POPULATION DYNAMICS OF THE WHITE SHARK,  
*Carcharodon carcharias*,  
AT MOSSEL BAY, SOUTH AFRICA  

By  

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Mossel Bay is internationally recognised as one of the centres of abundance of white sharks in South Africa. During 2008 – 2010 there were four sites within the bay i.e. Seal Island, Hartenbos, Kleinbrak and Grootbrak, which were sampled to gain insight into the population dynamics of this species. Currently, life history information on white sharks in this area is limited. This study used a combination of mark-recapture using photographic identification techniques and sight per unit effort methods. Inter-annual, seasonal and spatial patterns in abundance are assessed. The effects of environmental parameters on abundance are also investigated.

Photographic identification techniques were employed to identify unique individuals within the sampled population. This modified mark-recapture approach is therefore non-invasive and cost-effective. Open population POPAN parameterization was used to analyse the data in software program MARK. The total population was estimated at 389 sharks (351 – 428; 95% CI). Over the three year period, a marginal (yet non-significant) decline in numbers was observed, in terms of both monthly and seasonal population estimates.

Sightings per unit effort data were collected during sampling trips. The relative abundance and body size composition of white sharks demonstrated significant spatial and seasonal variation. The highest and lowest relative abundance was observed at Seal Island and Hartenbos, respectively, and is likely attributed to prey availability. Although white sharks were present year-round in Mossel Bay, the highest relative abundance occurred during summer and the lowest relative abundance occurred during spring.

White sharks were grouped into three main size classes based on estimated total length (TL): Young of the year (YOY) (125 – 174cm), juvenile (175 – 324cm) and adult (325 – 524cm). YOY white sharks were most prevalent at Grootbrak, with
juvenile and adult individuals concentrating at Seal Island. Although most size-classes were present throughout the year, seasonal differences were observed. YOY individuals were most abundant in the autumn months, juvenile size-classes appeared to concentrate in the study area during winter, and the adult individuals were most abundant in the spring months. Overall, there was a high concentration of white sharks ranging in size between 175 – 324cm TL, and it was thus hypothesised that Mossel Bay represents an interim nursery or grow-out area for white sharks in South Africa.

Data collected from 2008 and 2009 was used to investigate the relationship between specific environmental parameters, i.e. sea surface temperature and vertical water clarity, in relation to the relative abundance of white sharks. Sea surface temperature and vertical water clarity observed in this study ranged from 9.3 - 22.7°C and 0 – 10m, respectively. Sea surface temperature did not have a significant influence on the relative abundance of white sharks and this may be attributed to the thermoregulatory capacity of the species. Vertical water clarity, however, did significantly influence the relative abundance. Furthermore, the combined effect of site and season significantly influenced the relative abundance of white sharks and is probably linked to the distribution and abundance of inshore prey resources.
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DECLARATION

I, Rabiah Ryklief (20631101) hereby declare that the thesis for the degree of
Master of Science in Zoology is my own work and that it has not previously been
submitted for assessment or completion of any postgraduate qualification to
another University or for another qualification.

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CHAPTER 1
GENERAL INTRODUCTION

1.1 INTRODUCTION TO STUDY ANIMAL

*Carcharodon carcharias*, commonly referred to as the white shark, is a large mackerel shark (order Lamniformes) belonging to the family Lamnidae (Compagno *et al.* 1997). The white shark is distinctly grey with a white underbelly and is typically torpedo-shaped with a pointed snout, large pectoral and dorsal fins and a crescent-shaped caudal fin (Compagno *et al.* 1997). This species displays sexual dimorphism in that females attain a larger size than males (Compagno *et al.* 1997). The length at maturity varies between populations but in general, length at maturity in females is considered to be between 4.5 – 5.0m, and 3.4 – 4.1m for males (Bruce 2009). Due to the existence of a social hierarchy in which larger individuals are dominant over smaller individuals, females tend to be the dominant sex (Strong *et al.* 1992; Klimley & Anderson 1996). At birth, individuals are estimated to range in size from 109 – 165cm total length (Cailliet *et al.* 1985; Francis 1996; Uchida *et al.* 1996) and have a sex ratio close to 1:1 (Bruce 2009). The only morphological characteristic (over and above body size) to distinguish between the sexes is the presence of two claspers (reproductive organs) situated ventrally adjacent to the pelvic fins of males (Last & Stevens 2009).

As is the case with most sharks, white sharks are characterised by a K-selected life history and is thus a slow growing, long-lived species with low fecundity (Smith *et al.* 1998; Dudley & Simpfendorfer 2006). As the white shark is a marine apex predator it is able to maintain biodiversity through direct and indirect predation effects (Stevens *et al.* 2000; Heithaus *et al.* 2002; Myers *et al.* 2007) thus representing a keystone species essential to the functioning of coastal marine ecosystems (Van der Elst 1979; Stevens *et al.* 2000; Ferretti *et al.* 2010).
Despite a circum-global distribution (Last & Stevens 2009), many aspects of the basic biology and ecology of white sharks are still poorly understood, probably due to the difficulties of keeping this large, active pelagic species in captive conditions as well as the inherent obstacles associated with sea-based research.

Scientific studies on the white shark have focussed on age-growth dynamics (Cailliet et al. 1985; Mollet et al. 1996; Stevens & Bruce 1999; Wintner & Cliff 1999; Cliff et al. 2000), thermoregulation (Carey et al. 1982; Tricas & McCosker 1984; Block & Carey 1985; Goldman 1997), predator-prey interactions (Tricas & McCosker 1984; Klimley et al. 1992; Le Boeuf 2004; Martin et al. 2005; Hammerschlag et al. 2006; Johnson et al. 2008; Laroche et al. 2008), site fidelity (Klimley & Nelson 1984; Bruce et al. 2005; Kock & Johnson 2006; Johnson & Kock 2006; Domeier & Nasby-Lucas 2007; Weng et al. 2008; Jorgensen et al. 2010), and fine scale movements of individuals (Bruce 1992; Strong et al. 1992; Bruce et al. 2005; Johnson & Kock 2006; Johnson et al. 2009; Jorgensen et al. 2010). In addition, a growing number of studies are investigating transoceanic movements and linkages between populations previously thought to be distinct (Taylor 1985; Pardini et al. 2001; Bonfil et al. 2005; Weng et al. 2007; Jorgensen et al. 2010). Reproduction in this species is still poorly understood as knowledge has largely been founded on the capture of neonates and postpartum adults (Klimley 1985; Fergusson 1996; Francis 1996; Uchida et al. 1996) with no reports, to date, documenting visual accounts of the species mating. Although attempts have been made to quantify population numbers of white sharks, such estimates have generally been subjected to significant limitations (Cliff et al. 1996b; Strong et al. 1996; Chapple et al. 2011; Johnson unpublished). It is imperative to obtain robust estimates of population numbers over time for this species to allow for the detection of population trends and to enable effective conservation management.
1.2 DISTRIBUTION AND RANGE

White sharks have a circumpolar distribution in temperate waters concentrating in coastal waters of Australia, California, the northeast United States and South Africa (Fergusson et al. 2005). There are also records from tropical localities such as the Coral Sea (Last & Stevens 2009), Papua New Guinea (Burgess & Callahan 1996), the central Pacific (Taylor 1985), northern Brazil (Gadig & Rosa 1996) and the tropical southwest Indian Ocean (Cliff et al. 2000).

South Africa is internationally recognized as one of the global centres of abundance for white sharks (Compagno et al. 1997) and hosts a genetically distinct population from those found in the North Atlantic and Australasia (Jorgensen et al. 2010). White sharks actively migrate along the entire South African coast (Cliff et al. 1996b; Bonfil et al. 2005) and between the identified aggregation sites i.e. False Bay, Gans Bay and Mossel Bay (Bonfil et al. 2005; Kock & Johnson 2006; Johnson 2011). Recently, Algoa Bay in the Eastern Cape has been identified as a possible nursery aggregation site (M. Dicken, pers. comm.). South Africa thus hosts a metapopulation with movement between the different local populations.

White sharks utilize close inshore waters e.g. the intertidal zone (Compagno et al. 1997) through to offshore waters of the continental and insular shelves (Compagno et al. 1997) exceeding depths of 1 280m (Last & Stevens 2009). There is evidence that white sharks make pelagic migrations between ocean basins, however, the importance of such open ocean habitats are still unclear (Bonfil et al. 2005; Jorgensen et al. 2010).
1.3 SEASONAL PATTERNS AND THE EFFECTS OF ENVIRONMENTAL PARAMETERS ON ABUNDANCE

Seasonal patterns in habitat use in white sharks exists as they concentrate at pinniped island rookeries during the winter months and move close inshore during the summer months (Kock & Johnson 2006; Oelofse & Kamp 2006; Johnson unpublished). Several environmental parameters could potentially influence the relative abundance of white sharks. In KwaZulu-Natal there were significantly more catches of white sharks when turbidity was higher than the monthly mean, with 63% of individuals caught in warmer waters at temperatures between 19 – 22 °C (Cliff et al. 1989). Water visibility off the coast of KwaZulu-Natal ranged from 0.5 – 14m, with an average of 2.9m in the summer and 4.8m in the winter (Cliff et al. 1989) and catch rates were derived from individuals caught in the bather protection nets along the KwaZulu-Natal coast. The catch effort data were analysed using a general linear model to incorporate the environmental parameters (Cliff et al. 1989). Sea surface temperature (SST), rainfall and El Nino Southern Oscillation (ENSO), which causes reduced levels of rainfall in South Africa, in relation to catch rates was later investigated (Cliff et al. 1996a). A cyclical trend was evident in which every four to six years a peak in relative abundance was observed, however this was attributed to natural variation within the netted region (Cliff et al. 1996a). ENSO years were associated with low catch rates, and high rainfall coupled with low SST during the preceding summer (January – March) resulted in increased captures during the following winter (June – September) (Cliff et al. 1996a).

1.4 MANAGEMENT AND CONSERVATION OF WHITE SHARKS IN SOUTH AFRICA

In recent times, the white shark has become a highly sought after trophy species in sports fishing, targeted largely for its teeth and jaws (Fergusson et al. 2005).
As a result, South Africa, the first country to do so, provided protection to this species under its national fisheries legislation via the precautionary principle put forward in 1991 (Compagno 1991). This pre-emptive legislation stipulates that it is illegal to disturb, catch or kill and/or trade any products derived from a white shark unless permission is granted from the Director-General of the Department of Environmental Affairs and Tourism (Compagno 1991). On a global scale the white shark is listed on Appendix II of the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) and is listed as Vulnerable on the IUCN Red List of Threatened Species (IUCN 2011).

The notorious reputation of the white shark as a ‘man-eater’, arising from shark-attacks and negative media publicity, led to the installation of permanent bather protection nets off most of the KwaZulu-Natal coastline, initially at Durban in 1952 and subsequently elsewhere between the early- to mid-1960’s (Dudley 1997). Unfortunately, these bather protection nets are not only detrimental to sharks but also to other marine species i.e. dolphins, turtles, batoids and teleosts (Dudley & Cliff 1993). Approximately 36 white sharks are caught annually by these nets and a decline in the mean size of female specimens was observed (Dudley & Simpfendorfer 2006). In 1978, an initial sharp decline in population numbers was documented based on catch per unit effort data derived from the bather protection nets installed along the coast of KwaZulu-Natal (Cliff et al. 1989; Dudley 1997; Dudley & Simpfendorfer 2006), however, with additional data from 2004 – 2009, the catch rate appeared to be stable over the long term (S. Dudley, pers. comm.).

In the Cape Town metropolitan area, Western Cape, where bather protection nets do not exist, a shark-spotting programme has recently been established for the following beaches, Muizenberg, Fish Hoek, Monwabisi, Mnandi, Blue Waters, Strandfontein and Sunrise (Oelofse & Kamp 2006). Shark-spotters are provided with two-way radios, polarized sunglasses and binoculars to monitor the inshore area and a shark alarm is sounded to alert bathers of shark presence (Oelofse &
Beaches are monitored from 08:30 to at least 17:00 seven days a week during the summer season but year-round at Muizenberg and Fish Hoek (Oelofse & Kamp 2006). In addition to this programme, AfriOceans Conservation Alliance, a non-governmental organisation, has erected informative sign boards to create awareness of the presence of sharks inshore and of the shark-spotting programme (Oelofse & Kamp 2006). Although this method of avoiding shark attacks is more labour-intensive than managing shark nets, it has obvious conservation benefits.

Cliff et al. (1996b) executed the first mark-recapture study to estimate the white shark population size on the South African coast. The authors, in conjunction with the Oceanographic Research Institute (ORI) Tagging Programme, used dart tags to mark 73 individuals between Richards Bay and Struis Bay between January 1989 and December 1993, during which six individuals were recaptured. A modified Petersen estimate was employed to determine population size for the five 1-year periods and produced a single regional (Richards Bay, KwaZulu-Natal to Struis Bay, Western Cape) absolute estimate of 1 279 (839 – 1843; 95% CI) individuals (Cliff et al. 1996b).

Later, Kock & Johnson (2006) produced a preliminary minimum estimate of 128 individuals for False Bay and 198 individuals for Mossel Bay. The estimate for Mossel Bay was based on the successful identification of individuals for 70.25% of the white shark sightings between 2001 and 2005 (Kock & Johnson 2006). Sampling occasions were few and irregular i.e. taking place only a few days during a few months of each year, and the estimates produced were solely based on the number of unique individuals identified in the database (R. Johnson, pers. comm.). In addition to the latter, Johnson (unpublished) utilised photographic identification techniques to produce a more robust absolute estimate for Mossel Bay. Johnson (unpublished) identified 185 individuals between June 2001 and December 2005 and applied a Cormack-Jolly-Seber model to yield a baseline population estimate of 276 individuals.
1.5 BACKGROUND TO PHOTOGRAPHIC IDENTIFICATION

Photographic identification is both cost-effective and non-invasive, and can be executed by personnel with limited scientific training (Castro & Rosa 2005). Furthermore, photographic identification is particularly applicable to species that do not retain artificial tags for the duration of a study period (Gamble et al. 2008), or are not easily tagged due to their size and intractability (Kohler & Turner 2001). This technique has been used as a monitoring tool on a variety of species that have distinctive features, such as natural markings, which can be used to identify individuals (Stevick et al. 2001; Van Tienhoven et al. 2007). It has been widely applied on marine mammals (Karczmarski & Kockcroft 1998; Wilson et al. 1999; Hillman et al. 2003; Calambokidis et al. 2004; Mizroch et al. 2004; Coakes et al. 2005; Gilkinson et al. 2007), but also to several species of elasmobranchs such as whale sharks *Rhincodon typus* (Arzoumanian et al. 2005; Bradshaw et al. 2007; Rowat et al. 2007), raggedtooth sharks *Carcharias taurus* (Van Tienhoven et al. 2007; Bansemer & Bennet 2008), nurse sharks *Ginglymostoma cirratum* (Castro & Rosa 2005), manta rays *Manta alfredi* (Marshall et al. 2011) and white sharks (Anderson & Goldman 1996; Klimley & Anderson 1996; Domeier & Nasby-Lucas 2007; Chapple et al. 2011; Sosa-Nishizaki et al. in press).

