked and none of these events corresponded to hours of dawn or dusk.

Furthermore during night tracking, if the moon was ≥ ⅔ full, predatory activity continued close to Geyser Rock (this study). The predation advantages during bright moonlit nights may be comparable to those found at dawn and dusk in studies elsewhere (Laroche et al. 2008; Johnson et al. 2009). In the north-east Pacific, juvenile white sharks also make use of the moons phase; foraging deeper and more frequently during a full moon (Weng et al. 2007). This study also recorded deeper swimming at night with higher rates of movement (ROM) and linearity (LI) (Figure 3B, C; Figure 4A; Figure 5). Moonlit movements were back and forth over the entire southern stretch of Geyser Rock and the kelp ridge extending to the Drop Zone at an average distance of 520 m from Geyser Rock; this is roughly the maximum dive distance for Cape fur seals from Geyser Rock or the kelp and they must pass through this area to reach offshore foraging grounds (average dive distance of seals from Geyser Rock is ~ 400m Wcisel pers. comm.). No predations were recorded during this time but the sharks were deep in the water column (12.14m ± 1.25) and subsurface predations may have taken place. Domeier (2012) suggested this as a predation tactic used by white sharks at Guadalupe Island, Mexico; a study site where few surface predations are observed.

Studies using stomach content and stable isotope analysis show that the white shark is a cosmopolitan apex predator, regularly predating on species ranging from near shore pelagics, skate, ray and other shark species to large marine mammals and squid (Klimely 1985; Weng et al. 2007; Hussey et al. 2011; Carlisle et al. 2012; Hussey et al. 2012; Smale & Cliff 2012). However such studies are often limited to sporadic sampling or in bather netted regions where sharks are culled, often far from seal colonies. The stomach contents of a stranded 3.8m male white shark on Dyer Island in June 2012 contained 3 undigested 2 – 5 yr old, 3 undigested young of the year (YOY) and 3 skulls all from Cape fur seals. This suggests that, while at Dyer Island sharks gorge themselves on the seal resources available before making seasonal migrations away from the area (Bonfil et al. 2005; Dept. Environ. Affairs unpublished data). Whilst it is likely other prey items are opportunistically ingested at Dyer Island, Cape fur seals must be considered the main source of prey for large white sharks foraging at Geyser Rock during winter time.

Shark Alley, the Drop Zone and the Geldsteen reef system

Predatory behaviour between white sharks and pinniped species are often thought to be dependent on depth, with white sharks using large amounts of energy in short bursts to ambush prey from below and gain high reward from a kill (Anderson et al. 1996; Klimely et al. 2001; Martin et al. 2005; Laroche et al. 2008). In Mossel Bay resting then took place in reef systems as sharks digested prey before returning to hunt at the seal colony (Johnson et al. 2009). Shark Alley provides a unique setting as a narrow channel, which has no great depth (max 6 – 7 m) extremely close to a highly abundant prey source; the Cape fur seal colony of Geyser Rock (Johnson et al. 2008). The LI and ROM values recorded here were far lower than those recorded by Johnson et al. (2009) in the waters adjacent to Seal Island, Mossel Bay (LI 0.55, ROM 0.18 in Shark Alley; LI 0.70, ROM 0.70 at Seal Island). The limitations in space within the channel do not allow the onshore offshore movements recorded by foraging white sharks at Seal Island, Mossel Bay, the Farallon Islands, California and the Neptune Islands, South Australia (Strong et al. 1992; Goldman & Anderson 1999; Johnson et al. 2009). Instead movements were more circular, with white sharks moving close to the rafting seals at the edge of Geyser Rock before moving away to the middle of the channel and circling back around to restart the movement. Such movements were repeated for entire days in a row (Figure 3B). Seals were ambushed with short horizontal bursts of speed before being pulled away from the rocks and being consumed in the slightly deeper water mid-channel. Such movements would presumably expend far less energy than short bursts from deep and likely allowed sharks' longer durations of foraging and maximize feeding opportunities. Similar patrolling close to the kelp forest at the Drop Zone or Geldsteen may also provide opportunities to encounter Cape fur seals without expending large amounts of energy. The Geldsteen may also provide other feeding opportunities on other taxa such as sharks, fish and rays.

Swimming patterns, size of sharks and home ranges

Overall levels of LI and ROM at Dyer Island were comparatively lower than Johnson et al. (2009)'s results from Mossel Bay (LI 0.68, ROM 0.42 at Dyer Island; LI 0.76, ROM 0.52 at Mossel Bay). Johnson et al. (2009) also recorded higher ROM in larger sharks; something not found in this study (Figure 6B). However their sample size included sharks as small as 200 cm TL, whereas the smallest shark in this study was 300 cm. There were statistically significant differences between day and night at Dyer Island (Figures 3 – 6, present study), whilst in Mossel Bay day and night were similar in LI and ROM (Johnson et al. 2009). Both LI and ROM were a function of distance from Geyser Rock, with sharks moving straighter and at a higher rate as they moved into deeper waters.

The effect of shark size had little effect on the daily or nightly activity areas and Index of Reuse (IOR), both of which were a function of size at Mossel Bay (Jewell et al. 2012). In other species larger sharks need larger areas to forage (Morrissey & Gruber 1993; Speed et al. 2010). However, in other white shark studies smaller sharks were deemed to forage over greater site specific home ranges than larger conspecifics within the same aggregation site (Goldman & Anderson 1999; Jewell et al. 2012). Average home range of white sharks in Mossel Bay was 12.21 km^2 (Jewell et al. 2012), far greater than the 2.32 km^2 in this study. Although a more accurate method of home range which limits the bias of fixed positions and barriers (Benhamou & Cornélis 2011) is used (present study), this does not account for such a large difference in size. Food resources are more abundant at Dyer Island than Mossel Bay

(55 – 60,000 Cape fur seals in comparison to 5,500 Dept. Environ. Affairs unpublished data) which may allow sharks to limit their activity areas and home range without the need to migrate to different areas of the aggregation site.

Conclusion

This study suggests that white sharks forage in a very different way at Dyer Island than at other seal colonies at False Bay to the west and Mossel Bay to the east. The target prey species is the same at all locations (Kirkman et al. 2007) and a significant number of known sharks forage in at least two or all three of the locations (Bonfil et al. 2005; Johnson & Kock 2006; Jewell et al. 2011). One of the study animals from this investigation (S5) was sighted at Mossel Bay the previous year (unpublished data). This suggests that white sharks are able to adapt their foraging behaviour to suit the environment they are in and utilize prey resources in the most efficient way possible; thus making them site specific in their foraging ecology.

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Chapter 4: General Conclusion

Acoustic Telemetry & Home Range Analysis

This study successfully used acoustic telemetry to assess site specific home ranges and localised movement patterns of white sharks in Gansbaai. The limits of such telemetry mean home range estimates are very limited to the study site as in Rechisky & Weatherbee (2003), Heupel et al. (2004) and Jewell et al. (2012). In fact the study animals will certainly exceed these estimates once they begin their seasonal migrations away from the study area (Bonfil et al. 2005). Tracking further requires satellite telemetry and this has far less resolution in position estimates than active acoustic tracking (Teo et al. 2004; Jewell et al. 2011) and even then tracking is limited to the life of the tag. Very few studies will ever be able to track wild mega fauna from birth, to reproduction and death to get the true home range of a study animal. Equipment failure prevented us from improving the error in our positioning by using range tests, estimated direction and strength of ping received as in Heithaus et al. (2002). However I do not believe such adjustments would have significantly affected results. The method of Movement-based Kernel Density Estimate (MKDE) (Benhamou & Cornélis 2010) provided a useful alternative to the traditional fixed-based methods used to estimate white shark home range in previous studies (Jewell et al. 2012) and performed particularly well when accounting for the movements in and around Shark Alley (Chapter 2). As in Jewell et al. (2012) we were able to identify several core areas of habitat use using home range estimates but at Dyer Island these seem more focused on the Cape fur seal colony than at Mossel Bay (Fig. 1, 2, Chapter 3). Diurnal movement patterns were found to contrast those found elsewhere in South Africa by Johnson et al. (Mossel Bay, 2009) and Laroche et al. (False Bay, 2008) and suggest that the environment plays as large a role in shaping the movements of both predator and prey (Chapter 3; Wcisel pers. comm.).

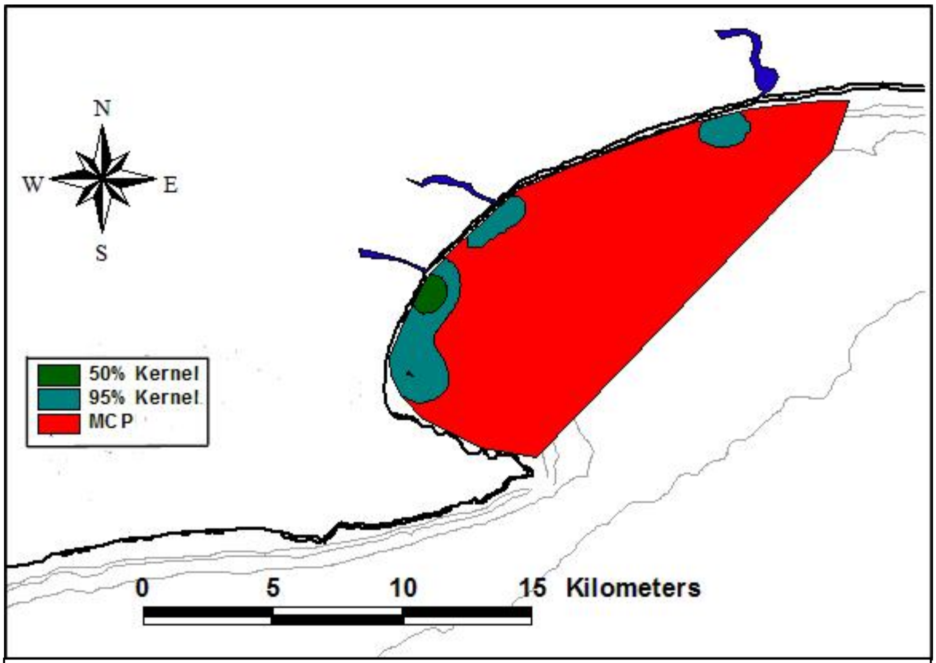

Figure 1. The combined home range and core habitat use of thirteen white sharks tagged and acoustically tracked within the confines of Mossel Bay (Jewell et al. 2012). Estimates determined by K95 (grey), K50 (green) and MCP (outer, red) calculations. The overall area of tracking took place over a large area, but within this the home range was limited to 10.19 km^2 with a core area of just 1.05 km^2.

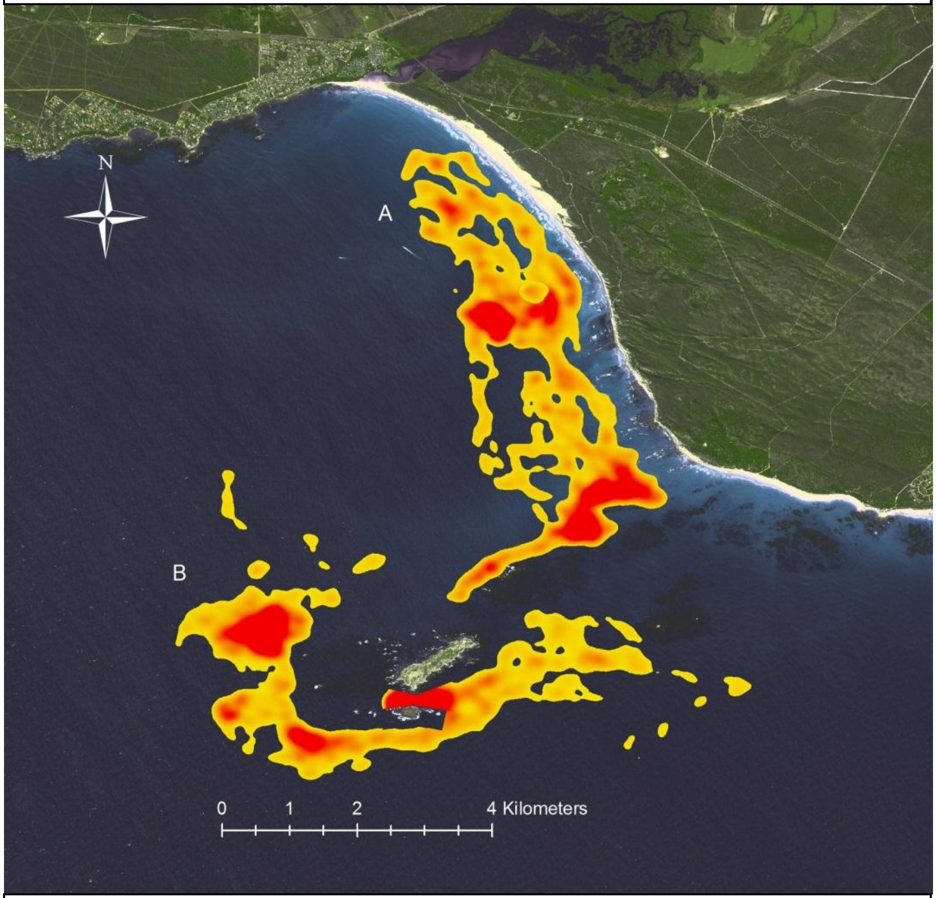

Figure 2. MKDE home range estimates of 6 white sharks in the Gansbaai/Dyer Island regions. Home range was estimated inshore (A, 1 shark) and at Dyer Island (B, 5 sharks) which allowed for comparison between the two areas of seasonal aggregation in the bay. Core areas inshore were on the reef systems of Joubertsdam (A – centre) and the kelp reefs to the east of the UD. Core areas at Dyer Island were found in Shark Alley, The Drop Zone and Geldsteen (B).

