Great White Sharks *Carcharodon carcharias* in Gansbaai, South Africa: Environmental Influences and Changes over Time, 2007–2011

by

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Declaration

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Alison Towner

Dedication

‘To my father Eric James Towner, I dedicate this thesis in your memory for inspiring my fascination with the ocean. To my mother Maureen and dear twin Lewis, this is also to you, for listening, supporting and loving me unconditionally every step of the way.’

Abstract

The South African Government introduced protective legislation prohibiting targeted fishing of the great white shark *Carcharodon carcharias* in 1991. This pre-emptive measure was intended to protect this species from increasing fishing pressure to allow researchers to gather information of this shark's distribution, basic life history traits, breeding behaviour, and habitat use. Following this, the species conservation status was placed on CITES Appendix II and classified on the IUCN (International Union for the Conservation of Nature) Red List as Vulnerable. This thesis investigates white sharks at Gansbaai, in particular their occurrence, changes over time and the influence of environmental variables on their numbers there.

The size and numbers of white sharks were recorded from an anchored cage diving vessel over a five-year period between 2007 and 2011. The study was conducted around Dyer Island and the inshore region of Gansbaai in the Western Cape of South Africa. A change in size frequency between seasons suggests that the white sharks are not resident for long periods, but that different size classes use the coastal bay at different times. There was a statistically significant change of size distribution over the five years for both male and female sharks. The trend of larger sizes recorded later in the study could infer a change in the cohorts visiting the bay or growth of the same individuals exhibiting site fidelity to the area.

Reduction of bather protection gill netted areas on the South African east coast in KwaZulu-Natal and reduced fishing pressure on the species are discussed in relation to the trend. Recruitment of white sharks subsequent to protection in 1991 has not been quantitatively documented to date thus this study could provide the first indication that this may be a recovering white shark population The collection of long term consistent data collection of this species is clearly warranted to follow this trend.

The occurrence of white sharks visiting Gansbaai was investigated through five years of cage diving boat sightings from 2007–2011. I used the generalized linear model to investigate counts of great white sharks per trip in relation to sexual composition of sharks, month, sea surface temperature and a multivariate ENSO Index. Shark sightings for both sexes were most frequent during winter months when water conditions are less variable than in summer when south-easterly winds intensify cold water upwelling Furthermore, Multivariate ENSO Index,(MEI) is an index to quantify the strength of the Southern Oscillation which affected male and female white sharks numbers in opposite ways, and these interannual trends were highly significant. These data suggest that water temperature and climatic phenomena may influence the abundance of white sharks at this coastal site. These findings ‘discussed in relation to size class, sex, and the influence of physiology.

The findings of both aspects of this study are discussed in relation to future white shark research. It is suggested that this work may contribute towards policymaking and management decisions for white sharks in South Africa. Furthermore the findings of this study could contribute to bather safety programmes because the incorporation of environmental parameters into predictive models may help identify times and localities of higher risk to bathers and help mitigate human white shark interaction.

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Acronyms

PCL: Pre caudal is length measurement of a shark's length from its snout to before the caudle fin/peduncle

TL: Total length, shark's length measured from snout to tip of upper caudal lobe.

ENSO: EL Nino Southern Oscillation is a quasiperiodic climate pattern that occurs across the tropical Pacific Ocean roughly every five years. The *Southern Oscillation* refers to variations in the temperature of the surface of the tropical eastern Pacific Ocean (warming and cooling known as *El Niño* and *La Niña* respectively) and in air surface pressure in the tropical western Pacific. The two variations are coupled: the warm oceanic phase, El Niño, accompanies high air surface pressure in the western Pacific, while the cold phase *La Niña*, accompanies low air surface pressure in the eastern Pacific.

MEI: Multivariate Enso Index is a multivariate measure of the ENSO signal in the first principal component of six main observed variables over the tropical Pacific: sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and cloudiness of the sky. The highest values of MEI values represent the warm ENSO phase (El Niño) while the lowest values of MEI represent the cold ENSO phase (La Niña).

MODIS: Moderate resolution Infrared (IR) Spectroradiometer. Instrument on NASA Aqua and Terra spacecraft that provide visible and IR data from 36 channels at sub-point resolutions from 250m to 1 km

SeaWiFS: Sea Viewing Wide Field of view Sensor. An optical remote sensing sensor on the OrbView satellite, a project run by NASA (National Aeronautical Space Agency).