Photographic identification has progressed from film-based photographs to digital photography. Digital photography is less labour intensive, more affordable and reliable (Markowitz et al. 2003). Similarly, the formation of slides and large photographic catalogues has now been upgraded using computer software for faster and more objective categorisation. The manual organisation of large photographic catalogues has led to the development of specific computer programs that use unique features in a string matching technique to produce recognition algorithms (Araabi et al. 2000). Although programs with recognition algorithms might be time consuming and costly during development, they avoid long-term setbacks such as high cost and time consuming analysis, which represent significant disadvantages in manual matching of photographs (Hillman
et al. 2003; Van Tienhoven et al. 2007). Nevertheless, automation does not produce perfect results since the final decision lies with the observer, once again introducing a degree of subjectivity to the analysis (Araabi et al. 2000; Kelly et al. 2001).

The white shark was one of the first elasmobranch species on which photographic identification techniques were implemented (Anderson & Goldman 1996; Anderson et al. 2011). Although white sharks are considered to be a wide-ranging species (Boustany et al. 2002; Bonfil et al. 2005) recapture studies show that they return to specific localities at regular intervals (Cliff et al. 1996b; Klimley & Anderson 1996; Jorgensen et al. 2010; Anderson et al. 2011; Chapple et al. 2011; Sosa-Nishizaki et al. in press) thus making photographic identification techniques feasible for estimating population sizes.

1.6 RATIONALE

The current status of sharks is of global concern (Baum et al. 2003; Dulvy et al. 2008; Simpfendorfer et al. 2011) and there is limited information available on the demographics and abundance of sharks (Heithaus et al. 2007). In South Africa, long-term data on the white shark is currently derived from the capture of individuals in the Natal Sharks Board bather protection nets (Dudley & Simpfendorfer 2006). Furthermore, a population trend for the white shark is not currently available (Fergusson et al. 2005) and photographic identification techniques represent a scientifically viable means to obtain such information in South Africa (Anderson et al. 2011). Results from this study can yield robust population estimates that can be used to monitor the population health of this species in South Africa.

Previous research on white shark behaviour and abundance investigated the influence of abiotic variables such as water clarity, sea surface temperature, swell height, ocean currents and lunar phase (Ainley et al. 1981; Casey & Pratt
Global climate change could potentially alter some of these environmental parameters. Thus, assessing the influence of abiotic variables on population abundance is of great value in order to facilitate objective examination regarding future expected changes in the white shark population.

1.7 STUDY OBJECTIVES

The chapters in this thesis were prepared to facilitate publication of the work. Although there may be some repetition, each chapter has unique objectives and key questions. The study was based at four known aggregation sites within Mossel Bay at which photographic and sighting data of white sharks were collected between 2008 and 2010.

The main objective of this research was to utilise a photographic identification technique in a mark-recapture framework to produce a robust population estimate for white sharks at Mossel Bay (Chapter 3). Inter-annual variation in seasonal and spatial patterns in relative abundance at four sites within the bay were also investigated using sightings per unit effort analysis, in addition to the body size composition being defined (Chapter 4). The effects of environmental parameters, specifically sea surface temperature and vertical water clarity, on abundance was furthermore investigated using general linear modelling (Chapter 5). Lastly, a multi-feature photographic identification technique is described which has been submitted as a technical report of Oceans Research (Appendix I).

1.7.1 KEY QUESTIONS

1. What is the population size of white sharks that utilise the waters in Mossel Bay?
2. What are the temporal (monthly, seasonal and annual) patterns in abundance of white sharks in Mossel Bay?

3. What are the seasonal and spatial variations in body size composition of white sharks in Mossel Bay?

4. What is the influence of environmental variability (sea surface temperature and vertical water clarity) on the relative abundance of white sharks in Mossel Bay?
CHAPTER 2

STUDY AREA: MOSSEL BAY

2.1 INTRODUCTION

Mossel Bay (34°11’00”S, 22°08’00”E) which is situated in the Indian Ocean, lies centrally in the Agulhas marine bioregion on the southern Cape coast of South Africa. Cape St Blaize, a characteristic rocky peninsula in this shallow, semi-enclosed bay, protrudes out into the sea in the western region of the bay. The southern Cape coast is considered to be an area of high wave energy and Cape St Blaize acts as a buffer to this by refracting the waves and reducing wave action (Mead et al. 2009). The rocky peninsula not only provides a degree of protection, but also facilitates the accumulation of sand along the northern and eastern regions of the bay creating an extensive dune system (Lubke & de Moor 1998).

The general topography of the bay is dominated by a sandy bottom with a gentle slope extending 5km from the shoreline, ranging up to 25m in depth (Johnson unpublished). There are three estuaries that lead into the bay i.e. Hartenbos, Kleinbrak and Grootbrak. Estuaries are dynamic environments and represent important nursery grounds for a number of marine species (Whitfield 1998). Hartenbos and Grootbrak are temporally closed estuaries and Kleinbrak is a permanently open estuary (James & Harrison 2008). Temporary closed estuaries are often characterised by the accumulation of deposits which subsequently results in large quantities of sediments being washed out into the immediate coastal zone, creating turbid conditions (Branch & Branch 1995). The most notable feature in the bay is Seal Island, a rocky outcrop 800m off the coast. Seal Island is a protected reserve for the Cape fur seal, *Arctocephallus pusillus pusillus*, with a rookery of over 4000 pinnipeds strong (Johnson et al. 2009).
Mossel Bay is recognised as a commercially significant area due to its sheltered conditions and relative proximity to the Port of Mossel Bay (Scott 1951). The bay is largely used by the fisheries and oil industry. Important recreation activities in the bay include deep sea fishing trips, seal and whale observation trips, scuba diving and white shark cage diving.

2.2 GENERAL CLIMATE

The physio-chemical and biological composition of the Agulhas Current strongly influences the waters around Mossel Bay (Branch & Branch 1995). The Agulhas Current is part of the Indian Ocean Gyre that brings down warmer waters from the tropics (Branch & Branch 1995). The Mossel Bay marine environment is therefore classified as a warm-temperate system (Lombard et al. 2004). As the Agulhas Current moves progressively south, it cools, and as a result supports different groupings of species, depending on the geographic locality (Branch & Branch 1995). During the summer season coastal upwelling occasionally occurs, bringing nutrient-rich waters to the surface (Scott 1951; Shannon 1989; Hanekom et al. 2009).

Alternating high and low pressure cells moving from the South Atlantic Ocean towards the tropical Indian Ocean creates the wave climate observed in Mossel Bay (Mead et al. 2009). Low pressure cells cause strong winds which create large waves with short wave periods (Mead et al. 2009). Thereafter, the subsequent high pressure cell causes a drop in wind strength resulting in swells with longer wave periods (Mead et al. 2009). Thus, the currents in Mossel Bay are wind-driven and are therefore not directly affected by the Agulhas Current (Mead et al. 2009). Two particular wind-types dominate the bay i.e. south-easterly and north-westerly winds in the summer and winter, respectively (Heydorn & Tinley 1980) (Fig. 2.1). Wave periods are generally between nine and sixteen seconds and are swell-dominated (Mead et al. 2009).
Fig. 2.1: Average wind direction for each season in Mossel Bay (a) summer, (b) autumn, (c) winter and (d) spring (Windfinder).

During the study period, ambient temperature ranged from 9 – 33°C (Windfinder). The lowest mean monthly ambient temperature was 13°C in August (Windfinder). The highest mean monthly ambient temperature was 24°C in February (Windfinder). Mean monthly wind speed ranged from 8 - 15 knots, as measured during the course of this study. The months of October through to January have the highest wind speeds after which it drops consistently until May, as measured during the course of this study.
2.3 MARINE TOP PREDATORS

Mossel Bay hosts a suite of marine predators including marine mammals, elasmobranchs and seabirds. The cetacean species that regularly utilise Mossel Bay are the southern right whale (*Eubalaena australis*), humpback whale (*Megaptera novaeangliae*), Bryde’s whale (*Balaenoptera edeni*), long-beaked common dolphin (*Delphinus capensis*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the Indo-Pacific humpback dolphin (*Sousa chinensis*) (Best 2007). In addition, there is a colony of Cape fur seals (*Arctocephalus pusillus pusillus*) that occupy Seal Island, a protected reserve for this species. On one rare occasion in 2010 there was the brief occurrence of a female southern elephant seal (*Mirounga leonina*) (Mertz & Bester 2011).

There are several shark species that utilise Mossel Bay, namely the white shark (*Carcharodon carcharias*), thresher shark (*Alopias spp.*), bronze whaler (*Carcharhinus brachyurus*), raggedtooth shark (*Carcharias taurus*), juvenile smooth hammerhead (*Sphyrna zygaena*), smooth hound shark (*Mustelus mustelus*) and soupfin shark (*Caleorhinus galeus*) (McCord *et al.* 2008).

The most notable seabird species that utilise Mossel Bay are the subantarctic skua (*Catharacta antarctica*), kelp gull (*Larus dominicanus*), Hartlaub’s gull (*Larus hartlaubi*), Sabine’s gull (*Larus sabini*), Cape cormorant (*Phalacrocorax capensis*), African black oyster-catcher (*Haematopus maquinii*) and terns (*Sterna spp.*) (pers. obs.). Following particularly rough storms, solitary juvenile African penquins (*Spheniscus demersus*) are occasionally seen (pers. obs.). The Cape gannet (*Morus capensis*) is present for a short period in the autumn-winter months. The presence of these particular birds appears to coincide with the occurrence of the sardine run that moves up along the South Africa coastline. On rare occasions a solitary wandering albatross (*Diomedia exulans*) may pass through the area (pers. obs.).
2.4 STUDY AREA

The study area ranges from the Port of Mossel Bay (34°10′44″S, 22°08′64″E) to Grootbrak River mouth (34°10′53″S, 22°15′91″E). There are four sites within the bay that were sampled, namely Seal Island, Hartenbos, Kleinbrak and Grootbrak (Fig. 2.2).

![Fig. 2.2: Mossel Bay indicating the four sampling sites.](image)

2.4.1 SEAL ISLAND

The Seal Island study site is characterised by a combination of rocky reef and rocky sea floor (Mead et al. 2009). Average sea surface temperature is 14.3 °C during the summer months and 13.5 °C during the winter months. The island itself is ±1.5ha in size and lies 800m from the mainland.
2.4.2 HARTENBOS

The Hartenbos Estuary mouth is often closed during the dry months, requiring heavy rains to flush out the system (Day 1981; Bickerton 1982). When closed, the Hartenbos Estuary mouth is sealed with a flat sandbar elevated between 1 – 2m above mean sea level (Bickerton 1982). The estuary mouth is shallow at 0.8m in depth (James & Harrison 2008). In the upper reaches of the estuary there is a sewage treatment works which discharges treated effluent into the estuary (James & Harrison 2008). Average surface water temperature is about 18.8°C and salinity 18.8% at the mouth during closed conditions (James & Harrison 2008) and 36% during open conditions (Day 1981). The average pH recorded during closed conditions ranges between 8.9 – 9.2 (James & Harrison 2008) and is more consistent with seawater readings during open conditions with pH readings of 8.0 – 8.2 (Bickerton 1982).

2.4.3 KLEINBRAK

The lower reaches of Kleinbrak Estuary is characterised by a large well-developed flood-delta which is strongly influenced by tidal currents maintaining a near-permanent connection with the sea (Cooper 2001). Surface water temperature at the mouth of the estuary is about 18.7°C (James & Harrison 2008). Average salinity is 9.1% at the surface and 28.1% at the bottom, which leads to a greater mean pH level at the bottom than at the surface i.e. 8.0 and 7.9, respectively (James & Harrison 2008).

2.4.4 GROOTBRAK

Before the construction of the Wolwedans Dam, located approximately 6.5km upstream, the Grootbrak Estuary was permanently open (Day 1981; Quinn et al. 1999). Following construction, management ensured that the mouth is artificially
opened during the spring-summer seasons (James & Harrison 2008). The depth of the Grootbrak Estuary mouth is about 1.0m (James & Harrison 2008). During open-mouth conditions, water temperature at the mouth of the estuary is about 19.1°C at the surface and 18.9°C at the bottom (James & Harrison 2008). The average salinity and pH value is 34.9% and 8.3, respectively, (James & Harrison 2008) and are consistent with seawater readings during open-mouth conditions (Bickerton 1982).
CHAPTER 3
ABUNDANCE ESTIMATES FOR WHITE SHARKS, *Carcharodon carcharias*, AT MOSSEL BAY, SOUTH AFRICA

3.1 ABSTRACT

The white shark *Carcharodon carcharias* is a keystone species influencing the structure and functioning of marine ecosystems. Currently, life history information on this species is limited. This study estimated absolute abundance of white sharks present in Mossel Bay, a known aggregation site in South Africa. Photographic identification techniques were applied to the dorsal fin of white sharks using a multi-feature approach. A total of 261 unique individuals were subsequently identified from photographs of 1297 sharks, taken between February and November, 2008 – 2010. Open population POPAN parameterization embedded in software program MARK was used to analyse the data. The population abundance was estimated at 389 sharks (351 – 428; 95% CI) for the three year period. The average annual rate of apparent survival was estimated at 0.90 (0.89 – 0.92; 95% CI). Furthermore, monthly population estimates and seasonal patterns in abundance were investigated. Monthly population estimates and seasonal patterns in abundance showed an overall slight but nonsignificant decline over the three year period. The mark-recapture approach used in this study is non-invasive and cost-effective, the continuation of which would facilitate the determination of long-term population trends for this species – a key statistic for successful conservation management.

**Keywords**: mark-recapture, photographic identification, population estimate
3.2 INTRODUCTION

The current status of sharks has received increased attention over the past few years (Baum et al. 2003; Dulvy et al. 2008; Simpfendorfer et al. 2011). Sharks are characterized by a K-selected life history and thus have a low intrinsic rate of increase (Hoenig & Gruber 1990). This makes them particularly vulnerable to exploitation (Baum et al. 2003). Furthermore, sharks play an important ecological role and their subsequent removal can have ecosystem consequences as they are often able to maintain biodiversity through direct and indirect predation effects (Stevens et al. 2000; Heithaus et al. 2002; Myers et al. 2007). Species such as the white shark, *Carcharodon carcharias*, consequently represents a keystone species, essential to the functioning of coastal marine ecosystems (Van der Elst 1979; Ferretti et al. 2010).

The white shark is listed as “Vulnerable” (Category VU A2cd + 3cd) on the International Convention for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2011) and on Appendix II of the Convention on International Trade of Endangered Species of Fauna and Flora (CITES). However, despite this, trade in white shark products still occurs (Duffy 2004; Shivji et al. 2005). In South Africa, the white shark is protected under the National Fisheries legislation via the precautionary principle (Compagno 1991). Direct threats to this species include the illegal targeting of white sharks for the curio trade and consumptive trade i.e. jaws, teeth, meat and fins (Smale 1996; IUCN Specialist Group 1998; Johnson 2003) and sports fishing (Ferreira & Ferreira 1996; Johnson 2003), incidental bycatch by fisheries (Cliff et al. 1996b; Johnson 2003) and the capture of white sharks by bather protective netting programmes (Cliff et al. 1989; Dudley & Cliff 1993; Cliff & Dudley 2011).