The results of these studies highlight the need to investigate aggregation areas of threatened marine species, as behaviour and life history of individuals can vary greatly from one area to another. Conservation is heavily reliant on such information, allowing more informed decisions on policy, resource allocation and coastal development (Simpfendorfer et al. 2010).

Future Work

The acoustic tracking of white sharks will continue in Gansbaai; in particular the inshore area of Joubertsdam will be investigated further (Towner unpub. data). Satellite telemetry (SPOT Tags, see appending chapter II for description) has also been deployed to 36 white sharks in Southern Africa. With the collaboration of others studying white sharks up and down the coastline, I intend to use the data to assess the home range of these sharks and highlight areas of particular concern for their conservation. Gaps in tracks, sometimes spanning several weeks or months and thousands of kilometres are created as tags only transmit when the dorsal fin breaks the surface, and require satellite coverage overhead in order for transmissions to be received (Teo et al. 2004; Weng et al. 2005). This creates a challenge as MKDEs require consistent tracks and fixed based methods overestimate areas by calculating successive positions as if they were unlinked (Benhamou & Cornélis 2010). A new method (ideally based on the MKDE method) will likely have to be developed to estimate home ranges of Southern African white sharks based on this data. The importance and urgency of this study has already been highlighted by the death of one of the study animals that was caught and killed in a gill net of Mozambique within a few months of being tagged (Ocearch unpub. data).

We are now close to publishing work on the first population estimate of white sharks in Ganbsaai (DICT work in progress) and are also developing techniques to estimate body size of white sharks using photogrammetry, which I intend to use for my PhD. Such studies are novel and much needed as at present we have very little information to tell us how many white sharks there are left, how quickly they grow, how much they eat and how quickly they can reproduce. Finally we are starting to learn where they go, which is exciting but will only be useful if we can use the data to enforce policy change and better protect this vulnerable species.

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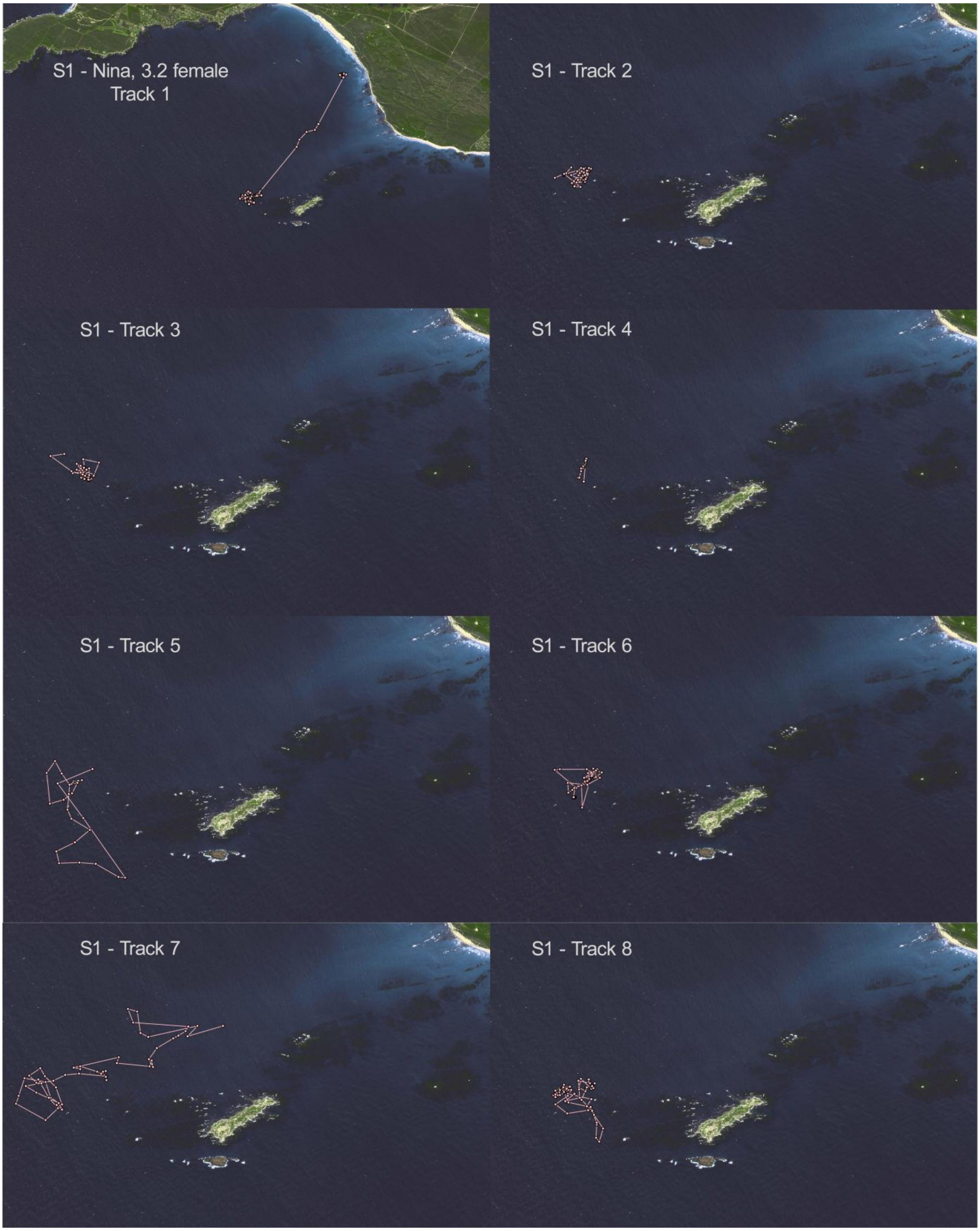
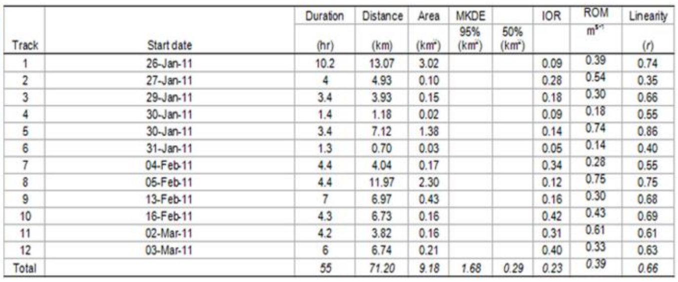
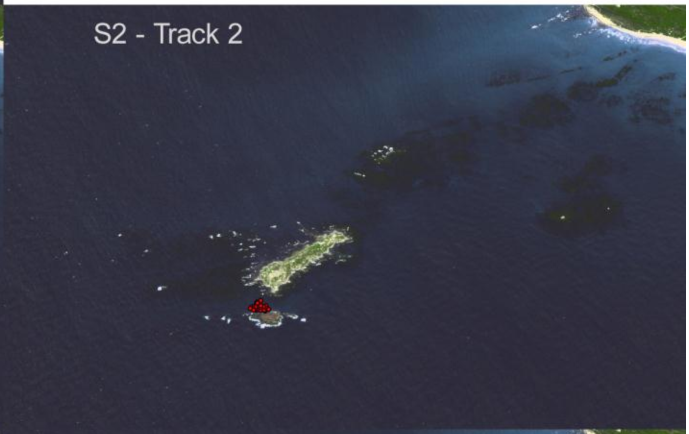
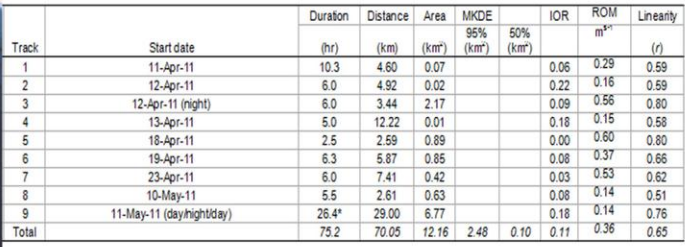
Appendix I: Dyer Island Shark Tracks



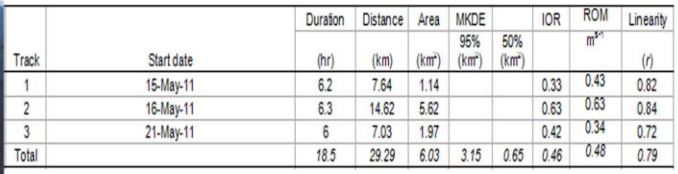


Track	Start date	Duration (hr)	Distance (km)	Area (km²)	MKDE 95% (km²)	50% (km²)	IOR	ROM $\mathrm{m}^{\mathrm{s}-1}$	Linearity (*r*)
1	26-Jan-11	10.2	13.07	3.02			0.09	0.39	0.74
2	27-Jan-11	4	4.93	0.10			0.28	0.54	0.35
3	29-Jan-11	3.4	3.93	0.15			0.18	0.30	0.66
4	30-Jan-11	1.4	1.18	0.02			0.09	0.18	0.55
5	30-Jan-11	3.4	7.12	1.38			0.14	0.74	0.86
6	31-Jan-11	1.3	0.70	0.03			0.05	0.14	0.40
7	04-Feb-11	4.4	4.04	0.17			0.34	0.28	0.55
8	05-Feb-11	4.4	11.97	2.30			0.12	0.75	0.75
9	13-Feb-11	7	6.97	0.43			0.16	0.30	0.68
10	16-Feb-11	4.3	6.73	0.16			0.42	0.43	0.69
11	02-Mar-11	4.2	3.82	0.16			0.31	0.61	0.61
12	03-Mar-11	6	6.74	0.21			0.40	0.33	0.63
Total		*55*	*71.20*	*9.18*	*1.68*	*0.29*	*0.23*	*0.39*	*0.66*