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Chapter 1

General Introduction

Photo: Alison Towner

Shark Evolution:

Evolutionary relationships within and among different groups of sharks have long been investigated by taxonomists (Compagno 1977; Schaeffer and Williams 1977). Fishes that were morphologically similar to modern day sharks swam in the seas during the Devonian when dinosaurs walked the land, and have survived multiple extinctions during the intervening 400 million years (Grogan and Lund 2004). The cartilaginous fishes, Class Chondrichthyes, to which sharks belong, are the oldest surviving group of jawed vertebrates (Wourms and Demski 1993). The Class is comprised of two subclasses: the Holocephali and the Elasmobranchii. They can be distinguished from the Osteichthyes (bony fishes) by the presence of dermal denticles, which have been replaced by scales in more modern fishes, a cartilaginous skeleton (Last and Stevens 1994), and the males have intromittent organs (claspers and their supporting structures) developed from extensions of the pelvic axis of mature sharks (Grogan and Lund 2004).

The Class Chondrichthyes (sharks, skates, rays and chimeras) are generally divided into four groups: the squalomorphs, galeomorphs, squatinomorphs and batoids (Compagno 1977). These include 51 families (Bonfil 1994). Fossil teeth are used to estimate the date of their evolutionary arrival. However this is a difficult task. Inconsistent and degraded specimens create complexities and much debate exists in the paeleontologists' arena about the emergence of many species (Martin 1996). It is generally accepted, however that their ancestral lineage is ancient, and that most of today's extant elasmobranch species originated or diversified from the early Jurassic and Late Cretaceous period, between 200 and 100 million years ago (Hubbell 1996; Long and Waggoner 1996; Martin 1996).

Throughout this long evolutionary history, sharks have evolved and adapted to take on many different forms, moving into various marine and freshwater habitats. Today out of c. 1,160 extant species of cartilaginous fishes (Pikitch et al. 2008) there are approximately 400 species of sharks. Taxonomists have grouped modern shark species together by their common external features. The two main groups from which all shark species stem are the Galea and the Squalea. From these two stems are derived each modern shark family, of which currently 21 are recognised (Martin 1996, Figure 1.1).

The mackerel sharks

During the carboniferous era, 320 million years ago, warm, shallow seas covered most of North America and Europe. At that point sharks were considered to be as diverse as present day reef-dwelling fishes (Maissey 1998). The Jurassic explosion, approximately 100 million years ago marked the emergence of thousands of shark species (Maissey1998).

The shark Order Lamniformes have remarkably diverse body forms. Their common features include five long gill slits, the presence of an anal fin, a mouth extending behind the eyes, and no nictitating membrane over the eyes (Martin

1996). The smallest member of the order, the crocodile shark *Pseudocarcharias kamoharai*, measures 1.1 m in length in contrast to the largest member of the order, the basking shark *Cetorhinus maximus* which attains a length of up to 12 m (Compagno 2001).

The family Lamnidae, the 'mackeral sharks', stems from this order. Fossils and molecular data indicate that this group may have originated during the Palaeocene or early Eocene. However their diversity and abundance are well documented from the later Cretaceous and Palaeocene (Capetta 1987; Siverson 1992). Today, although the lamnid sharks are a small group compared to their diversity in the Cenozoic times (Compagno 2008), they are cosmopolitan in distribution ranging from the polar seas to the tropics.

Physical and hydro-mechanical demands provided important selection pressures to optimise body design for locomotion during vertebrate evolution (Bernal et al. 2001). Lamnids and tunas, the two fastest swimming groups of fishes, have developed similar morphological and physiological adaptations that differ from those of most other fishes. They have evolved morphologyt for high-speed hunting which is supported by endothermy; which enables them to maintain an internal body temperature above that of ambient sea water (Carey et al.1982; Goldman 1997). The fastest of the mackerel sharks, the shortfinned mako *Isurus oxyrinchus* is capable of reaching burst speeds in excess of 45 km/h (Carlson et al. 2004; Bernal et al. 2005).

Of the five lamnid sharks, the most widely distributed is the white shark *Carcharodon carcharias* (Compagno 2008). During the later Jurassic era, 140–210 million years ago, the white shark was already highly evolved for ocean hunting/scavenging. Their modern form is almost identical to their form in the Tertiary period (Compagno 1990; Maissey 1998; Applegate 2001; Martin 2005).

This large active predator has attracted considerable notoriety (Compagno 2001; Bruce 2008). It has a popular, yet often controversial reputation in the media, largely due to it being one of the few shark species capable of fatally injuring humans. This combined with a negative stigma (largely generated by Peter Benchley's thriller series *Jaws*) has resulted in mixed and often conflicting public opinion towards the species. The realities of the white shark's life history have effectively been hidden by the mythical status this species has attained (Klimley and Ainley 1996b; Compagno et al. 1997).