Population abundance and the manner in which this changes on a spatio-temporal scale is central to the field of population ecology (Krebs 2001). However, in many instances it is challenging to obtain the necessary population metrics of
a species, especially of those that live in the marine environment (Williams & Thomas 2009). One effective means whereby population parameters can be obtained is by applying mark-recapture techniques to sample wild animal populations (Williams et al. 2002). Mark-recapture analysis relies on the ability to resight uniquely identified individuals over a given time period (Lebreton et al. 1992; Williams et al. 2002). The high degree of site fidelity displayed by white sharks makes this species suitable for long-term population studies (Bruce et al. 2005; Jorgensen et al. 2010; Anderson et al. 2011). Population estimation in white sharks through mark-recapture techniques is therefore considered to be feasible, conditional on the successful identification of individuals within the population (Anderson et al. 2011; Chapple et al. 2011; Sosa-Nishizaki et al. in press).

Mark-recapture techniques have previously been used to investigate the population parameters of white sharks in Australia (Strong et al. 1996), the northeast Pacific (Chapple et al. 2011) and South Africa (Cliff et al. 1996b; Johnson unpublished). In Spencer Gulf, Australia, Strong et al. (1996) tagged 40 individuals of 67 identified white sharks with dart tags. The authors used four mark-resight occasions to produce two abundance estimates using a Jolly-Seber model (Strong et al. 1996). Population abundance was estimated at 191 (37 – 1612; 95% CI) and 18 (4 – 158; 95% CI), respectively. Chapple et al. (2011) used photographs of dorsal fins to identify individuals and used a Bayesian framework to produce a population estimate of 219 sharks (130 – 275; 95% CI) for the northeast Pacific. Cliff et al. (1996b) produced a regional (Richards Bay, KwaZulu-Natal to Struis Bay, Western Cape) estimate of 1279 sharks (839 – 1843; 95% CI) using a modified Petersen framework. This estimate was derived from 73 tagged white sharks, of which six were recaptured. Later, Johnson (unpublished) used photographic identification of dorsal fins to produce a population estimate of 276 sharks (SE = 27.66) for Mossel Bay, Western Cape. This estimate was produced using a modified Cormack-Jolly-Seber method based on 185 identified individuals.
Although no overall population trend presently exists for the white shark (Fergusson et al. 2005), previous research indicated declines in abundance for white shark populations in the Northwest Atlantic Ocean (Baum et al. 2003; Burgess et al. 2006), the Mediterranean (Compagno 1984; Cavanagh & Gibson 2007) and Australia (Pepperell 1992; Reid et al. 2011). Studies in South Africa indicated an initial decline in abundance following 1968 (Dudley & Cliff 1993), however with the addition of data from subsequent years, the decline did not persist and the population was considered to be stable (Dudley & Simpfendorfer 2006).

The main objective of this study was to estimate the population number of white sharks at Mossel Bay, one of the major aggregating sites along the South African coast, during the period 2008 to 2010. In addition, the inter-annual patterns in abundance and seasonality were assessed.

3.3 METHODS

3.3.1 DATA COLLECTION

During the period 2008 to 2010 (February to November), dedicated research trips were conducted to the four identified sites in Mossel Bay (Fig. 2.2). Chum (a luring agent) was used to attract sharks and this is a widely used technique in the field of shark research (Klimley & Anderson 1996; Strong et al. 1996; Heithaus et al. 2002; Domeier & Nasby-Lucas 2007). Chum is used as an olfactory stimulus to attract sharks to the research vessel and the efficacy of this odour corridor is dependant on the dispersal conditions (current strength and direction) at the time of sampling. This was taken into consideration when employing the technique. Although chum is not selective, not all sharks that are attracted are available for sampling (Klimley & Anderson 1996). Fish (sardine Sardinops sagax or mackerel Trachurus trachurus) and fresh sea water was mixed to produce the chum, as has been used successfully elsewhere.
(Domeier & Nasby-Lucas 2007). This mixture was dispensed at a low rate and was adjusted to the current conditions at the time i.e. if the current was strong, more chum was dispensed into the water. The volume of chum dispensed never exceeded one litre per minute. One to three pieces of bait were tied to a rope kept afloat by a 10cm by 15cm float and drifted 1.5 to 3m astern the vessel. Bait used was one of the following: hake (*Merluccius paradoxus, M. capensis*), skipjack tuna (*Katsuwonus pelamis*), snoek (*Thyrsites atun*) or dorado heads (*Coryphaena hippurus*), and ranged in weight from 0.8kg to 3kg, depending on the size of the largest shark present.

Once an individual white shark arrived at the vessel, the bait was used to manipulate the shark's behaviour by gradually pulling the bait closer to the vessel so that its dorsal fin could break the sea surface sufficiently and in close proximity for it to be properly photographed. Simultaneously, an identification matrix was completed comprised of the following fields: shark reference number, estimated total length (TL), sex, white pigment presence (left-hand side (LHS) and right-hand side (RHS) of dorsal fin, and caudal fin tip), black pigment presence (LHS and RHS of dorsal fin), and fin deformities. Size was estimated as the sharks swam past a plumbing pipe of known length i.e. 2m, attached parallel to the vessel. Single-lens reflex (SLR) digital cameras with a resolution of over 10 mega pixels were used to take the photographs. Identity (ID) photographs were only taken when the subject was in close proximity to the vessel and the dorsal fin was perpendicular to the sea surface. Where possible, both sides of the dorsal fin were photographed. Experienced and trained photographers were used to take ID photographs. The SLR cameras were set to shutter priority and a minimum shutter speed of 1/400 per second was used to ensure photographs were sharp and sufficiently exposed.
3.3.2 DATA ANALYSIS

The white shark population at Mossel Bay is considered to be an open population (Cliff *et al.* 1996b; Bonfil *et al.* 2005). The use of simplistic population models, such as the Lincoln-Petersen model, would not suffice as these are structured for closed populations only (Williams *et al.* 2002). This makes the Jolly-Seber (JS) model the most appropriate method for population parameter estimation as it is designed to deal with immigration and emigration (Jolly 1965; Seber 1965). The two main assumptions underlying the JS model are homogeneity in both capture and survival probabilities (Jolly 1965; Seber 1965). Program MARK (White *et al.* 1999) offers a modified JS model i.e. the Cormack-Jolly-Seber (CJS) model that can be constrained should heterogeneity in capture and survival probabilities exist (Cooch & White 2010). The CJS model is designed for multiple recapture/resight studies in which there is no information on unmarked individuals, thus placing emphasis on estimating survival (Schwarz & Seber 1999). The development of program POPAN, currently an extension embedded in MARK, works within the CJS framework with the inclusion of the parameter $N$ denoting the size of the population (Schwarz & Seber 1999). The latter can be thought of either as (a) the total number of animals available for capture at any given time during the study, or (b) the total number of individuals within the sampled area between the first and last occasion of the study (Nichols 2005). Additional parameters estimated by this model are probability of apparent survival ($\Phi$), probability of capture ($P$), and probability of entrance of individuals ($\beta$).

All analyses available in MARK are based on likelihood theory and all estimates are maximum likelihood estimates (White *et al.* 1999). Maximum likelihood (ML) theory is robust in that estimators are consistent, asymptotically efficient and normally distributed (Cooch & White 2010). The design matrix is based on a general linear models approach and is essential for incorporating constraints into models, thus making analyses more robust (Cooch 1999). The only major
disadvantage is the need for strong assumptions to be made regarding the structure of the data (Cooch & White 2010).

Initially sighting histories were created for all the identified individuals, which were subsequently compiled into a resight history input file using Notepad++ v5.6.8. The input files were composed of binary data i.e. ‘0s’ (not-sighted) and ‘1s’ (sighted) arranged in a vertical series format. The data was grouped into a 30-occasion (i.e. 10 months per year; February to November, 2008 – 2010) format as this provided information on the inter-annual trends in abundance as well as the seasonal occurrence of identified individuals. A fully parameterized time-dependant model (or general model), was constructed and a Goodness of Fit (GOF) test was employed to validate the model assumptions using Program RELEASE (Burnham et al. 1987). Program RELEASE produces two tests i.e. TEST 2 and TEST 3 which, combined, yield a test statistic to assess departure from the model assumptions (see below). To correct for over-dispersion in the data, a post hoc variance inflation factor ($\hat{c}$) can be estimated (Lebreton et al. 1992). The general model was subsequently used as a template to construct the candidate model set composed of a range of 11 additional models with various constraints. These additional models were constrained to determine if seasonality was evident and to assess the degree of inter-annual variation. Seasonality was assessed by applying constraints in two ways: (i) summer, autumn, winter and spring, and (ii) spring-summer and autumn-winter, which were also tested per annum. Furthermore, a constraint based on sampling effort was applied to determine whether sampling frequency had any effect on capture probability (Table 3.1).

Akaike’s Information Criterion (AIC) was used to select the most parsimonious model from the candidate set (Burnham & Anderson 1998). The AIC not only weights the deviance (quality of fit) but also the precision (via number of estimable parameters) to select the model that best describes the data (Lebreton et al. 1992). In the case of post hoc analysis, the AIC is translated into a quasi-
Akaike Information Criterion (QAIC) (Lebreton et al. 1992) which is used in this study. Models with $\Delta$QAIC < 2 units represent good descriptions of the data (Burnham & Anderson 1998).

The assumptions associated with this study are: (i) sampling is instantaneous, (ii) survival probabilities are the same for all individuals (marked and unmarked) between each pair of sampling occasions i.e. homogenous survival, (iii) catchability is the same for all individuals (marked and unmarked) at each sampling occasion i.e. homogenous catchability, (iv) the study area is constant and, should the study area change over time, the population size may change in accordance to such alterations, (v) individuals are successfully identified, and (vi) individuals retain marks. We expect these assumptions to hold reasonably for the data (but see discussion).

### 3.4 RESULTS

A total of 702 sampling trips were undertaken during the course of the study period. Over the three years 2846 sharks were sighted of which 1297 were photographed. Over the three years, a total of 261 unique individuals were identified, of which 196 were female, 24 were male and 41 were of unknown sex. From these, 75.48% of individuals were seen only in one year (but often on multiple occasions), 14.18% were seen in two years and 9.58% were seen in all three years (Table 3.2). Some 54.02% of individuals were only seen once.

#### 3.4.1 GOODNESS OF FIT TEST

The results from TEST 2 + TEST 3 highlighted the violation of certain model assumptions (Table 3.3). To accommodate for over-dispersion in the data, a variance inflation factor of $\hat{\sigma} = 2.38$ was estimated and applied.
Table 3.1: Candidate model set used for population estimation of white sharks in Mossel Bay, using open population POPAN parameterization in program MARK.

<table>
<thead>
<tr>
<th>Modified Notation</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>{Φ(t) P(b/a) β(b/a)}</td>
<td>survival rate varies with time, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter) per annum</td>
</tr>
<tr>
<td>{Φ(.) P(b) β(b)}</td>
<td>survival rate is constant, capture rate and probability of entry varies per season (summer, autumn, winter)</td>
</tr>
<tr>
<td>{Φ(t) P(b) β(b)}</td>
<td>survival rate varies with time, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter)</td>
</tr>
<tr>
<td>{Φ(.) P(b/a) β(b/a)}</td>
<td>survival rate is constant, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter) per annum</td>
</tr>
<tr>
<td>{Φ(t) P(s) β(s)}</td>
<td>survival rate varies with time, capture rate and probability of entry varies per season (spring, autumn, winter, summer)</td>
</tr>
<tr>
<td>{Φ(a) P(s) β(s)}</td>
<td>survival rate varies annually, capture rate and probability of entry varies per season (summer, autumn, winter, spring)</td>
</tr>
<tr>
<td>{Φ(a) P(a) β(a)}</td>
<td>survival rate, capture rate and probability of entry varies per annum</td>
</tr>
<tr>
<td>{Φ(a) P(b/a) β(b/a)}</td>
<td>survival rate varies annually, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter) per annum</td>
</tr>
<tr>
<td>{Φ(.) P(a) β(a)}</td>
<td>survival rate is constant, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter)</td>
</tr>
<tr>
<td>{Φ(a) P(b) β(b)}</td>
<td>survival rate varies annually, capture rate and probability of entry varies seasonally (spring-summer, autumn-winter)</td>
</tr>
<tr>
<td>{Φ(t) P(e) β(t)}</td>
<td>capture rate varies with effort (monthly), survival rate and probability of entry varies with time</td>
</tr>
<tr>
<td>{Φ(.) P(t) β(t)}</td>
<td>survival rate, capture rate and probability of entry varies with time</td>
</tr>
</tbody>
</table>
Table 3.2: Overview of results for identified individual white sharks at Mossel Bay, February to November 2008 – 2010. \( n_i \) = number of identified individuals sighted at \( i \), \( m_i \) = number of identified individuals that were previously marked, \( u_i \) = number of identified individuals that were previously unmarked at \( i \), \( r_i \) = number of identified individuals that were re-sighted in subsequent years, \( z_i \) = number of identified individuals that were seen before and after \( i \) (Cooch & White 2010).

<table>
<thead>
<tr>
<th>Year</th>
<th>( n_i )</th>
<th>( m_i )</th>
<th>( u_i )</th>
<th>( r_i )</th>
<th>( z_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>137</td>
<td>0</td>
<td>137</td>
<td>47</td>
<td>NA</td>
</tr>
<tr>
<td>2009</td>
<td>109</td>
<td>39</td>
<td>70</td>
<td>46</td>
<td>25</td>
</tr>
<tr>
<td>2010</td>
<td>117</td>
<td>54</td>
<td>63</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

3.4.2 POPULATION PARAMETER ESTIMATES

The candidate model set and associated parameters are presented in Table 3.4. Of the 12 models tested, only three models adequately described the data i.e. model \( \{ \Phi(t) P(b/a) \beta(b/a) \} \) (survival rate varies with time, and capture rate and probability of entry varies per annum and season – spring-summer and autumn-winter), model \( \{ \Phi(.) P(s) \beta(s) \} \) (survival rate is constant, and capture rate and probability of entry varies with season – summer, autumn, winter and spring), and model \( \{ \Phi(t) P(b) \beta(b) \} \) (survival rate varies with time, and capture rate and probability of entry varies per season – spring-summer and autumn-winter).

The most parsimonious model was \( \{ \Phi(t) P(b/a) \beta(b/a) \} \) (\( \Delta QAI C_C = 0.00 \)) and for comparison, two alternative models were built i.e. model \( \{ \Phi(.) P(b/a) \beta(b/a) \} \) (\( \Delta QAI C_C = 3.98 \)) and model \( \{ \Phi(a) P(b/a) \beta(b/a) \} \) (\( \Delta QAI C_C = 7.00 \)), which had survival constrained to be constant and to vary annually, respectively (Table 3.4). According to the most parsimonious model, the total population size of white sharks at Mossel Bay is 389 sharks (351 – 428; 95% CI). Monthly population
Table 3.3: Program RELEASE goodness-of-fit results for the fully time-dependant Cormack-Jolly-Seber model tested in a mark-recapture analysis based on individual sighting histories of white sharks at Mossel Bay, February to November 2008 – 2010, using open population POPAN parameterization in program MARK.