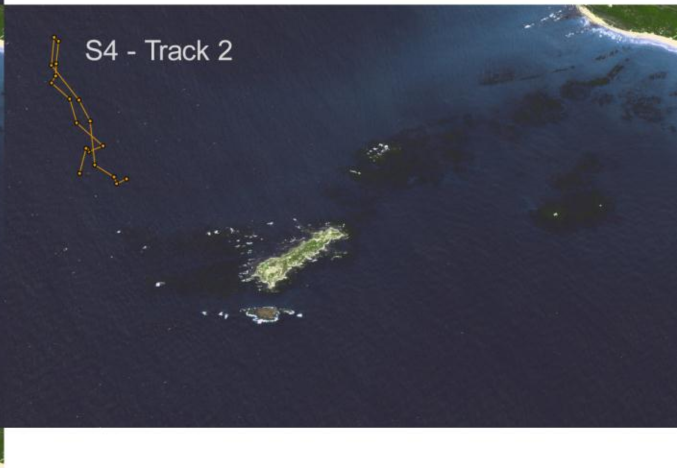


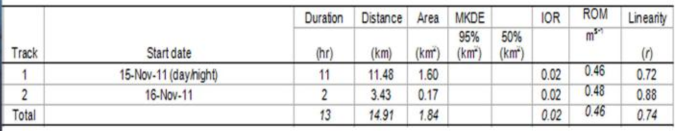


Track	Start date	Duration (hr)	Distance (km)	Area (km^2)	MKDE 95% (km^2)	50% (km^2)	IOR	ROM m^{s-1}	Linearity (*r*)
1	11-Apr-11	10.3	4.60	0.07			0.06	0.29	0.59
2	12-Apr-11	6.0	4.92	0.02			0.22	0.16	0.59
3	12-Apr-11 (night)	6.0	3.44	2.17			0.09	0.56	0.80
4	13-Apr-11	5.0	12.22	0.01			0.18	0.15	0.58
5	18-Apr-11	2.5	2.59	0.89			0.00	0.60	0.80
6	19-Apr-11	6.3	5.87	0.85			0.08	0.37	0.66
7	23-Apr-11	6.0	7.41	0.42			0.03	0.53	0.62
8	10-May-11	5.5	2.61	0.63			0.08	0.14	0.51
9	11-May-11 (day/night/day)	26.4*	29.00	6.77			0.18	0.14	0.76
Total		*75.2*	*70.05*	*12.16*	*2.48*	*0.10*	*0.11*	*0.36*	*0.65*



Track	Start date	Duration	Distance	Area	MKDE		IOR	ROM	Linearity
		(hr)	(km)	(km^2)	95% (km^2)	50% (km^2)		m^{s-1}	(*r*)
1	15-May-11	6.2	7.64	1.14			0.33	0.43	0.82
2	16-May-11	6.3	14.62	5.62			0.63	0.63	0.84
3	21-May-11	6	7.03	1.97			0.42	0.34	0.72
Total		*18.5*	*29.29*	*6.03*	*3.15*	*0.65*	*0.46*	*0.48*	*0.79*



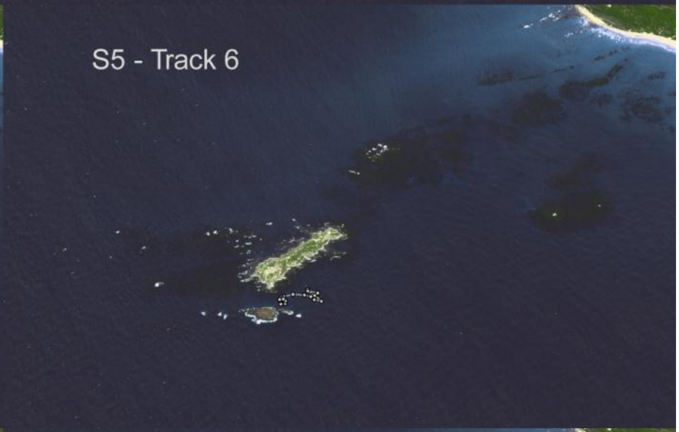


Track	Start date	Duration	Distance	Area	MKDE		IOR	ROM	Linearity
		(hr)	(km)	(km^2)	95% (km^2)	50% (km^2)		m^{s-1}	(*r*)
1	15-Nov-11 (day/night)	11	11.48	1.60			0.02	0.46	0.72
2	16-Nov-11	2	3.43	0.17			0.02	0.48	0.88
Total		*13*	*14.91*	*1.84*			*0.02*	*0.46*	*0.74*

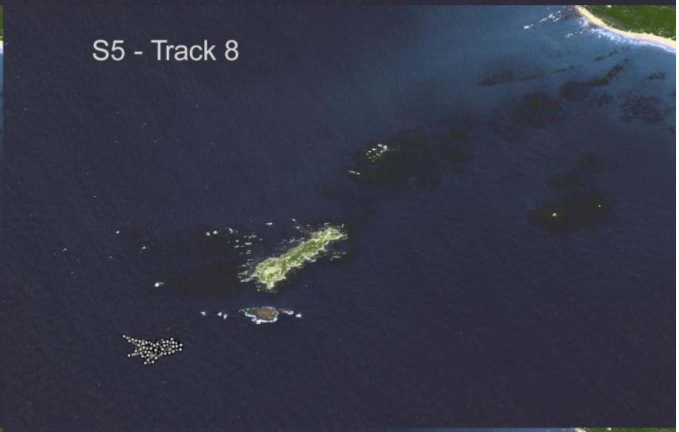

S5 - Track 3


S5 - Track 4


S5 - Track 5

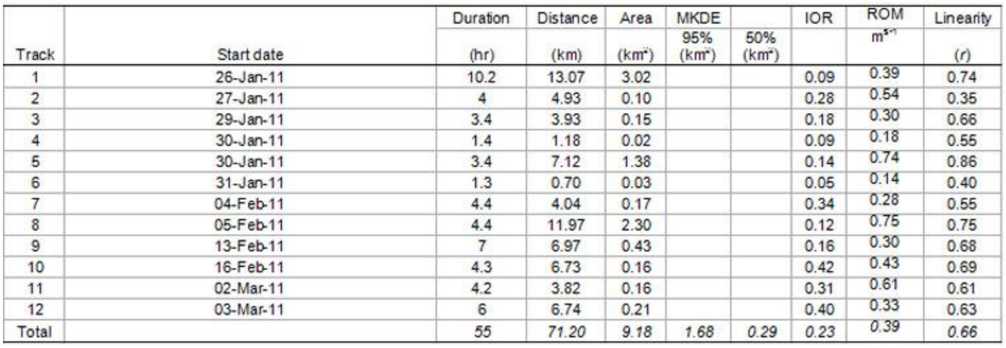

S5 - Track 6


S5 - Track 7


S5 - Track 8


S9 - Track 9


S10 - Track 10



Track	Start date	Duration (hr)	Distance (km)	Area (km^2)	MKDE 95% (km^2)	50% (km^2)	IOR	ROM ms^{-1}	Linearity (r)
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9	13-Feb-11	7	6.97	0.43			0.16	0.30	0.68
10	16-Feb-11	4.3	6.73	0.16			0.42	0.43	0.69
11	02-Mar-11	4.2	3.82	0.16			0.31	0.61	0.61
12	03-Mar-11	6	6.74	0.21			0.40	0.33	0.63
Total		*55*	*71.20*	*9.18*	*1.68*	*0.29*	*0.23*	*0.39*	*0.66*

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Appendix II:

Effects of Smart Position Only (SPOT) tag deployment on white sharks *Carcharodon carcharias* in South Africa. PLoS ONE 6(11): e27242. doi:10.1371/journal.pone.0027242

Authors

Oliver J. D. Jewell, Michelle A. Wcisel, Enrico Gennari, Alison V. Towner, Marthán N. Bester, Ryan L. Johnson and Sarika Singh

Abstract

We present 15 individual cases of sub-adult white sharks that were SPOT tagged in South Africa from 2003 - 2004 and have been re-sighted as recently as 2011. Our observations suggest SPOT tags can cause permanent cosmetic and structural damage to white shark dorsal fins depending on the duration of tag attachment. SPOT tags that detached within 12 - 24 months did not cause long term damage to the dorsal fin other than pigmentation scarring. Within 12 months of deployment, tag fouling can occur. After 24 months of deployment permanent damage to the dorsal fin occurred. A shark survived this prolonged attachment and there seems little compromise on the animal's long term survival and resultant body growth. This is the first investigation detailing the long term effects of SPOT deployment on the dorsal fin of white sharks.

Key Words: Tagging, dorsal fin, tag damage

Introduction

Monitoring the large scale movements of pelagic animals is logistically difficult due to the vast spatial ranges they transverse. Transmissions from satellite tags can not penetrate the water's surface, and acoustic telemetry requires receivers to be within a limited range to pick up tag transmission. The last decade of pelagic marine animal research has shown that satellite telemetry has greatly enhanced the documentation of these movements [1-5]. For white sharks (*Carcharodon carcharias*) specifically, two types of satellite tag have been used: Pop-off Archival Tags (PAT) and Smart Position Only/Temperature transmitting Tags (SPOT) [6-10]; PAT tags are considered to be low stress generating and a relatively non-invasive method of satellite tagging. White sharks are lured close to a research vessel and the tag is attached below the dorsal fin using a tagging pole as the free-swimming animal passes the vessel [5,11]. PAT tags remain attached for a predetermined period (days/months) before automatically “popping-off”, floating to the surface and transmitting a summary of data collected via satellite. In order to access the full archival record of the tag the tag needs to be retrieved. Tracks are determined from the ARGOS positioning system using data collected on light levels, which can then compare sunrise and sunset and estimated location. These tracks may have root mean square errors of 0.89- of longitude and 1.47- of latitude [12]. SPOT tags are manually attached by drilling through the dorsal fin, which requires the shark to be lifted from the water so that it may be operated on. SPOT tags use GPS based satellite telemetry and transmit data whenever the dorsal fin breaks the surface of the water. These are capable of operating for several years and generally have positioning errors under 1 km [3].

The methods used to attach SPOT tags have come under scrutiny from the press, public and conservation societies in the wake of documentaries detailing their deployment on large adult white sharks. Unlike smaller species, white sharks are not easily brought on board a vessel and released back to the ocean unharmed because of their size, weight, and strength. SPOT tags have also been attached to many other species, such as small cetaceans, and similar concerns have been raised about catching methods and long term damage. Tissue degradation and possible infection have been documented in bottlenose dolphin *(Tursiops truncatus)* [13], and tissue degradation of shark fins was suspected but only revealed recently [14]. We examine the long term effects of SPOT tag satellite transmitters placed on the dorsal fins of white sharks in South Africa using long term non-invasive dorsal fin identification of individual white sharks.

Methods

All data on re-sighted sharks is taken from incidental observations on either commercial cage diving or chumming research vessels. Initial data from SPOT tagging was collected by Marine and Coastal Management and published under Bonfil et al. [5]. We use photos from their archives but took no part in the actual tagging. As a result no ethics committee approval was required.

Archived data from the satellite tagging program [5] was compared to incidental observations from current and archived research and commercial operations. SPOT tags were deployed on 15 white sharks in South African waters between 24th May 2003 and 28th May 2004. These sharks were caught using a double hook baited line from an anchored research vessel. They were then brought on board a purpose built cradle attached to the research vessel and then lifted from the water. Total length (TL) was measured using a straight line to the nearest cm, and tags were then attached to the first dorsal fin using nylon pins, brass washers and steel nuts [5]. Anti-fouling paint was painted on the tag itself and the bolts, but not on the saltwater switch or the antennae, as this was deemed to interfere with transmissions. Tag attachments were designed to keep tags in place for a period of 9 - 12 months. Digital images of the sharks' dorsal fins were taken before and after deployment of the tags either while in the cradle, as the shark was being hooked, or as the shark was released as in Johnson [15, Figure 1A] and shark re-sightings were confirmed by matching photographic dorsal fin IDs as in Chapple et al. [16]. Re-sight images were taken either during research operations in Mossel Bay (2005-2011) or on commercial operations aboard the cage diving vessels of Marine Dynamics in Gansbaai (2007-2011).

Results

Eight of the instrumented white sharks were re-sighted without their SPOT tags and with the screw holes healed (Table 1; Figure 1B). One shark (GWS-7) was re-sighted 263 days after deployment, without the tag present but with raw scaring from tag bolts. Two further sharks were re-sighted with SPOT tags still in place. One of these sharks (GWS-1) was re-sighted in Mossel Bay 172 days after tagging. The tag displays fouling, but the shark has not been re-sighted since (Figure 2). The second (GWS-3) was seen in Mossel Bay on 31st August 2005, 822 days after deployment. The tag shows excessive fouling and the shark showed fin deformation with the fin leaning to the left (Figure 3A,B). The tag detached between that sighting in 2005 and subsequent sightings from 2008 onwards. Permanent deformation and a hole remain, leaving the shark extremely distinctive (Figure 3C,D). The shark has been sighted in 2008, 2009, 2010 and 2011 in Gansbaai, and in 2009 and 2010 in Mossel Bay. Observations of the shark's movement indicate that it is relatively unimpeded by the damages to the dorsal fin (Figure S1). The shark also has further unrelated damage to the left pectoral fin which occurred after the original tagging in 2003.