<table>
<thead>
<tr>
<th>Test</th>
<th>Chi-Square</th>
<th>df</th>
<th>p-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEST 2 + TEST 3</td>
<td>295.65</td>
<td>124</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TEST 2</td>
<td>214.76</td>
<td>73</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TEST 3</td>
<td>80.89</td>
<td>51</td>
<td>0.005</td>
</tr>
<tr>
<td>TEST 3.SR</td>
<td>66.69</td>
<td>27</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TEST 3.SM</td>
<td>14.20</td>
<td>24</td>
<td>0.942</td>
</tr>
</tbody>
</table>

estimates are presented in Figs 3.1 and 3.2.

Seasonal patterns in abundance (summer, autumn, winter and spring) were further assessed using the results derived from model \( \Phi(.) P(s) \beta(s) \) \( \Delta QAIC_c = 1.41; 383 \) sharks, 350 – 415; 95% CI) and are presented in Figs 3.3 and 3.4. As survival was constrained to be constant, this model was also used to determine the average annual rate of apparent survival which was estimated at 0.90 (0.89 – 0.92; 95% CI). To determine whether the inter-annual variation in seasonal patterns were significant, this seasonal model was compared to a similar seasonal model \( \Phi(a) P(s) \beta(s) \) \( \Delta QAIC_c = 5.22; 386 \) sharks, 352 – 420; 95% CI) without a year effect.

Effort was determined by the number of hours spent sampling and tallied for each month. The effort-constrained model \( \Phi(t) P(e) \beta(t) \) \( \Delta QAICC = 25.4 \) performed poorly. In addition, there was one model with annual but not seasonal
Table 3.4: Candidate model set for estimating population size for white sharks in Mossel Bay, using open population POPAN parameterization. QAIC = Quasi-Akaike Information Criterion value, NP = number of parameters, QDEV = quasi-deviance, $N$ = abundance estimate, SE = standard error, 95% CI = 95% confidence interval.

<table>
<thead>
<tr>
<th>Model</th>
<th>QAIC $c$</th>
<th>$\Delta$QAIC</th>
<th>QAIC weight</th>
<th>NP</th>
<th>QDEV</th>
<th>N</th>
<th>SE</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>${\Phi(t) p_{(b/a)} \beta_{(b/a)}}$</td>
<td>1080.07</td>
<td>0.00</td>
<td>0.44</td>
<td>27.00</td>
<td>37.05</td>
<td>389</td>
<td>19.55</td>
<td>351 - 428</td>
</tr>
<tr>
<td>${\Phi(.) p_{(s)} \beta_{(s)}}$</td>
<td>1081.47</td>
<td>1.41</td>
<td>0.22</td>
<td>10.00</td>
<td>74.42</td>
<td>383</td>
<td>16.58</td>
<td>350 - 415</td>
</tr>
<tr>
<td>${\Phi(t) p_{(b)} \beta_{(b)}}$</td>
<td>1081.99</td>
<td>1.92</td>
<td>0.17</td>
<td>20.00</td>
<td>54.01</td>
<td>380</td>
<td>17.95</td>
<td>345 - 415</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b/a)} \beta_{(b/a)}}$</td>
<td>1084.04</td>
<td>3.98</td>
<td>0.06</td>
<td>14.00</td>
<td>68.69</td>
<td>384</td>
<td>17.75</td>
<td>349 - 419</td>
</tr>
<tr>
<td>${\Phi(t) p_{(s)} \beta_{(s)}}$</td>
<td>1085.16</td>
<td>5.09</td>
<td>0.03</td>
<td>26.00</td>
<td>44.31</td>
<td>392</td>
<td>21.21</td>
<td>351 - 434</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b)} \beta_{(b)}}$</td>
<td>1085.29</td>
<td>5.22</td>
<td>0.03</td>
<td>12.00</td>
<td>74.10</td>
<td>386</td>
<td>17.29</td>
<td>352 - 420</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b/a)} \beta_{(b/a)}}$</td>
<td>1086.92</td>
<td>6.86</td>
<td>0.01</td>
<td>10.00</td>
<td>79.87</td>
<td>373</td>
<td>15.61</td>
<td>342 - 404</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b/a)} \beta_{(b/a)}}$</td>
<td>1087.06</td>
<td>7.00</td>
<td>0.01</td>
<td>16.00</td>
<td>67.52</td>
<td>391</td>
<td>19.19</td>
<td>353 - 429</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b)} \beta_{(b)}}$</td>
<td>1087.26</td>
<td>7.20</td>
<td>0.01</td>
<td>6.00</td>
<td>88.41</td>
<td>374</td>
<td>15.27</td>
<td>344 - 404</td>
</tr>
<tr>
<td>${\Phi(.) p_{(b)} \beta_{(b)}}$</td>
<td>1091.20</td>
<td>11.14</td>
<td>0.00</td>
<td>8.00</td>
<td>88.26</td>
<td>375</td>
<td>15.52</td>
<td>345 - 406</td>
</tr>
<tr>
<td>${\Phi(.) p_{(s)} \beta_{(s)}}$</td>
<td>1105.46</td>
<td>25.40</td>
<td>0.00</td>
<td>36.00</td>
<td>42.64</td>
<td>376</td>
<td>18.34</td>
<td>340 - 412</td>
</tr>
<tr>
<td>${\Phi(.) p_{(l)} \beta_{(l)}}$</td>
<td>1131.93</td>
<td>51.86</td>
<td>0.00</td>
<td>66.00</td>
<td>0.00</td>
<td>400</td>
<td>26.84</td>
<td>347 - 452</td>
</tr>
</tbody>
</table>
effects i.e. model \{\Phi(a)\ P(a)\ \beta(a)\} (\Delta QAICC = 6.86) which was also a poor representation of the data.

3.5 DISCUSSION

Despite an equal sex ratio at birth (Bruce 2009), female white sharks are observed more frequently throughout the year than male white sharks (Cliff et al. 1996b; Kock & Johnson 2006; Johnson unpublished). This is supported by the results from this study which also indicates that there is a strong sex-bias towards females. Kock & Johnson (2006) observed a discreet sex-based difference in the site fidelity of white sharks in Mossel Bay in which males moved in and out of the bay whereas females, particularly larger specimens, spent a few months in the bay. Sexual segregation in white sharks has been observed on a small spatial scale in South Australia, in which males utilised offshore and females inshore areas (Strong et al. 1992). Similarly, this pattern was observed in Gans Bay, South Africa, where male white sharks were more predominant in offshore areas, however, female white sharks were equally distributed between inshore and offshore sites (Johnson 2003). Consequently, the strong sex-bias observed in the present study highlights the possibility of sexual segregation occurring in Mossel Bay.

The low degree of site fidelity (54.02% individuals seen only once) observed in this study is surprising, as Mossel Bay is internationally recognized as a white shark aggregation site (Bonfil et al. 2005; Johnson et al. 2009). It may, however, be linked to low capture probabilities of individuals present within the study area. One of two scenarios may lead to this i.e. (i) no acceptable dorsal fin photograph was taken and thus the photograph was excluded and the shark could therefore not be identified, or (ii) the shark did not break the sea surface with it’s dorsal fin and thus no ID-photograph was taken at all, again preventing identification of the individual present. Anderson et al. (2011) conducted a photo-ID study between 1987 and 2008, identifying 364 individual white sharks. During 2006 and 2007,
76 new individuals were identified, but by 2008 only 35% of these new sharks were re-sighted (Anderson et al. 2011). Despite this low resight rate over a three-year period, individuals identified between 1987 and 2006 had a resight rate of over 60% (Anderson et al. 2011). Furthermore, identified individuals were not necessarily seen every year and this was attributed to unequal effort, spatially and temporally (Anderson et al. 2011). This indicates that a longer time series will likely yield a greater degree of repeat visits, contrary to what was observed in the present study.

The validation of model assumptions associated with mark-recapture studies is imperative for unbiased estimation of population parameters (Begon 1983). The results derived from TEST 2 and TEST 3 in program RELEASE (Table 3.3) highlighted a lack-of-fit in the data. TEST 2 deals with assessing homogeneity in capture probability and TEST 3 is concerned with assessing homogeneity in survival probability (Cooch & White 2006). This departure from model assumptions indicates over-dispersion in the data. There are several studies which indicate that there is limited impact on the parameter estimates produced, however the variance is influenced (Carothers 1978). To accommodate for this a post hoc variance inflation factor (\(\hat{c}\)) was estimated and applied (Lebreton et al. 1992). If the \(\hat{c}\)-value is \(\leq 3\), the lack-of-fit is deemed acceptable and the models are corrected with confidence (Lebreton et al. 1992).

Violation of the assumption of equal catchability is often a problem in mark-recapture studies (e.g. Reisinger et al. 2011). In theory, all individuals should have the same probability of being sampled as the use of chum for attraction serves as an olfactory stimulus and is therefore non-selective (Klimley & Anderson 1996). The fact that capture probability was not homogenous in this study is, however, not surprising as the factors contributing to heterogeneity are essentially inherent in this species. As white sharks display a dominance hierarchy in which larger individuals are dominant over smaller individuals, this may cause the latter to be under-sampled as they may not approach the
Fig. 3.1: Monthly population estimates for white sharks at Mossel Bay based on model \( \{ \Phi(t) \ P(b/a) \ \beta(b/a) \} \) for February to November 2008 – 2010. Vertical bars denote standard errors.
Fig. 3.2: Monthly population estimates for white sharks in Mossel Bay based on model \( \Phi(t) P(b/a) \beta(b/a) \) for February to November 2008 – 2010. Vertical bars denote standard errors.
Fig. 3.3: Seasonal abundance estimates for white sharks in Mossel Bay based on model \( \{\Phi(s), P_s, \beta(s)\} \) between 2008 – 2010. Vertical bars denote standard errors.
Fig. 3.4: Seasonal abundance estimates for white sharks in Mossel Bay based on model \( \Phi(s) P(s) \beta(s) \) between 2008 – 2010. Vertical bars denote standard errors.
research vessel when a larger conspecific is in close proximity (Strong et al. 1996). Despite this, there have been instances in which a larger individual has been frightened away by a smaller individual (pers. obs.). Failure to ‘capture’ individuals in terms of obtaining photographs of sufficient quality to facilitate identification may also introduce a degree of heterogeneity in terms of capture probability (see below). Another factor contributing to this is the change in behaviour when the distribution shifts toward Seal Island (foraging grounds) and the adjacent Hartenbos (resting grounds) (Johnson et al. 2009). During this time there is a predominance of larger white sharks present at these sites, thus smaller individuals are likely under-sampled as a result of this dominance hierarchy. White sharks experience an ontogenetic shift in diet in which individuals smaller than 300cm TL shift from a teleost/elasmobranch diet to a high-fat content diet i.e. pinnipeds and cetaceans (Tricas & McCosker 1984; McCosker 1985; Klimley 1985; Cliff 1989; Estrada et al. 2006). This is evidenced by an occasional lack of interest in the teleost bait displayed by larger individuals (pers. obs.). This may also contribute towards the capture heterogeneity observed in this study.

Individuals were successfully identified as only good quality photographs of the dorsal fin were used. A multi-feature approach was applied to confirm positive matches and to reduce pseudo-replication and false positives (Appendix I). The markers used were natural i.e. black and white pigmentation and notches, and successful identification of individuals is possible within a multi-feature framework (Johnson unpublished). The use of photographic identification techniques represents a non-invasive means to sample the population (Domeier & Nasby-Lucas 2007; Anderson et al. 2011). As a result, the probability of survival between sampling occasions should be equal amongst all individuals as no sampling-induced stresses are imposed. This is further validated by the high rate of apparent survival estimated in this study i.e. 0.90 (0.89 – 0.92; 95% CI). However, in terms of apparent survival, there was also a slight departure from homogeneity. Biologically plausible factors that were likely influencing this can be
related to the degree of residency, seasonality and transience of identified individuals. Although white sharks display strong levels of site fidelity to known aggregation sites (Bruce et al. 2005; Domeier & Nasby-Lucas 2007; Jorgensen et al. 2010) it is evident that white sharks utilizing Mossel Bay can be grouped into one of three main categories depending on length of stay in the study area i.e. long-term visitors or ‘residents’, seasonal visitors and transient individuals, based on monthly sighting histories of identified individuals. Site fidelity can be classified into four main categories: (i) mating, (ii) natal, (iii) pupping, and (iv) foraging (Speed et al. 2010). At Mossel Bay, site fidelity is linked partly to foraging due to the wide variety of prey available for exploitation and possibly serves a nursery function due to the predominance of juveniles (Chapter 4).

The total population is estimated at 389 sharks (351 – 428; 95% CI) based on the results from the most parsimonious model (Table 3.4). Even though the ΔQAIC<sub>C</sub> weights indicate that the models built for comparative purposes are not viable representations of the data, the population estimates derived from these alternative models were close to the best model’s population estimate. Johnson (unpublished) produced a baseline estimate of 276 sharks (SE = 27.66) for Mossel Bay. This study was conducted over a period of five years during which sampling occasions were few and irregular i.e. taking place only a few days during a few months for each year (R. Johnson, pers. comm.). Results from the present study (389 sharks; SE = 19.55) indicate that a more vigorous sampling approach does facilitate improved population estimation. Biologically plausible constraints were used when modelling population size which is furthermore a requirement for robust parameter estimation.

Results of this study indicate that population numbers vary on a monthly basis. Although this is to some extent consistent between years, inter-annual variation does exist, possibly a result of inter-annual variability in environmental conditions (Cliff et al. 1989; Adams et al. 1994; Cliff et al. 1996a). In 2010, October was seen as an anomaly as white sharks appeared to be very rare. Of the 18
sampling trips conducted, white sharks were only encountered on 5 (28%) trips at a mean sighting rate of 0.5 h\(^{-1}\). Although the reasons for this are unclear, by November 2010 white sharks were encountered on 67% of the sampling trips at a mean sighting rate of 2.93 h\(^{-1}\). Therefore monthly population abundance may indicate temporal fluctuations in environmental conditions that do not persist throughout an entire season, possibly highlighting particular water mass characteristics that are influencing white shark abundance.

Population numbers at Mossel Bay clearly varied on a seasonal basis, with models including seasonal effects having good support from the data (Table 3.4). This is in accordance with previous research in which white sharks displayed seasonal peaks in abundance elsewhere (Ainley et al. 1985; Patterson 1986; Reid & Krogh 1992; Malcolm et al. 2001; Kock & Johnson 2006; Weng et al. 2007). By comparing the abundance estimates for each season an overall pattern of slight decline was apparent over the three years (Fig. 3.4). This interannual variation was tested by comparing this model (\(\Delta Q\text{AIC}_C = 1.41\)) to a similar seasonal model but with abundance constrained over the three years (\(\Delta Q\text{AIC}_C = 5.22\)) and the decline was found to be insignificant.

The population estimate that is reported here was produced using the open population POPAN parameterization, which essentially estimates the total number of animals available for capture (Cooch & White 2006). Mossel Bay represents a single aggregation site in the Southern Cape – the white shark’s centre of abundance in South Africa (Bass 1978). Therefore it is hypothesised that white sharks utilising Mossel Bay likely represent a subset that forms part of a greater metapopulation. This is further substantiated by the large scale movements of this species along the entire South African coast (Cliff et al. 1996b; Bonfil et al. 2005; Kock & Johnson 2006).
CHAPTER 4
SPATIAL PATTERNS IN SIGHTING RATE AND BODY SIZE COMPOSITION OF THE WHITE SHARK, *Carcharodon carcharias*, AT MOSSEL BAY, SOUTH AFRICA

4.1 ABSTRACT

Although the white shark has a circum-global distribution, it displays site fidelity to specific localities along the South African coast. At Mossel Bay four sites within the bay were sampled to gain insight into the spatial and seasonal patterns in sighting rate and body size composition of white sharks. Sight per unit effort data was collected from February to December, 2008 – 2010 on individual free swimming white sharks. Sighting rate and body size composition of white sharks demonstrated significant spatial and seasonal variation. Seal Island had the highest sighting rate and Hartenbos had the lowest sighting rate observed in this study, which is likely attributed to prey availability. Although white sharks were present year-round, summer had the highest sighting rate and spring had the lowest sighting rate. Grootbrak had the highest frequency of young of the year (125 – 174cm total length (TL); 46.03%) and Seal Island had the highest frequency of juvenile (175 – 324cm TL; 53.08%) and adult (325 – 524cm TL; 52.21%) individuals. Most size-classes were present year-round, however, spring had the highest frequency of adult (27.21%) individuals observed in this study. Autumn had the highest frequency of young of the year (46.03%) individuals which may account for the highest frequency of juveniles (39.81%) occurring in winter. Overall, there was a predominance of individuals ranging between 175 – 324cm TL and it is thus hypothesised that Mossel Bay represents a nursery or grow-out area for white sharks in South Africa. Furthermore, results from this study indicate that sighting rate is not representative of white shark abundance.

**Keywords:** relative abundance, habitat use, body size composition, seasonality
4.2 INTRODUCTION

The white shark, *Carcharodon carcharias*, is a coastal apex predator occurring in temperate systems (Compagno 1997). Determination of patterns in the temporal occurrence and relative abundance of this vulnerable species is important to gain insight into the role this species plays in structuring communities (Ferretti *et al.* 2010). Insight into the population dynamics of an apex predator improves the understanding of the overall community dynamics to facilitate effective management and successful conservation not only for that particular species but also for the ecosystem to which it is interconnected (Wirsing *et al.* 2007; Jorgensen *et al.* 2010).

South Africa is internationally recognised as a centre of abundance for white sharks and specific localities along the South African coast have been identified to which this species displays site fidelity i.e. False Bay, Gans Bay and Mossel Bay in the Western Cape (Kock & Johnson 2006) and possibly Algoa Bay in the Eastern Cape (M. Dicken, pers. comm.). Yet, despite the site fidelity displayed by white sharks to aggregation sites such as Mossel Bay, there is limited information on the demographics of this species in this particular region (Johnson unpublished). By understanding the demographic structure of white sharks utilising Mossel Bay, insight can be gained into the ecology of this species e.g. spatio-temporal habitat preferences or habitat requirements for different sexes and size classes (Heithaus *et al.* 2007). The benefit derived from such knowledge is essential for the effective management of a species. Furthermore, the importance of insight gained links directly to a more comprehensive understanding of top-down effects and the degree of inter-dependency regarding ecosystem functionality (Stevens *et al.* 2000; Myers *et al.* 2007; Ferretti *et al.* 2010).

Catch per unit effort (CPUE) is one technique with which to determine the relative abundance of a species and has been widely used in assessments of fish stocks
(Richards & Schnute 1992; Williams et al. 2002). CPUE analysis was used to determine seasonal occurrence of white sharks in South Africa (Dudley & Simpfendorfer 2006). During the period 1978 to 2003, Dudley & Simpfendorfer (2006) used the Natal Sharks Board (NSB) bather protection netting programme in KwaZulu-Natal to determine the relative abundance of 14 shark species, one of them being the white shark. CPUE was based on the number of sharks caught per unit time over one kilometre of netting (Dudley & Simpfendorfer 2006). Although the population trend of white sharks appeared to be stable, a declining trend in the annual mean size of female white sharks was apparent (Dudley & Simpfendorfer 2006). At present, this is the only long-term data set on the population status of the white shark in South African waters.

The main objective of this study was to use sight per unit effort analysis to identify spatial and seasonal patterns in the relative abundance of white sharks at Mossel Bay. In addition, the body size composition was investigated to define the population structure of the white shark at Mossel Bay.

4.3 METHODS

4.3.1 DATA COLLECTION

Data collection was based on observations of individually recognised individuals per unit time. As individuals were not caught, but rather observed, we refer to this as sight per unit effort (SPUE) for the remainder of the document. Data were collected during February to December 2008 – 2010. Dedicated research trips were conducted to the four identified sites in Mossel Bay (Fig. 2.2). Sharks were attracted to the vessel by dispensing chum into the water – an accepted practice in the field of shark research (Klimley & Anderson 1996; Strong et al. 1996; Domeier & Nasby-Lucas 2007). Chum is used as an olfactory stimulus to attract sharks to the research vessel and the efficacy of this odour corridor is dependant on the dispersal conditions (current strength and direction) at the time of
sampling. This was taken into consideration when employing the technique. Although chum is not selective, not all sharks that are attracted are available for sampling (Klimley & Anderson 1996).

The chum was composed of a mixture of fish (sardine *Sardinops sagax* or mackerel *Trachurus trachurus*) that was mashed up into a pulp and combined with fresh sea water, as has been successfully used elsewhere (Domeier & Nasby-Lucas 2007). Current condition at the time influenced dispensing rate of chum i.e. if the current was strong more chum was dispensed into the water. A maximum of three pieces of bait were tied to a rope that was kept afloat by a 10cm by 15cm float and drifted 1.5 – 3m astern the vessel. Bait used was one of the following: hake (*Merluccius paradoxus, M. capensis*), skipjack tuna (*Katsumonous pelamis*), snoek (*Thyrsites atun*), dorado heads (*Coryphaena hippurus*), and ranged in weight from 0.8kg to 3kg, depending on the size of the largest shark/s present.

Once an individual white shark arrived at the vessel an identification matrix was completed comprised of the following fields: shark reference number, total length (TL), sex, white pigment presence (left-hand side (LHS) and right-hand side (RHS) of dorsal fin, caudal fin tip), black pigment presence (LHS and RHS of dorsal fin), and fin deformities. Sex was determined by the presence of claspers for males and the absence of claspers for females. Total length was estimated by experienced observers when a shark swam adjacent to a plumbing pipe of known length (2m), attached parallel to the vessel. Estimated total length was divided into eight categories: (i) 125 – 174cm, (ii) 175 – 224cm, (iii) 225 – 274cm, (iv) 275 – 324cm, (v) 325 – 374cm, (vi) 375 – 424cm, (vii) 425 – 474cm, and (viii) 475 – 524cm.
4.3.2 DATA ANALYSIS

The data were analysed to determine patterns in the relative abundance of white sharks at four sites within Mossel Bay. SPUE was defined as the number of uniquely identified sharks sighted per hour of attraction for each sampling occasion. Data were limited to records that had all trip information complete. The assumptions associated with this study are: (i) catch or observer effort is constant, and (ii) catchability is constant. We expect these assumptions to hold (but see discussion). To prevent pseudo-replication, only individuals that could be uniquely identified, per sampling session were used for analyses.

Inter-annual variation in spatial (Seal Island, Hartenbos, Kleinbrak and Grootbrak) and seasonal (summer, December – February; autumn, March – May; winter, June – August; spring, September - November) patterns were assessed using Analysis of Variance (ANOVA). Data resulting from morning and afternoon sampling trips were analysed separately to avoid potential bias associated with variability in diurnal activity patterns. Statistics software package Statistica 10 was used for all analyses. Standard errors (SE) of point estimates are provided.

To determine body size composition, individuals were placed into cohorts defined by size-class based on estimated total length. Variation in the spatial and seasonal patterns in body size structure were assessed using Chi-Square ($\chi^2$) and contingency table analysis. In addition, frequency histograms were applied to assess the seasonal and spatial frequency of specific size-classes.

4.4 RESULTS

Between February and December, 2008 to 2010, a total of 717 sampling trips were undertaken to the four aggregation sites within Mossel Bay (Fig. 2.2). Total observation effort was 1758hrs and 20mins with a mean of 2hrs and 49mins per trip. A total of 2648 white shark sightings were recorded at a mean sighting rate
of 1.33 h⁻¹. For the body size composition analysis, data from 481 of these sampling trips were used during which 1548 white shark sightings were recorded. White sharks observed in this study ranged from young of the year (YOY) through to adults at the top end of the size spectrum for the species i.e. 125 – 524cm TL.

4.4.1 PATTERNS IN RELATIVE ABUNDANCE

Morning trips constituted 493 sampling occasions during which 1827 white sharks were sighted at a mean sighting rate of 1.34 ± 1.43 h⁻¹. The sighting rate observed at each aggregation site within Mossel Bay differed significantly (F(3, 481) = 3.4076, p < 0.05) (Fig. 4.1). Seal Island had the greatest sighting rate (1.63 ± 0.10 h⁻¹) and Hartenbos had the lowest sighting rate (0.95 ± 0.20 h⁻¹). The sighting rates observed at Kleinbrak (1.35 ± 0.25 h⁻¹) and Grootbrak (1.34 ± 0.11 h⁻¹) were similar. Inter-annual variation in sighting rate was insignificant for all the sites except for Seal Island (F(2, 203) = 8.9787, p < 0.05), which differed significantly in sighting rate over the three years.

Afternoon trips constituted 224 sampling occasions during which 670 white sharks were sighted at a mean sighting rate of 1.32 ± 1.34 h⁻¹. The sighting rate observed at each aggregation site within Mossel Bay once again differed significantly (F(3, 212) = 2.8181, p < 0.05) (Fig. 4.2). Seal Island had the greatest sighting rate (1.63 ± 0.10 h⁻¹), followed by Kleinbrak (1.52 ± 0.50 h⁻¹), then Grootbrak (1.09 ± 0.35 h⁻¹), and lastly Hartenbos had the lowest sighting rate (1.04 ± 0.19 h⁻¹). Similarly, inter-annual variation in sighting rate was insignificant for all the sites except for Seal Island (F(2, 132) = 10.886, p < 0.05), which differed significantly over the three years.

Although white sharks were present year-round in Mossel Bay, sighting rate was significantly affected by season (F(3, 481) = 8.3973, p < 0.05) (Fig. 4.3). Summer was associated with the highest sighting rate (1.76 ± 0.17 h⁻¹), closely followed
Fig. 4.1: Spatial patterns in relative abundance based on sight per unit effort (SPUE) at Mossel Bay for morning sampling trips during February to December 2008 – 2010.

by winter \((1.71 \pm 0.11 \text{ h}^{-1})\). Autumn \((1.18 \pm 0.14 \text{ h}^{-1})\) and spring \((1.04 \pm 0.11 \text{ h}^{-1})\), were associated with much lower sighting rates. Inter-annual variation in sighting rate was significant for summer \((F(2, 61) = 3.3033, p < 0.05)\), winter \((F(2, 148) = 8.4228, p < 0.05)\) and spring \((F(2, 152) = 8.0888, p < 0.05)\).

Interestingly, when only using data collected during the afternoons no seasonal effect was apparent \((F(3, 212) = 1.1554, p = 0.32779)\), and similarly, there was no significant difference in inter-annual variation in sighting rate observed between the four seasons.
Fig. 4.2: Spatial patterns in relative abundance based on sight per unit effort (SPUE) at Mossel Bay for afternoon sampling trips during February to December 2008 – 2010.

4.4.2 PATTERNS IN BODY SIZE COMPOSITION

Observed size classes differed significantly between aggregation sites sampled in the study (Yates corrected $\chi^2 = 53.02$, df = 21, p < 0.05) (Fig. 4.4). Grootbrak had the greatest frequency and Seal Island had the second greatest frequency of YOY white sharks (125 – 174cm TL) i.e. 46.03% and 33.33% respectively, whilst Kleinbrak had the lowest frequency i.e. 4.76%. Seal Island had the greatest frequency of both juvenile (53.08%, 175 – 324cm TL) and adult (52.21%, 325 – 524cm TL) white sharks. Grootbrak (29.80%) had the second greatest frequency of juvenile white sharks and Hartenbos (22.06%) had the second greatest frequency of adult white sharks.
Fig. 4.3: Seasonal variation in relative abundance based on sight per unit effort (SPUE) for morning sampling trips at Mossel Bay during February to December 2008 – 2010.

Although most size classes were present year-round in Mossel Bay, size composition did vary significantly with season (Yates corrected $\chi^2 = 104.99$, df = 21, $p < 0.05$) (Fig. 4.5). The greatest frequency of YOY white sharks were reported during autumn (46.03%) followed by winter and spring (20.63% and 19.05%, respectively). During winter (39.81%) the greatest frequency of juvenile white sharks were reported, whilst spring (23.87%) and autumn (23.80%) displayed very similar results. Spring (52.21%) had the greatest frequency and winter (27.21%) had the second greatest frequency of adult white sharks observed in this study.
4.5 DISCUSSION

A sound understanding of habitat use is essential for effective population management (Kareiva & Wennergren 1995). Habitat use can be related to three main factors: (i) reproduction, (ii) shelter, and (iii) prey availability (Barnett et al. 2010). A number of studies have linked prey abundance and movement to shark species distribution (e.g. Sims & Quale 1998; Sims 2003; Dicken et al. 2006). This has been documented for white sharks in which the abundance and distribution of inshore prey resources have been linked to changes in abundance (Ainley et al. 1985; Martin et al. 2005; Kock & Johnson 2006).

Cailliet et al. (1985) estimated that the general age at maturity is between 9 and 10 years. Similarly, Wintner & Cliff (1999) determined the age of sexual maturity for males as 8 – 10 years, whereas females were slightly older between 12 and 13 years. The occurrence of sexually mature (female > 450cm TL, Francis 1996; male > 360 – 380cm TL, Pratt 1996; Malcolm et al. 2001) and YOY (120 – 150cm TL, Francis 1996) individuals in this study makes reproduction, to a lesser degree than foraging, a possible driving force associated with habitat use in Mossel Bay. Furthermore, at the top of the food chain, it is unlikely that shelter is an important determinant of habitat use. Mossel Bay provides fairly protected conditions during most of the year (Lubke & de Moor 1998; Mead et al. 2009), and white sharks have no known predators (Klimley & Anderson 1996). Larger white sharks could threaten smaller individuals but due to the low numbers of YOY and adult sharks (4.07% and 8.79% respectively) this is unlikely to be a significant factor in terms of habitat use at Mossel Bay.