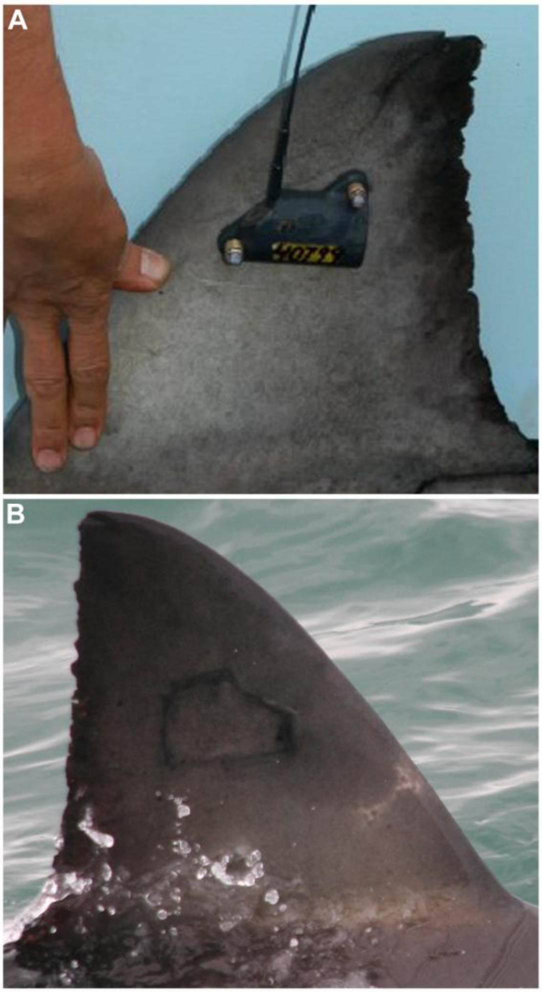


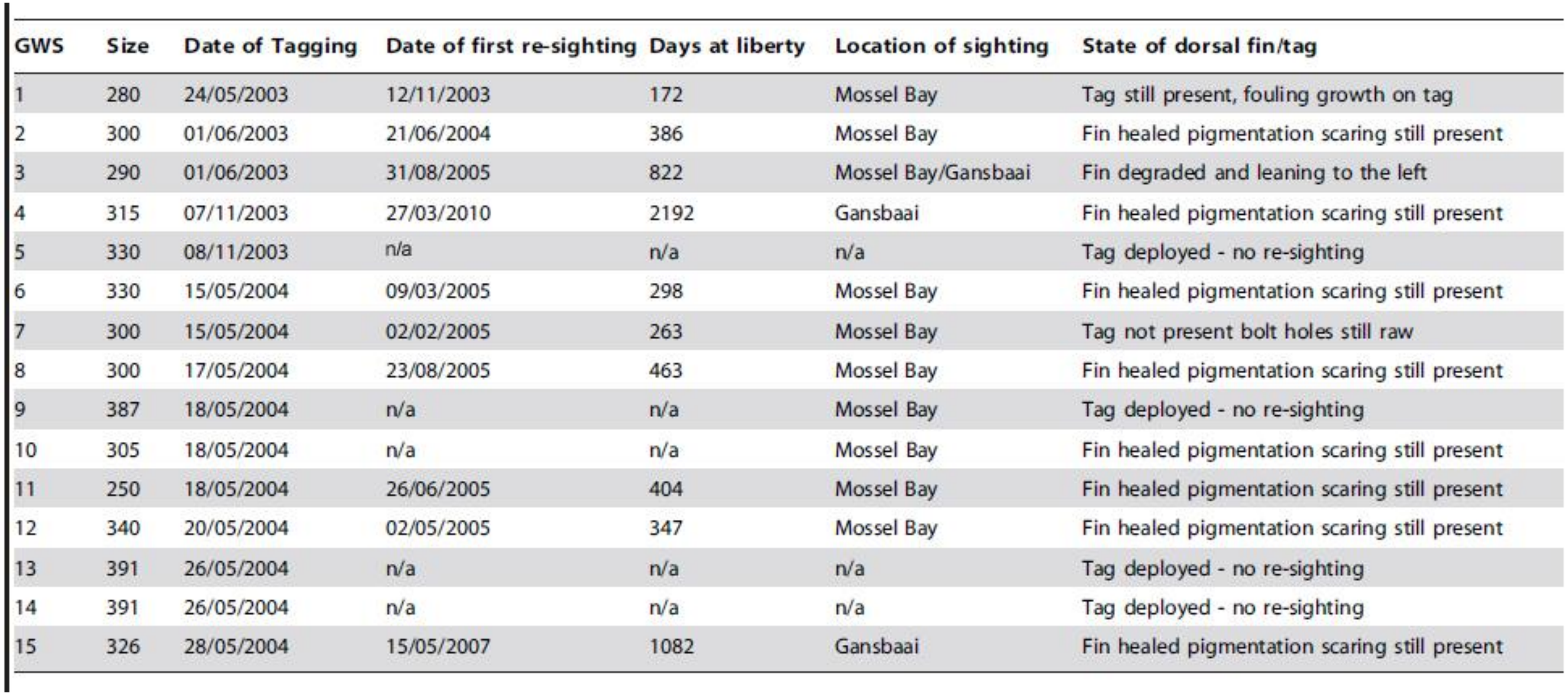
Figure 1. (left and left below) An example of a white shark with SPOT tag freshly deployed (A) and another with pigmentation scaring following SPOT detachment (B).

Figure 2. (below) White shark dorsal fin with SPOT tag in place 172 days after deployment with algal growth on tag. Sighted in Mossel Bay November 2003, after making a migration from Mossel Bay to Mozambique and back again.

The size of GWS-3 was estimated at 290 cm when sighted in 2005. Sightings in December 2010 estimated the sharks' length at 400 to 420 cm, using a 400 cm cage for perspective. This suggests a growth of between 110 and 130 cm in 5 years.

Another shark (GWS-15) tagged on 28/05/2004 was first re-sighted on 27th March 2010 in Gansbaai and was acoustically tagged in 2011. It is identifiable by dorsal fin pigmentation scaring and an amputated upper caudal fin (Figure 4). The caudal fin was healed upon capture (Figure 4B) and as a result is considered an unrelated injury to the tagging project. This shark represents the second oldest re-sight since the original tagging campaign in 2003, and suggests that pigmentation scarring caused by SPOT tags is permanent. The shark is estimated at between 420 and 440 cm TL

Table 1. Mark and recapture results of 15 white sharks tagged in South Africa from 24/05/2003 – 28/05/2004 with dates of tagging, first re-sighting, days at liberty, location of re-sighting and the state of dorsal fin/SPOT tag.



GWS	Size	Date of Tagging	Date of first re-sighting	Days at liberty	Location of sighting	State of dorsal fin/tag
1	280	24/05/2003	12/11/2003	172	Mossel Bay	Tag still present, fouling growth on tag
2	300	01/06/2003	21/06/2004	386	Mossel Bay	Fin healed pigmentation scaring still present
3	290	01/06/2003	31/08/2005	822	Mossel Bay/Gansbaai	Fin degraded and leaning to the left
4	315	07/11/2003	27/03/2010	2192	Gansbaai	Fin healed pigmentation scaring still present
5	330	08/11/2003	n/a	n/a	n/a	Tag deployed - no re-sighting
6	330	15/05/2004	09/03/2005	298	Mossel Bay	Fin healed pigmentation scaring still present
7	300	15/05/2004	02/02/2005	263	Mossel Bay	Tag not present bolt holes still raw
8	300	17/05/2004	23/08/2005	463	Mossel Bay	Fin healed pigmentation scaring still present
9	387	18/05/2004	n/a	n/a	Mossel Bay	Tag deployed - no re-sighting
10	305	18/05/2004	n/a	n/a	Mossel Bay	Fin healed pigmentation scaring still present
11	250	18/05/2004	26/06/2005	404	Mossel Bay	Fin healed pigmentation scaring still present
12	340	20/05/2004	02/05/2005	347	Mossel Bay	Fin healed pigmentation scaring still present
13	391	26/05/2004	n/a	n/a	n/a	Tag deployed - no re-sighting
14	391	26/05/2004	n/a	n/a	n/a	Tag deployed - no re-sighting
15	326	28/05/2004	15/05/2007	1082	Gansbaai	Fin healed pigmentation scaring still present

(based on comparison to cage diameters and taking into account the missing section of the upper caudal). At time of tagging, the sharks' total length was measured at 315cm, representing an estimated growth of 105-125 cm in TL over 7 years.

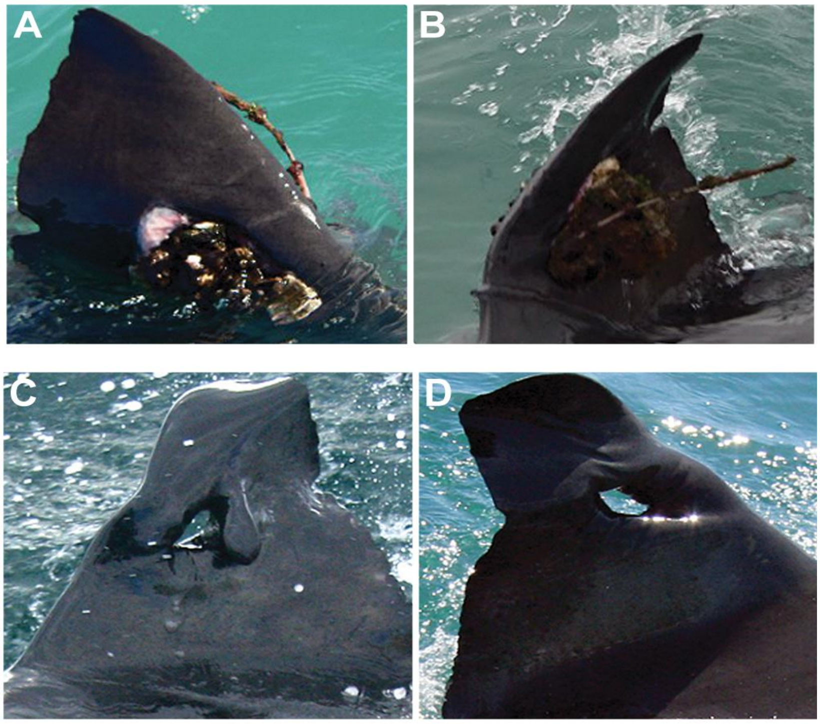


Figure 3. White shark dorsal fin with SPOT tag present over 24 months after deployment. (A and B) - tag is showing excessive fouling and fin is leaning to the left as a result of the weight; images taken in 2005 at Mossel Bay and without the tag (C and D) and with resulting hole and fin degradation after tag detachment; images taken in 2009 at Gansbaai.

Discussion

The use of SPOT tags in 2003 provided a unique insight into the large scale movement patterns of South African white sharks. However, the use of hooks to catch sharks and drills to attach the tags to the dorsal fins attracted negative press. The use of SPOT tags on white sharks in North America brought further public criticism, particularly in regard to the catching methods. We therefore embarked on the present investigation which represents the first South African record detailing the effects of SPOT tags to white shark dorsal fins after deployment.

Of the original 15 sharks, 8 sharks were sighted with healed fins and pigmentation scars, one with fresh scars suggesting recent tag detachment, one with the tag still in place and one shark with a deformed fin resulting from SPOT tag deployment. These observations suggest that SPOT tags designed to rust and fall out within 12 months are unlikely to cause permanent damage to the structure of the shark's fin as long as they detach within that time. We only observed permanent degradation to the structure of the fin on a shark's tag that was still present for between 24 and 60 months. The shark would have been considered sub-adult at the time of tagging and as a result growth rates would be expected to be relatively quick [17,18]. Damage to the fins structure was evident from the observation after 24 months. Potential causes of the damage could have been from the impediment of the growth of the fin, pulling it to the left, weight from algal build up on the tag itself which appeared quite excessive 24 months after tag deployment, or quite likely a combination of the two. This result suggests that white sharks yet to obtain full size - particularly while sub-adult and growing fast are unable to sustain SPOT tags in place much longer than 12 months without such damage occurring. Despite the dorsal fin damage to this shark, the shark survived to 2011 and had continued to grow post tag deployment. White sharks can recover from deep tissue wounds (that penetrate skin and muscle) providing vital organs and skeletal structure remain intact [19], however recovery from fin damage is still under investigation and it appears from our results full recovery to the fin has not occurred.