Results from this study indicate Seal Island had the greatest sighting rate, followed by Kleinbrak, Grootbrak and lastly Hartenbos, which had the lowest sighting rate. White sharks frequently prey on Cape fur seals (Arctocephalus pusillus pusillus) at rookeries off southern Africa and particularly so during winter.
Fig. 4.4: Frequency distribution of different size classes of white sharks at the four study sites at Mossel Bay for February to December 2008 – 2010.
Fig. 4.5: Frequency distribution of different size classes of white sharks in relation to season at Mossel Bay for February to December 2008 – 2010.
months when juvenile seals leave to forage offshore for the first time, making them vulnerable to white shark predation (Martin et al. 2005; Hammerschlag et al. 2006). Similarly, Ainley et al. (1981, 1985) observed that white shark occurrence coincided with the presence of juvenile Northern elephant seals, *Mirounga angustirostris*, at the South Farallon Islands, USA. This is evident at Seal Island where they target these pups (Johnson et al. 2008). Hartenbos lies adjacent to these hunting grounds and thus likely had the lowest sighting rate because it is generally used as a resting area (Johnson et al. 2009). Kleinbrak and Grootbrak are characterised by estuary mouths and reef systems, which are typical nursery areas for a number of teleost fish species (Houde & Rutherford 1993; Branch & Branch 1995; James & Harrison 2008). When present at these sites it is likely that the sharks target the large biomass of fish prey (James & Harrison 2008; McCord et al. 2008). Kleinbrak had the second highest sighting rate probably because it is an open estuary thus facilitating a constant exchange of teleost prey, making it more productive than Hartenbos and Grootbrak which are temporally closed estuaries (James & Harrison 2008). Through these feeding activities white sharks conceivably play a large role in influencing ecosystem dynamics through direct and indirect predation effects (Stevens et al. 2000; Heithaus et al. 2002; Myers et al. 2007). This is in accordance with Ferretti et al. (2010) who proposed that predators utilising large areas are important as they usually prey on multiple species in different systems and/or habitats.

Bruce et al. (2006) suggested that white sharks possibly experience switches in their diet between targeting marine mammals e.g. pinnipeds, and demersal teleost or chondrichthians in nearby habitats, and Martin et al. (2005) attributed this to seasonal changes. This is observed in the present study in which white sharks concentrate at Seal Island in the winter and move to Grootbrak in the summer. During summer, white sharks were seen to move close inshore making them more conspicuous (Oelofse & Kamp 2006), and this may have contributed to the increased sighting rate observed during this time. When white sharks utilise inshore areas they swim closer to the surface and can often be sighted at
a distance (Oelofse & Kamp 2006). The low sighting rate observed during the spring months may be a result of white sharks undergoing this shift in diet as they prepare to exploit inshore areas such as Kleinbrak and Grootbrak. Alternatively, the low sighting rate in spring may possibly be attributed to behavioural changes of individuals as it is thought that white sharks undergo parturition during this time (Klimley 1985; Fergusson 1996; Francis 1996; Uchida et al. 1996).

Results from the present study highlight the significant effect that season exerts on SPUE (Fig. 4.3). In some instances, certain sites were sampled to a lesser degree in summer (no January sampling) and therefore may exert a potential bias. The unequal spread of sampling trips to different locations creates a potential bias for site-specific analysis. Therefore, observed differences may not necessarily be directly related to differences in site utilization but are possibly a reflection of seasonal differences. Despite this, as the sites sampled in Mossel Bay represent different habitat types, it could be argued that these differences reflect differences in habitat use associated with possible seasonal shifts in diet (Martin et al. 2005; Bruce et al. 2006).

Although, traditionally, catch rates were assumed to be proportional to abundance (Harley et al. 2001), reservations exist regarding the accuracy of this method (Beverton & Holt 1957). This is evidenced in the present study by the fact that seasonal differences in sighting rate did not correspond to changes in abundance (highest abundance in spring – Chapter 3). This implies that sighting rate can not be used as a reliable indicator of population size.

The spatial variation in body size composition of white sharks in the study area appears to be largely influenced by prey availability. In this study, Seal Island and Hartenbos had the highest frequencies of adult white sharks. Seal Island is a hunting ground for Cape fur seals and only sharks larger than 300cm TL are considered capable of consuming marine mammals (Tricas & McCosker 1984;
McCosker 1985; Klimley 1985; Cliff 1989; Estrada et al. 2006). Although Hartenbos had a much lower frequency of adult sharks, it is the closest site to Seal Island and it is therefore not surprising that these sites host the greatest proportion of larger sharks observed in this study. The highest frequency of YOY white sharks were observed at Grootbrak – the farthest lying site in terms of proximity to Seal Island. Strong et al. (1996) found that smaller individuals appeared to limit their spatial use to reduce direct interactions with larger conspecifics within the species. Therefore, the presence of YOY individuals at Grootbrak is in accordance with Strong et al. (1996). Surprisingly, however, Seal Island had the second highest frequency of YOY individuals. This may be a result of the inexperience of YOY sharks to the dominance hierarchy displayed by this species (Strong et al. 1992; Klimley & Anderson 1996). Alternatively, Seal Island is associated with rocky reef likely attracting YOY sharks which may be exploiting this area when larger conspecifics are not present (Barros et al. 2001). Overall, Kleinbrak essentially had the lowest frequency across all body size classes.

From this study it is evident that Mossel Bay is dominated by white sharks ranging in size from 175 – 324cm TL (87.14%) and thus only beginning to switch to a diet dominated by marine mammals (Casey & Pratt 1985; Klimley 1985). Furthermore, the size range of white sharks present in False Bay (276 - 425cm TL, Kock & Johnson 2006) is greater than the subset found in Mossel Bay. This species displays a dominance hierarchy in which smaller individuals are submissive to larger individuals (Strong et al. 1992; Klimley & Anderson 1996). Therefore, the subset observed in Mossel Bay may be a result of these smaller individuals being excluded, and subsequently out-cancelled due to lack of experience, by larger individuals of this species present in False Bay. Johnson & Kock (2006) found a pattern in shark size as a function of longitude and latitude i.e. YOY sharks predominated KwaZulu-Natal, Mossel Bay and Gans Bay hosted an intermediate suite of size classes, and False Bay was dominated by the largest sharks encountered in South Africa. The size structure observed in this study is consistent with the results from Johnson & Kock (2006), indicating that
Mossel Bay likely serves as an interim nursery area where intermediate size classes can grow out before they move down along the coast towards False Bay.

Mossel Bay hosts a diverse array of prey species catering for all size classes of white shark (James & Harrison 2008; Johnson et al. 2009). However, despite the wide range of size classes observed in this study (124 – 524cm TL), 87.14% of sampled individuals were juveniles (175 – 324cm TL). It is therefore hypothesised that Mossel Bay represents an interim nursery area. Results from this study support the hypothesis of a seasonal shift in diet proposed by Martin et al. (2005) as white sharks were observed to concentrate at Seal Island during the winter and Grootbrak during the summer. Furthermore, SPUE is not a good representative of white shark abundance possibly due to behavioural differences between the seasons. The potential seasonal bias highlighted in this study will direct future research to ensure equal sampling of sites within each season to exclude this effect. In addition, the use of laser photogrammetry to better estimate the size of white sharks sampled in Mossel Bay will be investigated. Data derived from this method will also facilitate sex-confirmation and can be used to determine sex specific differences in spatial and seasonal use of Mossel Bay by white sharks.
CHAPTER 5
ENVIRONMENTAL INFLUENCES ON THE RELATIVE ABUNDANCE OF WHITE SHARKS, *Carcharodon carcharias*, AT MOSSEL BAY, SOUTH AFRICA

5.1 ABSTRACT

Global climate change is becoming increasingly evident and changes in specific environmental parameters hold the potential to alter the distribution and abundance of species. Although the white shark has a broad geographical range, it displays site fidelity to specific localities. Mossel Bay is an internationally recognised centre of abundance for white sharks. Four sites within the bay were sampled to investigate the relationship between certain environmental parameters and the sighting rate as an index of abundance of white sharks. Data was collected from February to December, 2008 – 2009. Sea surface temperature (SST) ranged from 9.3 – 22.7°C with a mean of 15.4°C. Mean vertical water clarity was 2.5m and was very similar across all sampled sites and during each season. In this study SST did not have a significant influence on the abundance of white sharks and this may be attributed to the thermoregulatory capacity of this species. Vertical water clarity, however, was observed to have a significant influence on the abundance of white sharks. In addition, the interaction between site and season influenced the abundance of white sharks significantly and is likely attributed to the distribution and abundance of inshore prey resources.

**Keywords:** sea surface temperature, vertical water clarity, generalized linear modelling
5.2 INTRODUCTION

The white shark, *Carcharodon carcharias*, has a circum-global distribution (Last & Stevens 2009). Although this species occurs largely in temperate systems (Compagno 1997), it also visits tropical localities (Taylor 1985; Burgess & Callahan 1996; Gadig & Rosa 1996; Cliff *et al.* 2000), and is capable of trans-oceanic movements (Taylor 1985; Pardini *et al.* 2001; Bonfil *et al.* 2005; Weng *et al.* 2007; Jorgensen *et al.* 2010). Due to this large-scale distribution, and the ecological importance of white sharks in coastal marine ecosystems, numerous studies have been conducted to determine the relationship between white shark abundance and/or behaviour in relation to environmental parameters (Adams *et al.* 1994; Cliff *et al.* 1996a; Martin 2004; Robbins 2008).

Lamnid sharks have a unique trait separating them from most other elasmobranchs and teleosts in that they are able to thermoregulate (Carey *et al.* 1982, 1985; Tricas & McCosker 1984; Goldman *et al.* 1996), a contributing factor allowing for their broad geographical range. White sharks possess internal stomach temperatures of up to 14.3°C above ambient temperature (Goldman 1997). The occurrence of endothermy is therefore a likely cause for the broad temperature tolerance displayed by white sharks i.e. 4.8 - 26°C (Casey & Pratt 1985; Boustany *et al.* 2002). Martin (2004) found that in the North Pacific white sharks occurred between sea surface temperatures (SST) of 5 - 16°C, however were more abundant between temperatures of 9 - 10°C. Off the coast of Florida, white sharks were only present during winter and early spring when lower SST's occurred i.e. between 18.7°C and 21.6°C (Adams *et al.* 1994). Furthermore, in the Mediterranean white sharks seem to disappear when the SST at certain localities exceed 25°C when they are likely to remain in the deeper isothermal waters (Fergusson 1994).

In South Africa, limited studies have investigated the abundance of white sharks in relation to SST (Cliff *et al.* 1989; 1996(a); Ferreira & Ferreira 1996), rainfall
(Cliff et al. 1996(a)) and water clarity (Cliff et al. 1996(a)). There were significantly more catches of white sharks in KwaZulu-Natal (KZN) bather protection nets when turbidity was higher than the monthly mean, and 63% of individuals caught were entrapped between 19 - 22°C (Cliff et al. 1989). Water visibility ranged from 0.5 – 14m, with an average of 2.9m in the summer and 4.8m in the winter (Cliff et al. 1989). Later, Cliff et al. (1996a) investigated SST, rainfall and El Niño Southern Oscillation (ENSO), which causes reduced levels of rainfall, in relation to catch rates. Catch rates were derived from individuals caught in the bather protection nets and were analysed using a general linear model to incorporate the environmental parameters (Cliff et al. 1996a). A cyclical trend was evident in which every four to six years a peak in relative abundance was observed, however, this was attributed to natural variation within the netted region (Cliff et al. 1996a). ENSO incurred low catch rates, and high rainfall and low SST during the preceding summer (January – March) resulted in increased captures during the following winter (June – September) (Cliff et al. 1996a). At Struis Bay and Dyer Island in the Western Cape, SST did not appear to significantly affect abundance as individuals were sighted across all temperature ranges (Ferreira & Ferreira 1996). However, higher SST’s (18 - 23°C) were associated with a peak in abundance and sightings decreased substantially when SST dropped to 11 - 12°C (Ferreira & Ferreira 1996). The temperature range recorded at Struis Bay and Dyer Island was 17 – 23°C and 11 - 20°C, respectively (Ferreira & Ferreira 1996).

The objective of this study was to determine if a relationship exists between the relative abundance of white sharks and specific environmental parameters. In particular, the influence of sea surface temperature and vertical water clarity on the relative abundance of white sharks at Mossel Bay.
5.3 METHODS

5.3.1 DATA COLLECTION

Data were collected during February to December, 2008 – 2010. Dedicated boat-based research trips were conducted to four identified sites in Mossel Bay (Fig. 2.2). Sharks were attracted to the vessel by dispensing chum (luring agent) into the water – an accepted practice by researchers studying this species (Klimley & Anderson 1996; Strong et al. 1996; Domeier & Nasby-Lucas 2007). Chum is used as an olfactory stimulus to attract sharks to the research vessel and the efficacy of this odour corridor is dependant on the dispersal conditions (current strength and direction) at the time of sampling. This was taken into consideration when employing the technique. Although chum is not selective, not all sharks that are attracted are available for sampling (Klimley & Anderson 1996).

Chum was created by combining fish (sardine Sardinops sagax or mackerel Trachurus trachurus) and fresh sea water, a mixture that has been successful elsewhere (Domeier & Nasby-Lucas 2007). The volume of chum dispensed never exceeded one litre per minute and was subsequently adjusted to the current conditions at the time. If the current was strong, more chum was dispensed and if the current was weak, less chum was dispensed into the water. One to three pieces of bait (hake (Merluccius paradoxus, M. capensis), snoek (Thyrsites atun), dorado heads (Coryphaena hippurus) or skipjack tuna (Katsumonous pelamis)) were tied to a rope and kept afloat by a 10cm by 15cm float. The bait ranged in weight from 0.8kg to 3kg, depending on the size of the largest shark/s present and was drifted 1.5 – 3m astern the vessel.

An identification matrix was completed for each individual that arrived at the vessel. Data recorded comprised the following fields: shark reference number, estimated total length (TL), sex, white pigment presence (left-hand side (LHS) and right-hand side (RHS) of dorsal fin, and caudal fin tip), black pigment
presence (LHS and RHS of dorsal fin), and fin deformities. Sex was determined by the presence (males) or absence (females) of claspers. Total length was estimated by experienced observers when a shark swam adjacent to a plumbing pipe of known length (2.0m), attached parallel to the vessel and was divided into eight categories: i) 125 – 174cm, (ii) 175 – 224cm, (iii) 225 – 274cm, (iv) 275 – 324cm, (v) 325 – 374cm, (vi) 375 – 424cm, (vii) 425 – 474cm, and (viii) 475 – 524cm. During each trip, sea surface temperature was measured using a thermometer and vertical water clarity was measured using a Secchi disc.

5.3.2 DATA ANALYSIS

The presence of a relationship between the relative abundance of white sharks and specific environmental parameters, specifically sea surface temperature and vertical water clarity, were tested for. To reduce the bias that additional environmental parameters (e.g. wind speed, atmospheric condition) may induce, the analysis was limited to records of sampled individuals that clearly surfaced and therefore such prevailing weather conditions would not have influenced sighting probability. Furthermore, data were limited to records where both sea surface temperature and vertical water clarity were recorded.