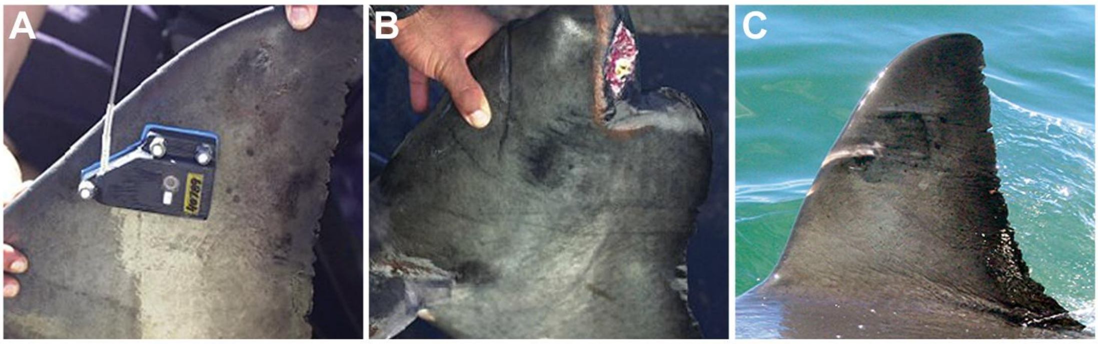


Figure 4. Photo ID of a male white shark tagged in Mossel Bay 2004 with missing upper caudal fin (A and B) re-sighted in Gansbaai 2010 and 2011 from Marine Dynamics cage diving vessel displaying pigmentation scaring from tag (C).

We therefore conclude that based on the tags deployed in South Africa in 2003 - 2004, SPOT tags did not cause long term damage to the sharks when detached within 12 - 24 months, but they had the ability to cause permanent structural damage to the dorsal fin when left in place for longer periods. These tags were deployed to relatively sub-adult members of the population (< 450 cm) and as such it may be recommended that a review of the tag design is considered for long term deployments to sharks of this size. Observing re-sightings of SPOT tagged white sharks in areas such as Guadalupe or South California would allow a comparison to see if adult white sharks are affected in a similar way. The structural damage to the dorsal fin caused by SPOT tags did not appear to negatively effect the long term survival of the shark and the re-sighting of individuals post tagging and of tracks of individuals not re-sighted suggest there were no mortalities as a result of this programme. However, the effects of removing large (> 450 cm) white sharks from the water in order to deploy SPOT tags are still unknown and should also be considered.

Acknowledgements

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Figure S1. White shark displaying damage to the dorsal fin as a result of SPOT tag deployment breaks the water at Gansbaai, South Africa during a Marine Dynamics cage diving trip. Photo courtesy of Michelle Wcisel, Marine Dynamics.

Appendix III:

Fine scale movement patterns and activity areas of white sharks (*Carcharodon carcharias*) at Mossel Bay, South Africa**.** **(**2012) Environmental Biology of Fishes

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Authors

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Abstract

Previous work on white sharks indicate the species show seasonally limited movement patterns, at certain aggregation sites small areas may play vital roles in the life history of a large amount of the population. Acoustic telemetry was used to estimate habitat use of white sharks, *Carcharodon carcharias*, while aggregating at Mossel Bay, South Africa. Total range of all shark tracks combined accumulated 782 hrs and covered an area of 93.5 km^2 however, within this range, sharks were found to highly utilise a core habitat (50% Kernel, K50) of just 1.05 km^2 over a reef system adjacent to a river mouth. Individual tracks revealed additional core habitats, some of which were previously undocumented and one adjacent to a commercial harbor. Much was found to be dependent on the size of the shark, with larger sharks (>400cm) occupying smaller activity areas than subadult (300-399 cm) and juvenile (<300 cm) conspecifics, while Index of Reuse (IOR) and Index of Shared Space (IOSS) were both found to increase with shark size. Such results provide evidence that larger white sharks are more selective in habitat use, which indicates they have greater experience within aggregation sites. Furthermore, the focused nature of foraging means spatially restricted management strategies would offer a powerful tool to aid enforcement of current protective legislation for the white shark in similar environments of limited resources and capacity.

Key Words: *Acoustic Telemetry; Manual Tracking; Home Range; Kernel Analysis Habitat Use; White Sharks*

Short Title: Fine scale movements and activity areas of white sharks

Introduction

The white shark *Carcharodon carcharias* (Linnaeus, 1758) is globally threatened and has been listed under Appendix II of the Convention on International Trade in Endangered Species (CITES) and the World Conservation Union (IUCN) (Ferguson et al. 2005). It is of particular interest due to their tendency to aggregate close to shore and the perceived danger they represent to humans (Kock et al. 2012). The species is protected by both local and international legislations (Compagno 1991; Dulvy et al. 2008). However, widespread public support for this legislation has been difficult to generate, often due to fear of shark attacks (Peschak 2006). The species can make large-scale oceanic migrations whilst displaying patterns of site fidelity, often linking aggregation sites, occupying previously unforeseen areas and entering waters which may not fall under their protection (Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007; Nasby-Lucas et al. 2009; Jorgensen et al. 2010; Duffy et al. 2012; Jorgensen et al. 2012). Despite the legislations, trade in white shark products has continued; particularly of those fished offshore in international waters by the shark finning industry (Shiviji et al. 2005). Other threats include incidental by-catch in commercial fisheries and mortalities in shark nets or drumlines set at popular swimming beaches in South Africa, Australia and Singapore (Compagno et al. 1997; Baum et al. 2003; Dudley & Simpfendorfer 2006). Along with other species, white sharks have now gained commercial value in tourist trade, since the advent of shark diving in the late 1980’s and early 1990’s (Gallagher & Hammerschlag 2011).

Within South Africa, aggregation sites are often coastal and associated with pinniped colonies (Compagno et al. 1997). Such aggregations are particularly well documented in the South Western Cape at three locations; Seal Island, False Bay (Kock and Johnson 2006); Dyer Island, Gansbaai (Johnson 2003; Wcisel et al. 2010) and Seal Island, Mossel Bay (Johnson et al. 2009). Movements of individuals between these sites and others along the coastline have been confirmed with acoustic and satellite telemetry as well as visual identification (Bonfil et al. 2005; Johnson & Kock 2006).

In order to protect a species we must first understand their movements and habitat use patterns (Simpfendorfer et al. 2010). In the marine environment acoustic telemetry systems have lead to a better understanding of sharks' role as apex predators in ecosystems (Sundström et al. 2001; Voegeli et al. 2001). Such studies allow for a better understanding of concepts such as home range (the day to day, spatial extent or outside boundary which an animal utilises Burt 1943; McNab 1963) to be explored and have often formed the basis for assessing the boundaries and potential effectiveness of marine protected areas (Heupel et al. 2004; Bruce et al. 2005; Meyer & Holland 2005; Wilson et al. 2009; Hearn et al. 2010). These protected areas are considered vital tools for science based protection of marine species (Heupel and Simpfendorfer 2005; Simpfendorfer et al. 2010). Active tracking has the advantage over passive monitoring in that it can reveal fine scale movement patterns, particularly in areas which are frequented by an individual for long periods of time (Johnson et al. 2009; McCord & Laberth 2009). It also produces tracks of a finer scale than satellite telemetry, which is limited by the water column itself (Teo et al. 2004; Jewell et al. 2011). The obvious disadvantage with active tracking is the long hours involved in collecting data and the limitation of weather conditions; as such finding a study site with some protection from the ocean is often preferable (Johnson et al. 2009).

Previous studies indicate that white sharks may limit their activity areas while foraging on pinnipeds; Goldman & Anderson (1999) and Klimely et al. (2001) documented foraging of white sharks at the Farallon Islands over mulit-day periods, whilst Johnson et al. (2009) tracked tagged white sharks for several months in Mossel Bay. In a separate study Johnson (in prep) found white sharks year round in Mossel Bay and over 40% were found to be seasonal residents, being detected by an acoustic array at least 50% of days during a study of the seven month high season. Such studies used Rate of Movement (ROM) Swimming Linearity (LI) to assess movement patterns (Goldman & Anderson 1999; Sundström et al. 2001) and we further examine habitat use with home range analysis (Kernel and Minimum Convex Polygon; Silverman 1986). We define the activity areas projected as at least temporary or seasonal home ranges as many of the individuals have been documented to return to Mossel Bay over many years (Johnson unpublished data), however it is important to note that during its entire life history a white shark may roam many thousands of km spanning entire oceans.

We report on the seasonal home range size and overlap of acoustically tagged and manually tracked white sharks utilising Mossel Bay, South Africa. We further determine whether home range size and overlap is independent of shark size (total length). Already established as an important habitat for this protected and vulnerable species, we examine if a marine protected area in Mossel Bay, and similar systems, could be a viable and effective tool to aid the survival of white sharks.

Materials and Methods

Study Site

Mossel Bay lies approximately 400 km to the east of Cape Town on the Indian Ocean side of South Africa's Western Cape (Fig. 1; S'34º10, E'22º10). The bay provides an ideal study site for acoustic telemetry surveys as it is partially protected from the winter prevailing winds from the west and south west by the Cape St. Blaize peninsula, and fully protected to the north and east by the curvature of the bay. The bay is home to a moderate sized colony of Cape fur seals *Arctocephalus pusillus pusillus* (Schreber 1775) of *circa*, 4500 - 5000 individuals (excluding pups of the year), which reside on Seal Island (Kirkman *pers. comm.*). There are three river mouths within the bay (Hartenbos, Kleinbrak and Grootbrak), each with reef systems adjacent to them.

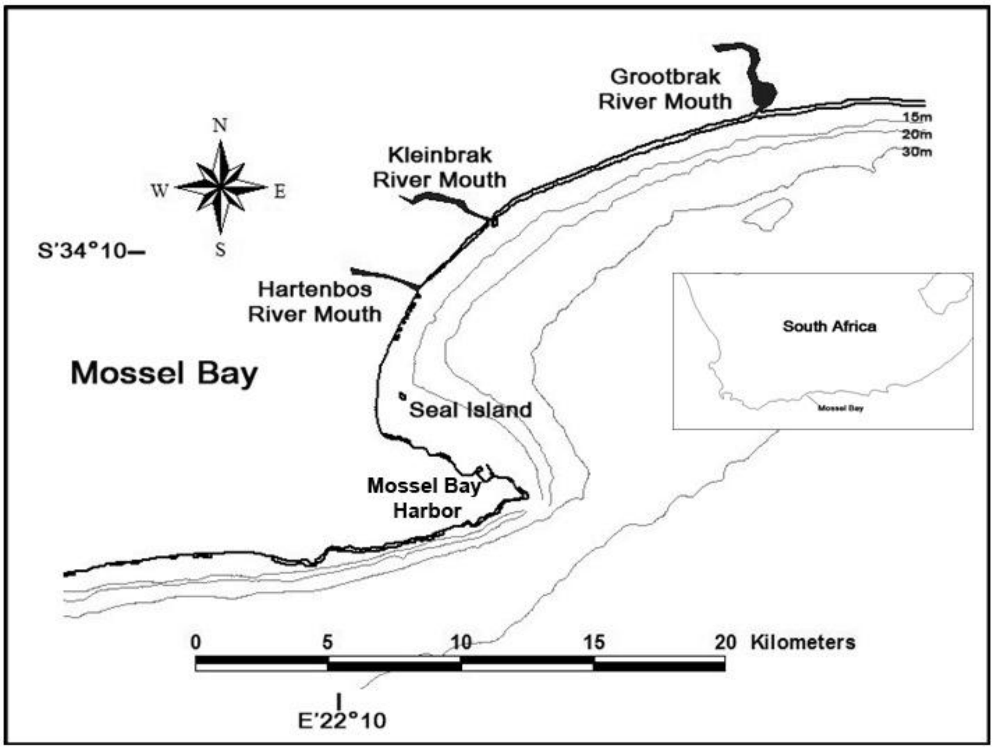


Figure 1. Study Site, Mossel Bay South Africa

Acoustic Telemetry

All relevant permit and ethics approval were obtained prior to initial tagging from Marine and Coastal Management (MCM now operating under Oceans and Coasts) and University of Pretoria Animal Use and Care Committee. A total of 13 sharks were tagged with acoustic transmitters and tracked by research vessels in Mossel Bay between June 2005 and October 2008 (Table I). Sharks were attracted to a research vessel with the use of bait and chum in order to be tagged externally while free swimming (as described in Johnson et al. 2009). Body markings and any other individual traits such as dorsal fin ID and shark total length (TL) were recorded to recognise each shark throughout the study. Total length was estimated by comparison to known dimensions of research vessels as sharks swam close. Sharks were tagged with VEMCO V16 frequency-specific continuous transmitters (pinging rate every 1000 - 2000 ms), with the use of a tagging pole. These sharks were then actively tracked by a boat-mounted hydrophone connected to a VEMCO VR60 (GWS’s 1 - 3) or VEMCO VR100 (GWS’s 4 - 13) acoustic receiver. Every 10 minutes, the tracking boat would position itself 30 - 40 m (equivalent to signal strength of about 70 dbs) from the shark to approximate the shark’s position in comparison to the onboard GPS’s position. The vessel would not try to follow the shark closer than 20 - 30 m (*circa* 80 dbs) to minimise any potential interaction between the shark and the tracking vessel. Time and position of the shark were recorded manually every 10 min, while the VR100 recorded boat’s GPS positions continuously.

When conditions permitted, sharks were continuously tracked for a minimum of 24 h. Crew changes involved a second research vessel in order to minimise disruption to the continuity of the track. When a second vessel was unavailable for crew change, the research vessel would dock in the harbor which led to gaps of 40-70 min in tracking data. When sea conditions deteriorated or the tag signal was lost, tracking was abated until favourable conditions returned. On occasions a tagged shark would be picked up opportunistically by the research vessel while on unrelated excursions and tracking would recommence.

Data analysis

Home Range Analysis

Data of tracked sharks was filtered to one data point for every 10 min as in Johnson et al. (2009). Home ranges were determined using both Minimum Convex Polygon (MCP) and Kernel (K) methods using the 'Animal Movement' extension of ArcView 3.2 (Hooge & Eichenlaub 2000). We defined 'activity area' from MCP, 'home range' from K95% and 'core-area' from K50%. Kernels of both 95% and 50% (K95/K50) were derived using least squares cross validation smoothing parameters as suggested by Warton (1995) and Carr & Rogers (1998). In the event that a kernel extended over land, the land was clipped using the X-tools extension of ArcView as in Heupel et al. (2004).

Total Range

Separate tracks of the same shark were synthesised (i.e. calculated as if they were continuous) to produce a cumulative track for each shark. These cumulative tracks were then synthesised for all the tracked white sharks to give a total range of tracking efforts. This range was then tested for activity area, home range and core area use.

Size Class/Home range

Individual tracks of each shark were subjected to home range analysis and then tested against size class with one-way Analysis of Variance (ANOVA) to determine if home range estimates varied significantly between different size classes of shark. We determined size class after Bruce (1992), who considered sharks under 300 cm as juvenile and presumed to have diet and physiology more adapted to teleost and cephalopod prey (Ferrara et al. 2011; Smale & Cliff 2012; n = 5). Subadult white sharks are expected to be 300 - 450 cm, however, our size range only extended to 420 cm and there is much debate on exactly what size white sharks become mature (it is impossible to tell visually while free swimming). As a result we avoided the term 'mature' and rather determined 'large' sharks at ≥ 400 cm (n = 4) and 'subadult' between 300 and 399 cm (n = 4).

Activity area over time

A comparison for activity area over time was plotted in a similar way to Goldman & Anderson (1999). We used the observation-area curve recommended by Winter and Ross (1982) and used by Rechisky & Weatherbee (2004) to determine optimal tracking time (the time at which the animal reaches the full extent of it's movement and home range estimates become more accurate) for white sharks in Mossel Bay, based on 5% activity area change.

Swimming linearity

Linearity of sharks' individual tracks were determined using the Linearity Index (LI) of Bell & Kramer (1979):

$LI = (Fn - F1)/D$

Where Fn is the last position taken for the shark, F1 is the first position taken for the shark, and D is the total distance travelled by the shark. A linearity of 1 indicates linear movements without returning to the vicinity (i.e. straight line travel). A LI near zero indicates little movement from the area with a great deal of overlap and reuse of the activity space. LI was determined after every 5 hrs of tracking on individual tracks lasting longer than 10 hrs as in Johnson et al. (2009).

Index of Reuse

Index of Reuse was used to determine the level of reuse from one day-to-day movement to the next. Home ranges (K95), determined from individual tracks of less than 24 hrs, were overlapped with each other, and those from longer tracks periods (12 or 24 hr) were compared as in Rechisky & Weatherbee (2004):

$IOR = [OV(A1 + A2)]/(A1 + A2)$

Where [OV(A1+A2)] is the area of overlap between two home ranges (K95), and (A1 + A2) is the total area of both home ranges ((Morrissey & Gruber (1993) modified from Cooper (1978) and McKibben & Nelson (1986)). The effect of shark body size was measured with Linear Regression from TL and IOR.

Home range overlap

We developed an Index of Shared Space (IOSS) from home range overlap using methods of Bull & Baghurst (1998) and Morrissey & Gruber (1993), K95 overlap from one individual's home range with each of the other sharks' home range was calculated using the X-tools feature of Arc View:

$IOSS = OV/[(A1+A2)/2]$

Where OV is the area of overlap from one conspecific's home range to another and A1 and A2 are the total home ranges of the two conspecifics (K95). The mean home range overlap was used to describe individual's general level of home range overlap with con-specifics (Table II). Kruskal-Wallis test was used to determine if home range overlap was inversely correlated to TL.

Migration away from Mossel Bay

Most tracks ranged from the harbor mouth to the Grootbrak River Mouth, but one shark (GWS-9) moved out of Mossel Bay using a near linear swimming pattern (Fig. 2A). The shark was not detected during any research operations in the bay for the following two months but was sighted back in Mossel Bay later on the 2 July 2008, by which time the tag had ceased transmitting. As the study’s focus was to examine home range of sharks whilst residing in Mossel Bay, the track of this shark was cut to the point at which it began moving away from Mossel Bay.

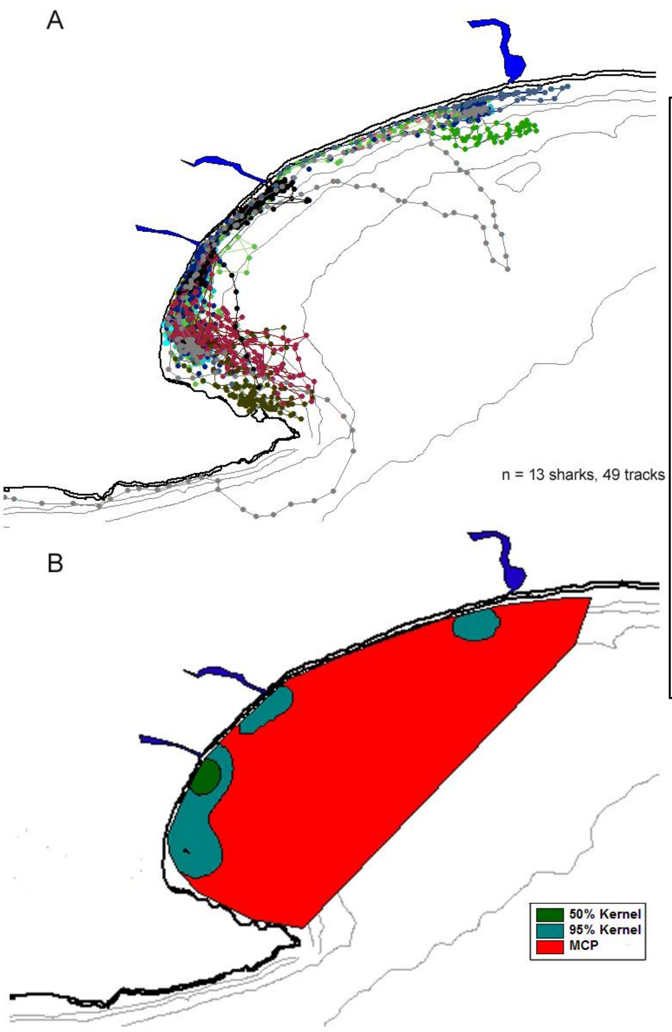


Figure 2. Active tracks of 13 white sharks tagged at Mossel Bay (A) and combined home range and core habitat use of thirteen white sharks acoustically tracked within the confines of Mossel Bay (B). Estimates determined by K95 (grey), K50 (green) and MCP (outer, red) calculations.

Results

The total activity area of the thirteen sharks, as determined by MCP, encompassed an area of 93.5 km^2 (Fig. 2B). This extended from Mossel Bay harbor to past the Grootbrak river mouth. The area was primarily restricted to near shore coastal habitat within the natural boundary of Mossel Bay. The home range (K95) within this area comprised 10.19 km^2 covering the habitats of Seal Island, Hartenbos, the waters adjacent to Kleinbrak and Grootbrak river mouths. The core area was 1.05 km^2 and located in the Hartenbos area.

Individual activity areas ranged from 6.4 km^2 (GWS-05) to 55.5 km^2 (GWS-02) (Table 1), whilst home range (K95) of these individuals varied from 3.52 km^2 (GWS-13) to 21.15 km^2 (GWS-06). Ten of the sharks confined their home range to one, or more, of the previously identified core habitats, namely Seal Island, Hartenbos, Kleinbrak and Grootbrak (Fig. 3). Two sharks (GWS's 10 and 12) displayed fidelity to an area adjacent to Mossel Bay harbor and one (GWS-09) moved into an area offshore of the Grootbrak. Incidentally GWS-10 also adopted an anomalous behaviour of entering the harbor during tracking and remaining within the harbor for several hours. Whilst at the harbor mouth, GWS-12 frequently circled a sardine purse-seine fishing vessel as it apparently cleaned its fish holds (as determined by the presence of a chum type slick).