A generalized linear model (GLM) was applied to the data using a Poisson distribution with a LOG link function. Raw shark count data was square-root transformed as some of the observations were zero (Zar 2010) and was subsequently used as the dependent variable. Effort was used as an offset variable in this analysis. Site and season were selected as categorical factors, and sea surface temperature and vertical water clarity were selected as continuous predictors. The analysis was executed using statistics software package Statistica 7.
5.4 RESULTS

Between February and December 2008 – 2009, 478 sampling trips were conducted to four aggregation sites within Mossel Bay (Fig. 2.2). Observed SST ranged from 9.3 – 22.7 °C in this study with a mean of 15.4°C. Recorded vertical water clarity ranged from 0 – 10m and a mean of 2.5m.

According to the generalized linear model, SST, site and season did not significantly influence sighting rate. Vertical water clarity and the combined effect of site and season did have a significant influence on the sighting rate of white sharks (Table 5.1). Although site and season were not significant indicators, the combined effect of these two factors highlight the differences in relative abundance between the four sites in different seasons (Fig. 5.1). Vertical water clarity significantly influenced overall sighting rate, but did not seem to have a large effect at the respective study sites. A marginal positive effect on the relative abundance of white sharks was observed across all sites (Fig. 5.2). Despite the broad temperature range, the effect of SST on sighting rate was insignificant (Fig. 5.3).

Table 5.1: Generalized linear model results for environmental effects on relative abundance of white sharks at Mossel Bay using a Poisson distribution.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Log-Likelihood</th>
<th>Chi-Square</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>1</td>
<td>-803.99</td>
<td>2.76</td>
<td>0.097</td>
</tr>
<tr>
<td>Vertical water clarity</td>
<td>1</td>
<td>-823.60</td>
<td>41.98</td>
<td>≤0.001</td>
</tr>
<tr>
<td>Site</td>
<td>3</td>
<td>-805.71</td>
<td>6.19</td>
<td>0.103</td>
</tr>
<tr>
<td>Season</td>
<td>3</td>
<td>-803.29</td>
<td>1.34</td>
<td>0.719</td>
</tr>
<tr>
<td>Site x Season</td>
<td>9</td>
<td>-863.90</td>
<td>122.58</td>
<td>≤0.001</td>
</tr>
</tbody>
</table>
Fig. 5.1: The combined effect of site and season on the relative abundance of white sharks in Mossel Bay during 2008 and 2009. Vertical bars denote standard errors.

5.5 DISCUSSION

Mossel Bay is characterised by two habitat types i.e. Seal Island which represents a Cape fur seal (*Arctocephalus pusillus pusillus*) rookery, and Hartenbos, Kleinbrak and Grootbrak which are associated with estuary mouths and reef systems hosting a suite of teleost prey (Houde & Rutherford 1993; James & Harrison 2008). In the present study, the interaction between site and season had a significant influence on the relative abundance of white sharks (Table 5.1, Fig. 5.1), a likely result due to the distribution and availability of inshore prey resources (Ainley *et al.* 1985; Kock & Johnson 2006).
Abiotic factors which change with the seasons affects the frequency and success of predation attempts (Martin et al. 2005; Hammerschlag et al. 2006). Furthermore, Bruce et al. (2006) suggested a seasonal switch in diet from targeting marine mammals, such as pinnipeds, to demersal teleost species, thereby accounting for the use of specific sites in particular seasons by white sharks in Mossel Bay e.g. Seal Island in winter. Although SST in this study had a fairly broad range, from 9.3 – 22.7°C, it did not, however, significantly influence the relative abundance of white sharks observed in this study (Table 5.1). Despite this, SST had a positive influence at Grootbrak and Kleinbrak, an almost neutral influence at Hartenbos, and a negative influence at Seal Island on the relative abundance of white sharks in this study (Fig. 5.3). Although not supported in this study, SST may be indirectly influencing white shark presence.
Fig. 5.3: The influence of SST on the relative abundance of white sharks at the four sites sampled in Mossel Bay between 2008 and 2009.

as a function of prey availability (Barnett et al. 2010). This is in accordance with previous research investigating the distribution of shark species where it was evident that the movement and abundance of prey species are more probable factors influencing the relative abundance of sharks (Sims & Quale 1998; Sims 2003; Dicken et al. 2006; Wirising et al. 2007). In this case the availability of seals in the winter months at Seal Island, and the availability of teleost and smaller elasmobranch prey in the summer months at Kleinbrak and Grootbrak.

It is conceivable that prey species targeted at Mossel Bay are not strongly governed by SST resulting in the negligible influence of SST on the relative abundance of white sharks utilising this area. In addition, the thermoregulatory capacity of white sharks enables them to tolerate a broad range of temperatures
thereby allowing them to exploit a wide variety of habitats and geographic ranges (Casey et al. 1982, 1985; Tricas & McCosker 1984; Goldman et al. 1996; Goldman 1997).

Results from the present study indicate that vertical water clarity has a significant influence on the relative abundance of white sharks (Table 5.1). Previously, there was an association between reduced levels of vertical water clarity and increased catches of white sharks (Cliff et al. 1989). However, in the present study increased frequencies of white sharks were generally associated with increased levels of vertical water clarity (Fig. 5.2). This highlights the possibility that all sharks are not necessarily attracted to the research vessel via chumming and that a number of individual sharks may not be seen at all. Particular factors that may be affecting vertical water clarity are atmospheric conditions (e.g. clear, overcast), turbidity and high wind speed. Atmospheric condition can influence vertical water clarity by limiting the amount of sunlight penetrating down the water column. When atmospheric condition is clear there is a greater degree of sunlight available to penetrate the water column resulting in higher vertical water clarity readings. Conversely, cloudy conditions restrict the amount of sunlight available to illuminate the water column and reduce vertical water clarity readings. Another factor that can influence vertical water clarity is turbidity. Temporally closed estuaries (e.g. Hartenbos and Grootbrak) are susceptible to the accumulation of sediments, often resulting in highly turbid water (Branch & Branch 1995). Consequently, after storm events this highly turbid water is flushed out of the estuarine system and into the immediate coastal zone. Three of the four sites sampled in Mossel Bay i.e. Hartenbos, Kleinbrak and Grootbrak, are associated with estuarine systems and are therefore vulnerable to temporary high-turbidity conditions (Allanson et al. 1997). In addition, when high wind speeds occur, the sea surface becomes choppy and it is thought that white sharks may be reluctant to approach the research vessel during such conditions, possibly because of the increased level of noise created by waves lapping against the vessel (pers. obs.). Although the aforementioned conditions affect vertical water clarity, these factors
should not affect sighting rate observed in this study, as records were limited to individuals that closely approached the research vessel.

Although SST did not significantly influence relative abundance, there was reasonable support for a temperature effect on abundance ($p = 0.097$; Table 5.1). Based on large scale influences of rising temperatures associated with global change on biodiversity (e.g. Johnson & Welch 2010; Knowlton et al. 2010; Hogg et al. 2011), a more thorough investigation on the influences of SST on white shark behaviour and possibly demographics should be implemented. As is the case for many marine systems, the challenge is to study the effect of one variable, in this case SST, in isolation without additional confounding environmental variables.
CHAPTER 6
SYNTHESIS AND CONCLUSIONS

Quantitative studies on the abundance and demographic structure of large sharks is limited, despite the value of such information (Heithaus et al. 2007). White sharks in South Africa are genetically distinct from the populations present in the coastal waters of the U.S. and Australia (Pardini et al. 2001; Jorgensen et al. 2010). This study therefore aimed at increasing knowledge on the white shark at an aggregation site in South Africa. Mossel Bay is internationally recognised as a year-round centre of abundance for white sharks (Bonfil et al. 2005; Johnson & Kock 2006; Johnson unpublished). There are four aggregation sites within the bay that were sampled i.e. Seal Island, Hartenbos, Kleinbrak and Grootbrak. This study was conducted between February and December, 2008 – 2010, and used a combination of photographic identification techniques and sight per unit effort methods.

This study identified 261 unique individuals using a multi-feature approach that was applied to the dorsal fin of white sharks. The photographic identification technique employed in this study represents an excellent, cost-effective and non-consumptive means to sample protected species such as the white shark (Anderson et al. 2011; Chapple et al. 2011; Sosa-Nishizaki et al. in press). In addition, data derived from this method facilitates the compilation of a national photographic database in which identified individuals can be monitored on a greater spatial scale, providing further insight into the movements and residency patterns of white sharks along the entire South African coastline. Datasets from areas such as Gans Bay and False Bay in the Western Cape, as well as possibly Algoa Bay in the Eastern Cape, can be combined to yield very strong regional population estimates that would better reflect white shark abundance in South Africa.
Total abundance of white sharks was estimated at 389 individuals (SE = 19.55). Recently, a baseline estimate of 276 sharks (SE = 27.66) was produced for Mossel Bay (Johnson unpublished.), however, results from the present study support the notion that a more vigorous sampling approach produces more accurate population estimates as biologically plausible constraints can be factored into the analysis. The population estimate presented here represents an index of abundance for white sharks at Mossel Bay. Currently there is no overall population trend for the white shark (Fergusson et al. 2005). However, previous research has indicated declines in abundance for white shark populations in the Northwest Atlantic Ocean (Baum et al. 2003; Burgess et al. 2006), the Mediterranean (Compagno 1984; Cavanagh & Gibson 2007) and Australia (Pepperell 1992; Reid et al. 2011). The monthly and seasonal population estimates produced in the present study indicated an overall pattern of slight decline, however further analysis rendered the decline insignificant.

The sighting rate and body size composition of white sharks observed in this study differed significantly on a spatial and seasonal scale. Seal Island had the highest sighting rate and the highest frequency of juvenile and adult white sharks. This pattern in spatial abundance is likely a function of foraging behaviour. YOY white sharks were most prevalent at Grootbrak, the farthest sampling site from Seal Island – evidence of the effects of the dominance hierarchy observed in this species (Strong et al. 1992; Klimely & Anderson 1996). Overall, there was a high concentration of white sharks ranging in size between 175 – 324cm TL, and it is thus hypothesised that Mossel Bay is used as an interim nursery area for white sharks in South Africa.

To improve body size estimates of white sharks, paired-laser photogrammetry represents a useful tool that can be employed to obtain this type of data. Paired-laser photogrammetry uses two parallel lasers attached to a single camera device. The lasers project two points of known distance onto the subject. These parallel lasers subsequently provide a scale for accurate measure and are used
to estimate the total length of the subject. This method has been successfully applied to whale sharks *Ryncodon typus* (Rohner *et al.* 2011) and manta rays *Manta alfredi* (Deakos 2010). In addition, footage collected from this method will enable the confirmation of sex for recorded individuals. The main limiting factor hindering the successful implementation of this particular method in Mossel Bay is the poor water clarity. However, it would prove useful in ‘ground truthing’ results based on methods for size estimation in the current study.

Interestingly, the peaks in relative and absolute abundance occurred in different seasons. In this study, relative abundance represents the number of white sharks observed per hour of attraction, and absolute abundance represents the total number of white sharks estimated within a mark-recapture framework. For relative abundance, the peak was observed in summer and the trough was observed in spring, however, for absolute abundance it was the opposite i.e. the peak was observed in spring and the trough was observed in summer. This difference may be attributed to behavioural differences between seasons, as for some reason they are more visible, even though less abundant, in summer versus spring. In summer, white sharks swim close inshore and at the surface making them more visible (Oelofse & Kamp 2006). The behavioural difference in spring may possibly be linked to parturition as it is hypothesised to occur during this time of the year (Klimley 1985; Fergusson 1996; Francis 1996; Uchida *et al.* 1996). Despite this, given the body size composition of white sharks observed at Mossel Bay, only a limited proportion of sharks would experience this. However, the effects of these larger sharks, possibly undergoing parturition, on the behaviour of the rest of the population is unclear. Furthermore, the differences observed between relative and absolute abundance indicate that sight per unit effort methods are not a viable proxy to determine white shark abundance.

Vertical water clarity appeared to have a slight positive influence on the relative abundance of white sharks observed in this study. Factors such as atmospheric condition (e.g. overcast), high levels of turbidity resultant from estuarine outflow,
and high wind speeds have the capacity to temporarily reduce vertical water clarity. Although previous studies have indicated an increase in white shark occurrence coinciding with certain environmental characteristics (e.g. Cliff et al. 1996a) or related to availability of prey species (e.g. Malcolm et al. 2001), it is thought that correlation with sea surface temperature is poor (Bass 1978; Ferreira & Ferreira 1996; Pyle et al. 1996). Rather, it may be that environmental characteristics are indirectly influencing the presence of white sharks by possibly influencing the occurrence and/or availability of prey species (Barnett et al. 2010). Despite this, sea surface temperature did not have a significant influence on the relative abundance of white sharks observed in this study. It is not surprising that the effects of sea surface temperature were negligible as white sharks have thermoregulatory capabilities enabling them to have a wide tolerance i.e. 4.8 - 26°C (Casey & Pratt 1985; Goldman 1997; Boustany et al. 2002). Thus, it may be the presence and/or movement of certain prey species that have a greater influence on white shark numbers than sea surface temperature itself.

White sharks utilising this area are considered to be a subset that forms part of a greater metapopulation (Kock & Johnson 2006). The population parameter estimates presented here provide a basis for understanding the behavioural and population dynamics of white sharks at Mossel Bay. Although the current dataset is limited to a three-year time series, inter-annual variation could be deduced, providing insight into the degree of variation over time. Nevertheless, a longer-term time series is required to determine population trends, and the continuation of this project is a scientifically viable means to obtain such information (Anderson et al. 2011).
APPENDIX I

CATALOGUING, COMPARING AND MATCHING OF PHOTOGRAPHICALLY IDENTIFIED WHITE SHARKS, Carcharodon carcharias, USING A MULTI-FEATURE APPROACH

This appendix describes a systematic approach for the manual identification of individual white sharks is presented using a multi-feature analysis (Gubili et al. 2009) applied to the dorsal fin. The use of image database software for the creation and management of a photographic catalogue is evaluated. In addition, guidelines for manual fin-matching are given and potential concerns about this method are discussed. The appendix is divided into two sections. The first section outlines basic operational knowledge for using Adobe Photoshop Lightroom 2 software. The second section instructs on how to apply the photographic identification technique described in this paper when using Adobe Photoshop Lightroom 2 as an organisational platform.

SECTION ONE

ADOBE PHOTOSHOP LIGHTROOM 2

Adobe Photoshop Lightroom 2, subsequently referred to as Lightroom 2, is a software program developed specifically for the organisation of large photographic databases. It is designed for post-production work on digital photographs and to prepare images for further development in Adobe Photoshop software. The main features in Lightroom 2 are Library (review of image collection and optional application of organisational tags), Develop (editing tools), Slideshow (tools and export features), Print (layout options and preferences for printing) and Web (automatic gallery creation and upload functions). Thus, Lightroom 2 is not a fin-matching program, but merely a platform that photographers can use to organise and apply simple manipulations to their
photographs. A great feature of Lightroom 2 is that any changes and progress made is saved automatically by the program. In addition, Lightroom 2 facilitates non-destructive editing of image files i.e. the adjustments are only visible in the program itself while the original file remains intact. A project in Lightroom 2 is referred to as a *Catalog* which stores all the metadata regarding a particular project. *Metadata* refers to all the information relating to the manipulations that have been applied to a photograph and any keywords, colour labels and/or ratings that have been assigned to it. Lightroom 2 is sensitive to filepath changes, so if any folder or file names are altered, the program will not automatically pick this up – any changes made will have to be synchronized.

**INTERFACE**

The Lightroom 2 interface is fairly user-friendly and is divided into four key areas i.e. the Module Picker, the Main Content Area, the Panels and the Filmstrip. The menu bar at the top represents the general menu standard in all programs. Below this, to the right, the secondary menu bar is located i.e. the *Module Picker*, which facilitates navigation between the main functions in Lightroom 2. The *Library* and *Develop* tabs represent the two main functions that will be used for maintaining a photographic identification database. The *Main Content Area* is bordered on either side by the *Panels* and represents the view chamber. When switching between the Library and Develop tabs, this viewing chamber remains constant whilst the left and right panels change. Located below the Main Content Area is the *Filmstrip* which displays an overview of all the photographs from a selected folder. Just above this, there is a *Filter* menu which can be toggled to display selected photographs.

The Library tool bar is located below the Main Content Area and is composed of a series of icons. The first four icons adjust the view i.e. Grid View (all images in a selected folder are arranged in the view chamber in grid format), Loupe View (a single selected image will be displayed), Compare View (two selected images will
be displayed in a split screen format) and Survey View (similar to the compare view but is not limited to two images). The next two icons are flags i.e. a white flag and a reject flag. The next five icons are a row of stars and can be used for rating. Following this is a selection of colour labels i.e. red, yellow, green, blue, purple, white and black. Lastly, there are two arrows which can be used to rotate the image 90° at a time in the respective direction.

When the Library module is selected, the left panel has the Navigator box at the top which displays the selected photograph. There are different options that can be toggled to alter the zoom i.e. Fit, Fill, 1:1 and 1:x (custom). Below this is the Catalog box which offers the following options: All Photographs, Quick Collection +, Previous Import and Already In Catalog. The last box is Folders and provides a hierarchical breakdown of the directory structure of all the images uploaded into Lightroom 2. At the bottom of this left panel there are two quick tabs i.e. Import and Export, which are used to upload and save photographs, respectively. There are more specific import and export options available under the File tab in the primary menu bar. When exporting photographs, options are available to alter the file name and/or create specific folders in which to save them.

The right panel houses the Histogram box at the top which displays a graphic breakdown of the composition of the photograph in terms of the relation of the three primary colours i.e. red, blue and yellow. At the bottom of the Histogram box the basic camera settings under which the photograph was taken are displayed e.g. shutter speed. The next box is Quick Develop which provides options for basic manipulations e.g. white balance, however, the Develop module has a more extensive range of options which are likely more preferable. The third box is Keywording in which keywords are assigned through manual input. Next is the Keyword List box in which a list of keyword tags can be created and assigned to selected photographs simply by checking them. The last box is Metadata which provides general information about the selected photograph e.g. file name,
and has fields that may be edited e.g. caption. At the very bottom are two quick tabs i.e. *Sync Settings* and *Sync Metadata*.

When the Develop module is selected, the *Navigator* box at the top remains the same. The *Presets* box below the latter allows the application of default or customised presets. The last box is *History* which tracks all the manipulations that have been applied. At the very bottom are two quick tabs i.e. *Copy* and *Paste*, which allows executed manipulations to be copied from one photograph and pasted onto another.

For the right panel, the *Histogram* box remains largely the same, with the addition of five icons representing the following functions: *cropping, spot removal, red eye correction, graduated filter and adjustment brush*. Below this are a series of editing boxes i.e. *Basic, Tone Curve, HSL / Color / Grayscale, Split Toning, Detail, Vignettes and Camera Calibration*. At the bottom are two quick tabs i.e. *Previous* (similar to the common “Undo” option) and *Reset* (facilitates the reversion to the original image).

**IMPORT PHOTOGRAPHS AND SYNCHRONIZE FOLDERS**

There are two main ways in which folders, and subsequently photographs, can be entered in Lightroom 2 – via importing images and folders, or synchronising folders. The *Import* option from the left panel (under the *Library* tab) or the *File* tab (on the main menu bar) can be used to upload folders and images into Lightroom 2. Another option is to right-click on the relevant folder under the *Folders* box (the left panel under the *Library* tab) where a menu will be displayed from which the “*Synchronize Folder*” option should be selected. Lightroom 2 will automatically read any changes made to the selected folder and calculate how many photographs need to be imported and/or removed. Simply click the “*Synchronize*” option and Lightroom 2 will do the rest.
SECTION TWO

PHOTO SELECTION PROCESS

Subsequently, the photographs were entered into a catalogue (created using Adobe Photoshop Lightroom 2) containing all the previously recorded individuals, arranged in a hierarchical format in the following manner: year, month, day, and individual specimen which was assigned a reference number for that particular day i.e. 00x-ddmmyy. A keyword system was developed containing the following fields i.e. white pigmentation, black pigmentation, fin amputations, notch structure, total length, sex, and tag presence (Table 6.1). Lightroom 2 has a built-in filter in which fields can be selected to reduce the number of potential candidates. Once matches were found through the correlation of key words, they were either confirmed or rejected through visual discernment. Confirmed matches were based on as many distinguishing features as possible, thus reducing the possibility of false positives (Gubili et al. 2009). Affirmative matches were assigned the same reference number. If no matches were located, the shark was assigned a new reference number i.e. WS-00X. Every two months, all the photographs for identified individuals were double-checked to reduce false positives and pseudo-replication.

RATING, CROPPING AND SELECTING

Under the Library tab, every photograph in each individual folder i.e. 00x-ddmmyy, is rated on a scale from 1-star to 5-stars. 1-starred photographs are those deemed completely useless e.g. images that are underwater or underexposed beyond correction, and 5-stars are assigned to photographs in which the entire dorsal fin is completely out of the water and perpendicular to the sea-surface, as well as sufficiently exposed and in-focus. Essentially, one star is gained for sufficient quality in (a) exposure, (b) composition, (c) focus, (d) protrusion of dorsal fin out of the water and (e) orientation of dorsal fin. Once all
the photographs have been rated all those that have been awarded with 3-stars or higher are cropped using the cropping function under the *Develop* tab. In addition, photographs may subsequently be manipulated to improve clarity and exposure where necessary. Switching back to the *Library* tab, the filter just above the *Filmstrip* is used to find the best photograph for both the left-hand side and the right-hand side of the dorsal fin, if both sides were photographed. Only photographs that are rated with three stars or higher are used for matching. Once the best photograph for each side has been selected, a colour label is applied. A red colour label is applied if the photograph has been rated with either four- or five-stars, and a yellow colour label is applied if the photograph has been rated with three stars. If the only photograph available is useless or difficult to match, it is assigned a green colour label and flagged with the reject flag.

**APPLYING KEYWORDS**

Keywords are only applied to photographs that have been assigned a red or yellow colour label. Most of the information required for key-wording is obtained from the individual identification matrix data sheet with the exception of Black Pigment and Notches. Many white sharks have small black pigments present on the dorsal fin as well as shallow notches on the dorsal trailing edge. As these keywords are only used for filtering for potential candidates, only black pigments and notches that are equal to, or exceed, a certain size are acknowledged.

Once an affirmative match has been made the appropriate keyword tag e.g. WS-028, under the keyword *GWS Number* is applied. If the dorsal fin represents a new individual, a new keyword tag is created by right-clicking next to the keyword *GWS Number* and selecting the *Create Keyword Tag inside “GWS Number”* option, after which a window will pop-up prompting for the relevant information to be filled in; click *Create* to complete the action.
KEYWORD LIST

The following table is a breakdown of the list of keywords that have been created for the photographic identification database (Table 6.1).

Table 1: List of keywords for dorsal fin photographic identification

<table>
<thead>
<tr>
<th>Amputations</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Caud Amp-A</td>
<td>Caudal Amputation Absent</td>
</tr>
<tr>
<td>Caud Amp-P</td>
<td>Caudal Amputation Present</td>
</tr>
<tr>
<td>Dorsal Amp-A</td>
<td>Dorsal Amputation Absent</td>
</tr>
<tr>
<td>Dorsal Amp-P</td>
<td>Dorsal Amputation Present</td>
</tr>
<tr>
<td>Pec-LHS Amp-A</td>
<td>Pectoral Left-Hand Side Absent</td>
</tr>
<tr>
<td>Pec-LHS Amp-P</td>
<td>Pectoral Left-Hand Side Present</td>
</tr>
<tr>
<td>Pec-RHS Amp-A</td>
<td>Pectoral Right-Hand Side Absent</td>
</tr>
<tr>
<td>Pec-RHS Amp-P</td>
<td>Pectoral Right-Hand Side Present</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Black Pigment</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>BP-LHS-A</td>
<td>Black Pigment Left-Hand Side Absent</td>
</tr>
<tr>
<td>BP-LHS-P</td>
<td>Black Pigment Left-Hand Side Present</td>
</tr>
<tr>
<td>BP-RHS-A</td>
<td>Black Pigment Right-Hand Side Absent</td>
</tr>
<tr>
<td>BP-RHS-P</td>
<td>Black Pigment Right-Hand Side Present</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Gender</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td></td>
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</table>

<table>
<thead>
<tr>
<th>GWS Number</th>
<th>Unique Identification Code</th>
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<tbody>
<tr>
<td>WS-001</td>
<td>Example</td>
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<table>
<thead>
<tr>
<th>Notches</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>BN-A</td>
<td>Bottom Notch Absent</td>
</tr>
<tr>
<td>BN-P</td>
<td>Bottom Notch Present</td>
</tr>
<tr>
<td>MN-A</td>
<td>Middle Notch Absent</td>
</tr>
<tr>
<td>MN-P</td>
<td>Middle Notch Present</td>
</tr>
<tr>
<td></td>
<td>TN-A</td>
</tr>
<tr>
<td>----------------</td>
<td>-----------------------</td>
</tr>
<tr>
<td></td>
<td>TN-P</td>
</tr>
<tr>
<td>Side</td>
<td>LHS</td>
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<td>Tagging</td>
<td>Tag-Pres</td>
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<td>Total Length</td>
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<td></td>
<td>TL-275-374</td>
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<td>TL-375-524</td>
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<td>White Pigment</td>
<td>WP-Caud-A</td>
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<tr>
<td></td>
<td>WP-Caud-P</td>
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<tr>
<td></td>
<td>WP-LHS-A</td>
</tr>
<tr>
<td></td>
<td>WP-LHS-P</td>
</tr>
<tr>
<td></td>
<td>WP-RHS-A</td>
</tr>
<tr>
<td></td>
<td>WP-RHS-P</td>
</tr>
</tbody>
</table>

**APPLYING THE FILTER**

Under the *Library* tab, the photograph that is to be matched is selected and then all the folders that are to be searched for potential matches are highlighted on the left panel. When the *Grid View* option is selected, the *Library Filter* will be displayed at the top of the view chamber, which has the following fields: *Text*, *Attribute*, *Metadata* and *None*. The red and yellow colour labels, under the *Attribute* field, should be selected. Under the *Metadata* field, the filter for each column should be set to *Keyword* so that the keywords applied to each photograph can be used to filter for potential candidates. Each column represents a single field that can be filtered for and a maximum of nine columns.
can be used for filtering. The right panel will display all the information and keywords assigned to the highlighted photograph. This is useful when selecting features that need to be filtered for.

Always start by first filtering for White Pigment i.e. WP-Caud-A/P, WP-LHS-AP and WP-RHS-A/P. The next feature to filter for is Amputations only if there are any amputations present, otherwise filter for Notches next i.e. BN-A/P, MN-A/P and TN-A/P. As the database grows, the amount of potential candidates will increase accordingly. If there are still far too many potential candidates, the next feature to filter for is Black Pigment i.e. BP-LHS-A/P and BP-RHS-A/P. Side is useless if that particular side has not been previously photographed. If the individual has a tag, this may reduce the number of potential candidates, however, that is dependant on whether the individual had previously been photographed with a tag present. Once filtering for potential candidates has been completed the task of finding an affirmative match may commence.

**FIN MATCHING**

The *Compare View* option at the bottom of the view chamber should be selected. The photograph that is to be matched will be displayed on the left-hand side in the *Select* box and the potential candidate will be displayed on the right-hand side in the *Candidate* box. All the photographs of the potential candidates will be displayed in the *Filmstrip* below the view chamber. The latest photograph is found at the extremity to the right and the oldest photograph is found at the extremity to the left.

If the photograph represents a new individual, it is assigned a new white shark number under the *GWS Number* keyword e.g. WS-087. However, if an affirmative match is found, the candidate photograph is highlighted and under the *GWS Number* keyword the dropdown list is opened to locate the keyword tag that had been assigned to that candidate. Subsequently, this keyword tag is
applied to the photograph that was to be matched. The keyword tag is then opened to ensure that all the dorsal fins with that particular unique code represent the same individual and that the match is successful. If the match was unsuccessful, the keyword tag is removed from the photograph and the matching process continues.

**DISCUSSION**

Dorsal fin matching through visual discernment is a dynamic process. The following are a few tips that should aid in the reduction of pseudo-replication and to prevent misidentifications. The most important feature to look at when trying to match dorsal fins is the dorsal trailing edge. Although it can and does change, it is very rare that the entire dorsal trailing edge will change – usually, only a section will be altered (Anderson *et al.* 2011). An effective means of comparing the dorsal trailing edge of two individuals is to find a pattern in the notch structure. Notches can and do change with time, thus it is important to keep an open mind when searching through potential candidates. Notches are likely a result of wear-and-tear but may also arise from the negative effects of parasites attached to the dorsal trailing edge (pers. obs.). Thus, do not rule out potential candidates whose trailing edges do not look exactly the same. Scarring, and to a greater degree trauma-induced wounds can be used to affirm matches. However, it is important to keep in mind the duration of such markings, as the previous photograph of that individual may not have had any scars or wounds present. Another sound feature to consider is black pigmentation. The smaller black pigments are not always evident in every photograph, likely due to the dorsal fin being wet coupled with the ambient light conditions at the time. Nevertheless, if present, black pigmentation can be used to confirm matches in instances of doubt.

The absence of dorsal fin-matching software for white sharks during the course of this study has subsequently led to the creation of the photographic identification technique described here. Consequently, the use of image
database software such as Adobe Photoshop Lightroom 2 represents an effective medium to facilitate the compilation of a photographic identification catalogue. A significant hindrance for the proposed fin-matching process is that it is time-consuming due to the manual-nature of the method. In addition, the constant possibility of the notch structure being partially altered presents its own challenges when distinguishing between individuals, thus a keen eye is required to pick up any changes. Although successful identification of distinct individuals is shown to be possible using a multi-feature approach, experience is certainly a key factor to effectively identify unique individuals and can only be gained through consistent practice.
REFERENCES CITED


Specialist report compiled by Enviro-Fish Africa for CCA Environmental on behalf of Irvin and Johnson Limited.