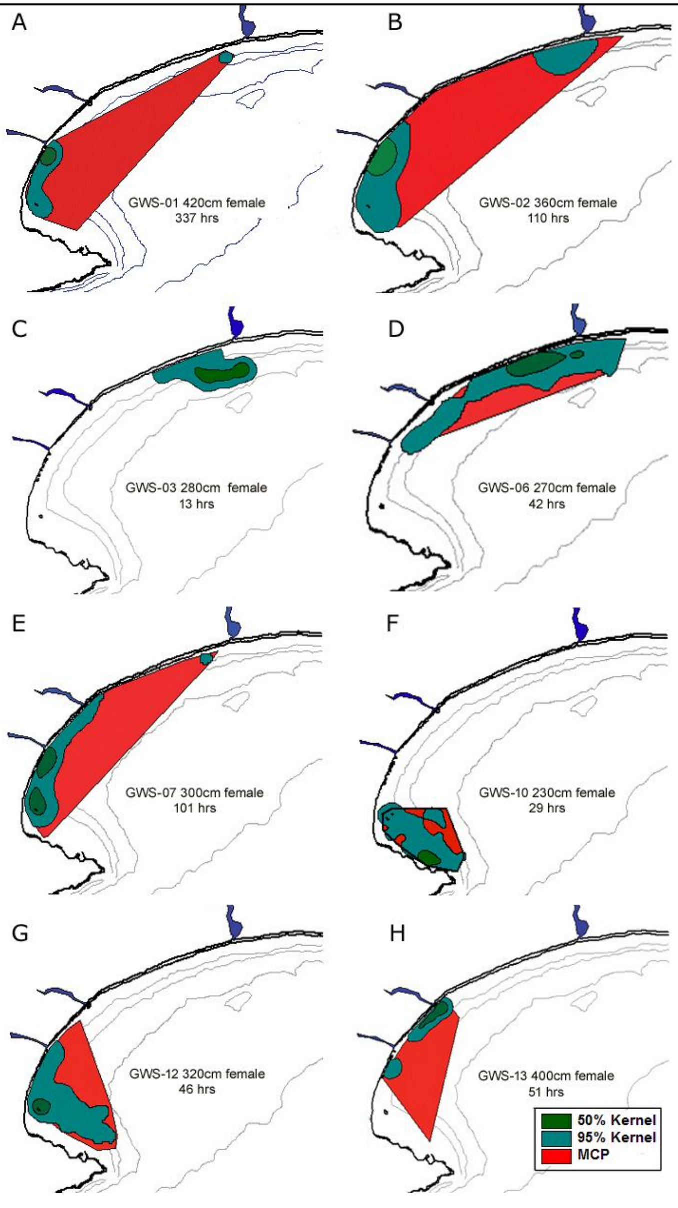
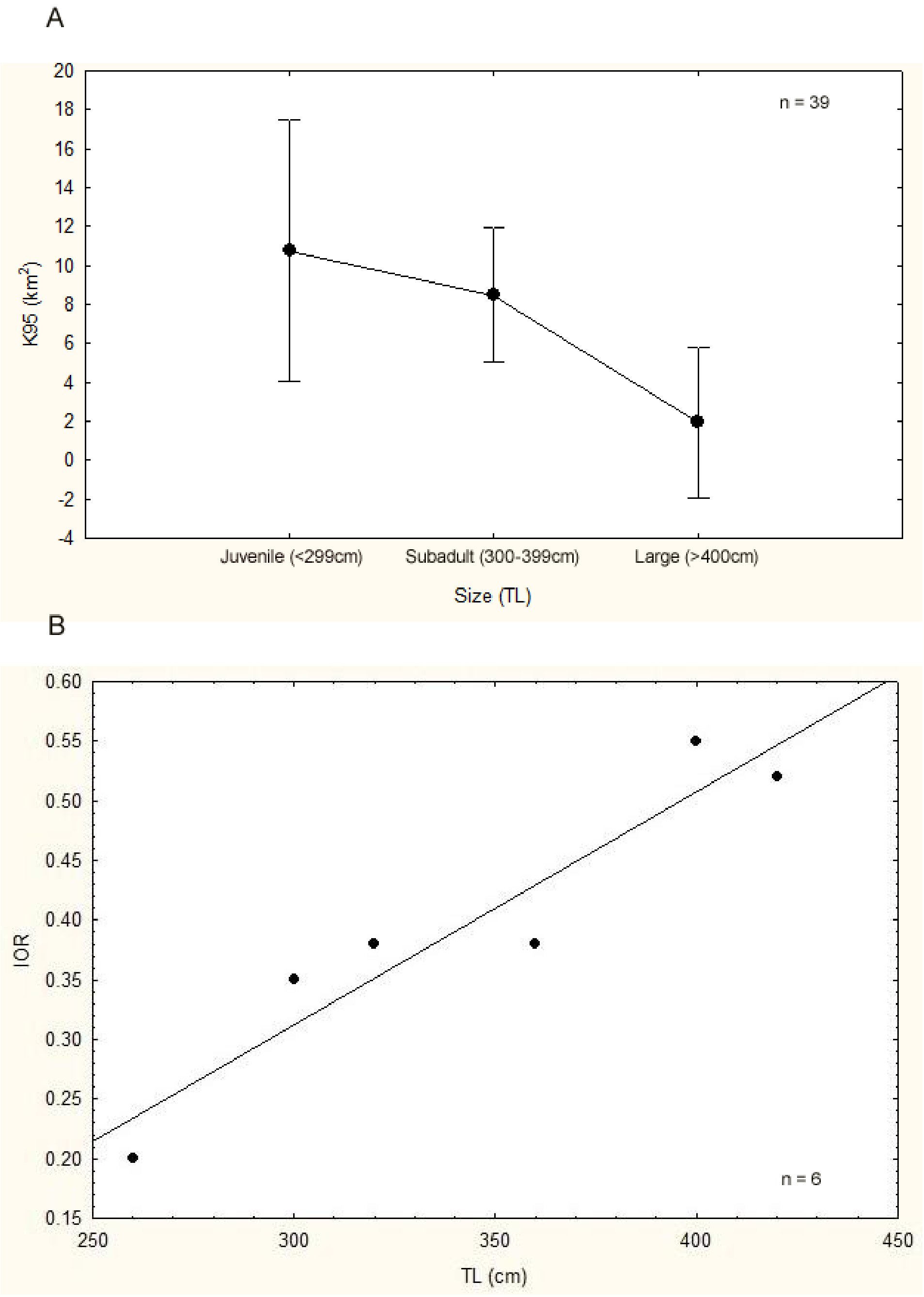


Figure 3. Activity area, home range and core habitat use of 8 individual white sharks tracked at Mossel Bay as determined by MCP, K95 and K50 calculations. A. GWS-01, B. GWS-02 350 cm female, C. GWS03 280 cm female, D. GWS-06 270 cm female, E. GWS-07 300 cm female, F. GWS-10 230 cm female, G. GWS-12 330 cm female, H. GWS-13 400 cm female.

Linearity varied depending on the sharks movements either away from core areas (higher) or remaining within them (lower). When GWS-09 moved into the area of Grootbrak its movement in this area was linear (LI = 0.696) before returning back to the coast and continuing to move linearly (LI = 0.495 - 0.454) until reaching Seal Island where linearity lowered (0.045). After 11 hours in this area (22:00 – 09:00 hrs) the shark began to move directly out of the bay toward south west (LI = 0.698). In comparison both sharks using the harbor mouth area showed low levels of linearity while there (LI of 0.019 and 0.041 respectively). Several other tracks also displayed high linearity; GWS-06 (LI = 0.885 between hours 5 – 15) which travelled from Hartenbos to Grootbrak and back to Seal Island and GWS-12 track 3 (LI = 0.692) which extended from Seal Island to Kleinbrak. Each of these movements followed costal routes from and back to the island or reef systems. GWS-13 moved from Kleinbrak towards the harbor, possibly as the shark moved away from Mossel Bay (LI = 0.777, the shark was not detected again despite several search transects in the weeks following). Lowest levels of LI were observed when tracks remained in core areas (GWS-01, Track 7; 0.006; GWS-06, Track 32; 0.007; GWS-07, Track 36; 0.010).

LI was independent of TL (ANOVA, $F_{(2,36)} = 1.488$, $P > 0.5$, $n = 39$), but significantly related to K95 (t-test $p < 0.01$, $n = 39$). However, the home range of individual tracks were found to be dependent on TL (ANOVA, $F_{(2,36)} = 4.315$, $P < 0.05$, $n = 39$) with large sharks using a more refined home range in comparison to small and medium sized individuals (Fig. 4A). IOR was found to be a function of size with larger sharks showing higher levels of reuse (Fig. 4B; Linear regression; $r^2 = 0.896$, $P < 0.01$, $n = 6$). In particular GWS-01 and GWS-13 showed high fidelity to the areas of Hartenbos and Kleinbrak respectively with the former repeatedly returning to the same site and the latter remaining at the same site for 80% of its total track. In contrast, GWS-06 used several different areas of the same reef system at Grootbrak which resulted in low levels of reuse.

Figure 4. A; Test for variance between home range size (K95) of white sharks tracks in relation to shark total length (TL). ANOVA, $F_{(2,36)} = 4.315$, $P < 0.05$, $n = 39$ and B; the effect of total length (TL) on Index of Reuse (IOR) measured with Linear Regression; $r^2 = 0.896$, $P < 0.01$, $n = 6$.



IOSS revealed an average of 0.273 (equivalent to less than 30%) shared space between one individual to all other conspecifics tracked, and showed a significant relationship to body size (Table2; Fig. 5; Kruskal-Wallis$_{(7,156)}$ = 21.65, $P < 0.1$, n = 13 sharks, 156 IOSS values). Highest levels of shared space were recorded between sharks at Hartenbos and were particularly high between two sharks tagged and tracked within the same 24 hrs (GWS-04 and GWS-05; 0.692). GWS-01 had the highest level of shared space with all other conspecifics at 0.400. Cases of zero overlap occurred between individuals whose tracks were either confined to one area (GWS-03) or several areas which did not include the Hartenbos reef system (GWS- 06 and GWS-10). Duration of tracking did not appear to play a major role in degree of overlap with several sharks tracked for just one shift showing higher overlap than others tracked for several days. GWS-09's track overlapped all other conspecifics as it covered the entire bay, but its IOSS was lower than those from Hartenbos (0.240) because its home range covered such a large area. Dorsal fin identification revealed five of the eight sharks tagged in 2008 and one from 2007 were present in Mossel Bay during October 2008 (GWS's 05, 06, 09, 10, 12 and 13).

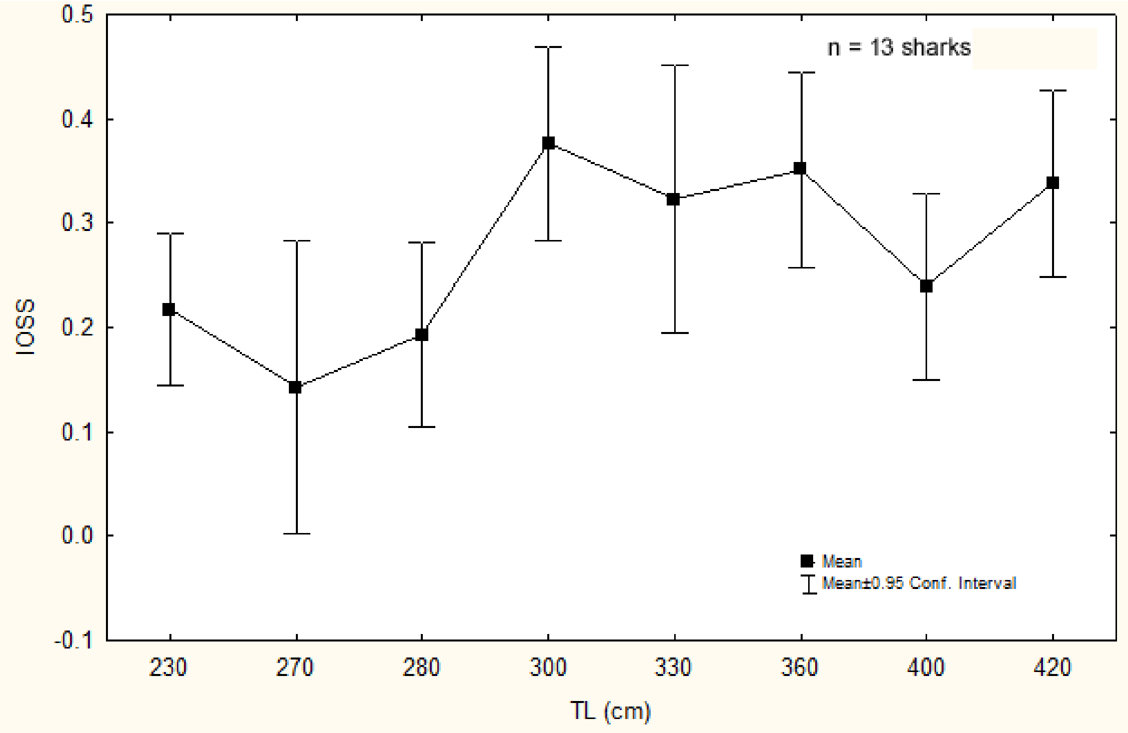


Figure 5. Index of shared space (IOSS) to total length (TL) Kruskal-Wallis$_{(7,156)}$ = 21.65, P > 0.005, n = 13

Comparing MCP over time displayed the rate of change in activity area as more tracking occurs (Fig. 6A). Activity area plateaus once a shark remains in the same area, or areas for prolonged periods of time. Steep rises in activity area are an indication of either high level of linearity or as a result of a shark being detected in a new area between different tracking shifts. Observation-area curve (Fig. 6B) showed that the optimum tracking duration in Mossel Bay was 72 hrs, a duration of which we surpassed three times in this investigation.

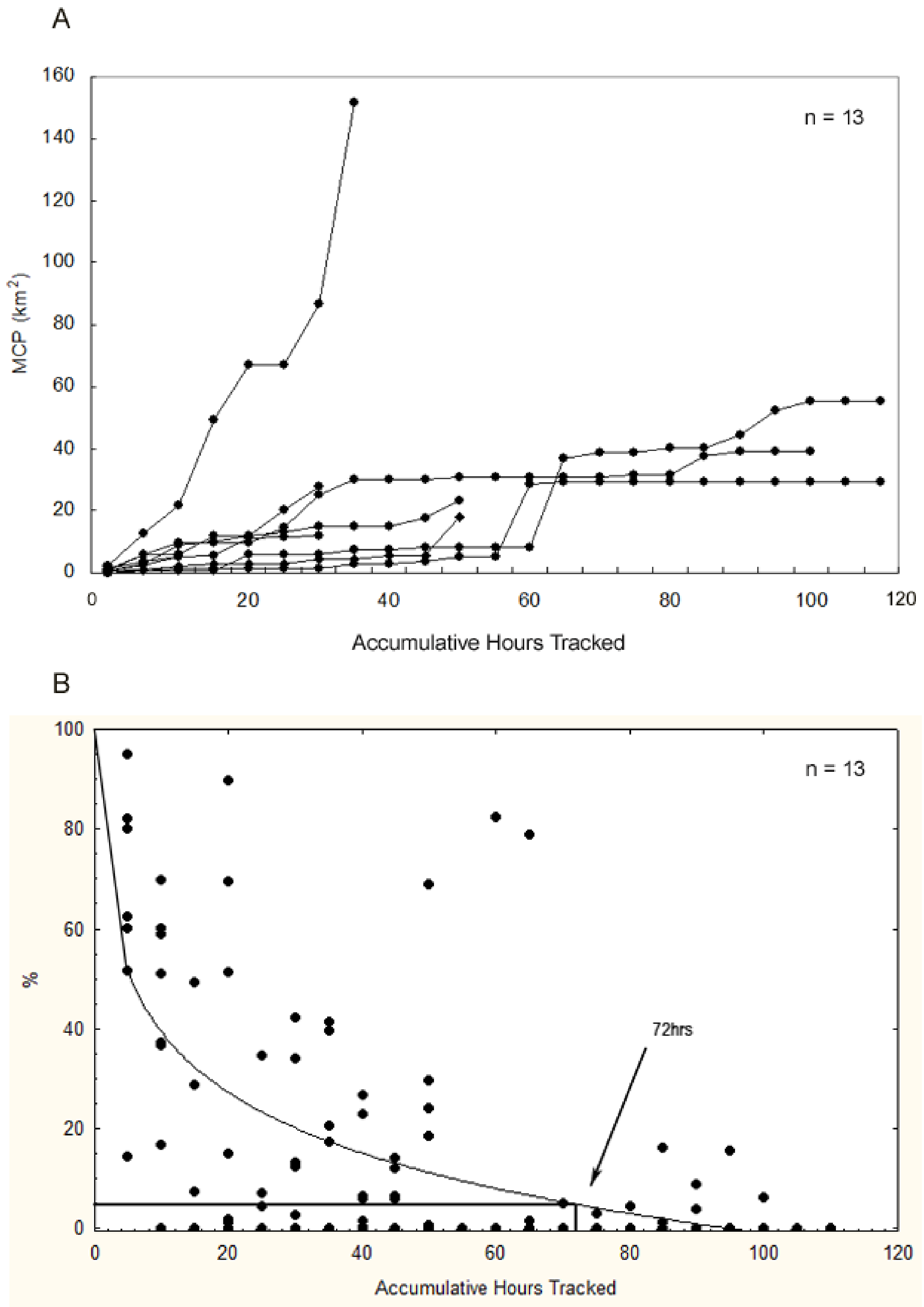


Figure 6. A, Effect of tracking duration on activity area (MCP) and B, Observation-area curve derived from activity area (MCP) change over time.

Discussion

The total range (MCP) of sharks tracked encompassed most of Mossel Bay; however 95% and 50% kernel analysis revealed a spatial pattern of highly utilised core habitats that fell within this range. Some of these core habitats have been previously identified, such as Seal Island, Hartenbos and Grootbrak (Johnson & Kock 2006; Johnson et al. 2009), whilst others, such as Kleinbrak and Mossel Bay Harbor represent newly identified areas.

Hartenbos was the most frequently used core habitat identified during this study. Johnson et al. (2009) found this site to be frequented by white sharks during a hiatus between morning and evening patrolling bouts at Seal Island. Lower levels of movement and linearity were observed and it was suggested this could be a site for resting or social purposes. This may explain why Hartenbos displayed higher levels of white shark home range use than Seal Island, contradicting earlier studies that suggest waters directly adjacent to Cape fur seal colonies would have the most dense aggregations of white sharks in the Western Cape (Compagno 1997). Johnson (in prep.) went on to suggest that when not foraging for seals, sharks in Mossel Bay fulfil other life history requirements, such as resting to digest food and conserve energy for the next Seal Island patrol or patrolling for other prey items in areas away from Seal Island.

Seal Island was frequented by the majority of tracked sharks, but did not fall in the core habitat of as many sharks as Hartenbos. This parallels the findings of Johnson et al. (2009) who found a daily effort of 8.9 to 10.7% spent patrolling at Seal Island which was much lower than that observed in California (Klimely et al. 2001). Our results show that whilst waters adjacent to pinniped colonies may represent a primary hunting ground for white sharks, they do not necessarily represent the most commonly used areas of an aggregation site. The Grootbrak river mouth was highly frequented by four sharks in this study and has the potential to support a feeding ground for white sharks due to the extensive reef areas harboring prominent teleost and elasmobranch populations (Johnson et al. 2009). The area adjacent to the Kleinbrak river mouth presents a new core habitat. GWS-13 spent the majority of its tracked time in this area following initial tracking at Hartenbos. Two other sharks

(GWS-6 and GWS-7) also utilised Kleinbrak area in a similar way to GWS-13, but with lower levels of overall fidelity. The final core habitat was adjacent to Mossel Bay Harbor. This area was frequented by two sharks; one juvenile (GWS-10) and one subadult (GWS-12). The harbor is an active commercial fishery and the potential overspill of fish being unloaded or discarded could produce a chum slick similar to those used to attract white sharks for viewing purposes. The repeated presence of olfactory stimulus, and potential food, may motivate a number of white sharks to actively forage in this area.

Our data suggests that home range size is dependent on shark total length and that larger sharks show higher levels of reuse within Mossel Bay. Goldman & Anderson (1999) also found that larger sharks utilised a smaller activity area compared to smaller conspecifics. These findings differ from lemon shark acoustic telemetry studies that found positive correlations between length and home range of individuals (Gruber et al. 1988). Goldman & Anderson (1999) suggested that larger white sharks were experienced hunters within South Farallon Islands and that experience could lead them to utilise certain areas efficiently whereas smaller, less experienced, individuals roamed greater areas in search of prey. On the other hand, Gruber et al. (1988) suggested that as juvenile lemon sharks in Bimini Lagoon grew they were able to expand their home range and venture away from nursery areas. We suggest that smaller white sharks need to fulfil life history requirements in spatially separate areas to larger sharks. As such, Grootbrak may provide a high abundance of teleost and cartilaginous prey, which smaller white sharks are considered more adept at hunting (Bruce 1992; Ferrara et al. 2011; Smale & Cliff 2012). Larger and medium sharks are more adept at hunting marine mammals, and therefore utilise the food resources of Seal Island. Medium sharks which have switched to marine mammal prey more recently (Bruce 1992; Estrada et al. 2006; Ferrara et al. 2011), need to learn the best areas and methods in which to hunt these prey and therefore may utilise these areas less efficiently than the larger individuals. The predictable occurrence of Cape fur seals in waters adjacent to Seal Island may enable large white sharks to gain sufficient food resources without the need for extensive horizontal searching.

Conservation Implications

Our study suggests that white sharks in Mossel Bay have limited home ranges, focused core areas, and that their individual home ranges overlap significantly with one another. The results could be used to provide guidance to management authorities in the implementation of a marine protective area in Mossel Bay as an effective means for the protection of the species. Costal developments at these sites have the potential to impact the life histories of the white sharks which seasonally inhabit them. The protection of these coastal areas will benefit the recovery of white sharks in South Africa which has begun to stabilise post protection in 1991, but still remains a fraction of the numbers 50 years ago (Dudley & Simpfendorfer 2006; Kock & Johnson 2006).

This study provides a further demonstration that active tracking can aid conservation efforts for endangered marine species. These methods are applicable to white sharks across the Western Cape of South Africa and beyond and could also be used where similar partially residential species are threatened. An increase in the knowledge of the species movements can only increase the effectiveness of conservation efforts for the species, improving survival rates and aiding recovery.

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The following persons assisted in tracking (2005) J. Mourier, J. Charivas, M. Cuvier, H. Medd, A. B. Casagrande, L. Ewing, S. John, G. Horton, L. Hancke, T. Snow, S. A’bere, T. Seckler, G. Wright, C. Jurk, M. Scholl, A. Riodon. 2008-2009: S. Swanson, B. Oh, L. Brits, A. Blaison, A. Dell'Apa, J. Lang, J. Swinton, D. Zaveta, Be. Contrella, C. Graham, N. Harrison, S. Peake, J. Yee, M. Orr, L. Belleni, K. Stewart, J. Silbernagel, C. Moore, A. Johnstone, A. Blessington, T. Coyne, J. Anderson, N. Tonachella, V. Cardinale, D. Uhlig, S. Lewis-Koskinen, V. Vasquez, A. Jodice, E. Teel, F. Munding, N. Julien, F. Jaine, R. G. Elliott, A. Prentice.

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Final Thanks…

Tracking Sharks


(c) Katja Vinding Petersen, Dyer Island Cruises


(c) Katja Vinding Petersen, Dyer Island Cruises

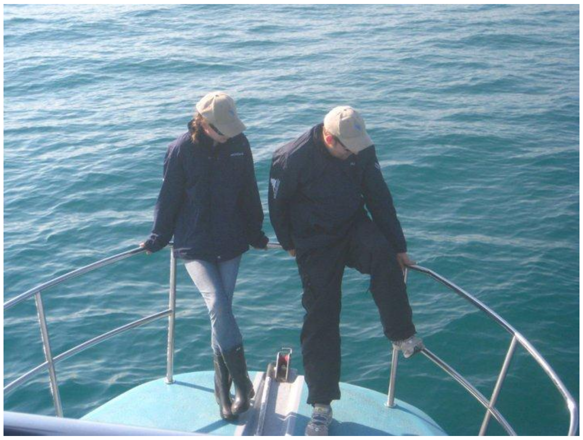
(above and right) Tracking sharks from Lwazi at dusk with Michelle, Alison, Katja and Zack.
(below) Our research vessel Lwazi with Alison, Ed and volunteers. Fuel was sponsored by VW South Africa as part of its Think Blue campaign.

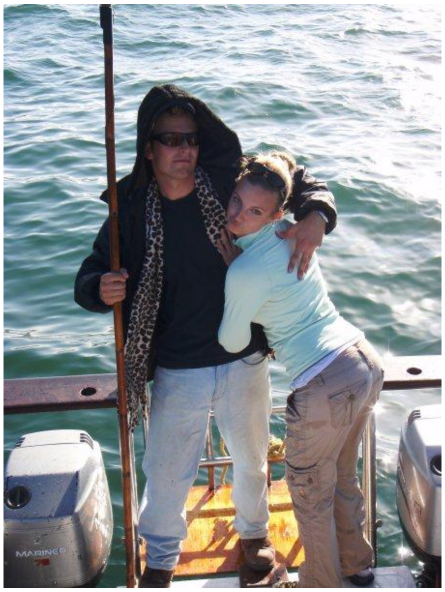
Marine Dynamics, VW & LWAZI


© Ben Arthur

(above) Working with Marine Dynamics, I've met some great people over the years and seen some amazing wildlife. Thank you for choosing Marine Dynamics and making a difference.

Friends met along the way…





(above left) Michelle Wcisel and I onboard Lwazi.
(above right) Nick Jones & Oliver Jewell, night tracking and braaing dream team!
(above left) Alison Towner, 'The Raz' & myself on Shark Fever 2010.
(above right) Old days from Mossel Bay with Michelle Wcisel 2009.
(below left) Alison & Oli tracking sharks on Lwazi.
(below right) With our interns, volunteers and crew from Marine Dynamics.
Thank you to all of you, the sharks were amazing but the people met along the way even more so.