Global distribution and migration patterns

Understanding the movements of large marine predators has been hindered by the scale of extensive roaming in an environment that has long challenged marine scientists (Klimley et al. 2002). Until the 1990s, it was thought that white sharks primarily inhabited temperate coastal and offshore waters of continental and insular shelves (Compagno 1984a; Bruce 2008). This was largely due to the fact that earlier white shark research had been focused on subadult and adult sharks greater than 3 m in length at pinniped colonies (Pyle et al. 1996a; Strong et al. 1996; Goldman and Anderson 1999; Malcolm et al. 2001; Bruce et al 2005a, b; Martin et al. 2005; Domeier and Nasby-Lucas 2007; Robbins 2007; Robbins and Booth 2012). Since 2000, there have been significant advances in our understanding of habitat use and behaviour of white sharks, due to advances in ultrasonic telemetric tagging (Hammerschlag et al. 2011).

White sharks occur circumglobally in temperate and tropical regions, including all major ocean basins and the Mediterranean Sea (Compagno 2001). They form seasonal aggregations at predictable locations around the globe. The main locations at which aggregations occur are in California, Mexico, South Africa, New Zealand, South Australia (Compagno et al. 1997) the North East Atlantic Ocean (Carey et al. 1982; Casey and Pratt 1985; Skomal et al. 2012) and to a lesser extent the Mediterranean Sea (Fergusson 1996; Francis 1996). Satellite tagging studies have revealed that white sharks spend large amounts of time in the open oceans and tropics when they leave these aggregation sites (Boustany et al. 2002; Bruce and Stevens 2004; Bonfil et al. 2005; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2009; Bradford et al. 2012; Bruce and Bradford 2012; Duffy et al. 2012; Francis et al. 2012; Jorgensen et al. 2012, Figure 1.2).

White sharks are able to navigate across ocean basins to return to the same locality , and their navigation has been attributed to their ability to use a number of cues, including those which are celestial, magnetic and topographic (Klimley et al. 2002; Bonfil et al. 2005; Weng et al. 2007b).

Coastal vs oceanic movements.

While undertaking migration, white sharks show marked differences in behaviour when inhabiting shelf waters as opposed to oceanic habitatsLongmigrations coupled with coastal site fidelity are documented as typical behaviour in most regions where white sharks are abundant, including South Africa (Bonfil et al. 2005; Bruce and Bradford 2012; Werry et al. 2012), Australia (Bruce et al. 2006), New Zealand (Duffy et al. 2012), California and Mexico (Boustany et al. 2002; Weng et al. 2007b, Domeier and Nasby-Lucas 2008; Jorgensen et al. 2009; Nasby-Lucas et al. 2009; Jorgensen et al. 2012). Furthermore, some differences in white shark migratory behaviour occur between regions. In the northern hemisphere, large scale movements of white sharks are mainly North-South in direction. In South Africa both South North West East and East West movement occurs where as new Zealand white sharks migrate South North.(Francis et al. 2012). Their migrations from New Zealand, California and Mexico have all shown ocean basin crossing whereas in South Africa and Australia preference for the continental shelf is more prevalent in records collected to date (Bonfil et al. 2005; Dudley 2012). In contrast, relatively few examples of excursions across entire ocean basins have been documented in the southern hemisphere (Bonfil et al. 2005; Bruce et al. 2006; Bruce and Bradford 2012). To date, however there has been only one published study from the southern African region which concluded that subadult female white sharks are capable of transiting from South Africa to Australia (Bonfil et al. 2005). Clearly this merits further investigation.

Studies of white sharks off Mexico showed that their deepest dives correspond to the depth of the oxygen minimum layer which occurs at approximately 500–1,000 m and 0.1–0.5 ml·l^{-1} of oxygen (Weyl 1965; Nasby-Lucas et al. 2009). In the south west Pacific and Indian Oceans, the oxygen minimum layer's depth is much deeper at 2,000 m and 3–4 ml·l^{-1} and here white sharks appear to occur at depths of greater than 900m more frequently (Bonfil et al. 2005; Duffy et al. 2012; Francis et al. 2012).

Fine scale movements: swimming patterns at aggregation sites.

Evidence collected to date suggests that white sharks may well be site specialists, displaying regionally specific behaviours in the areas to which they show fidelity (Bradford et al. 2012; Bruce and Bradford 2012; Duffy et al. 2012; Francis et al. 2012). Exploration of these fine scale behaviours has been made possible by advances in acoustic telemetry. Carey et al. (1982) were the first to deploy an acoustic transmitter onto a large adult white shark, estimated to be 4.5 m in length (Total length (TL)), which was feeding on a whale carcass off the east coast of the USA. During 83 hours of continuous tracking, the shark moved 190 km, and displayed a range of swimming patterns and sustaining swimming speeds of 3.2 km·h^{-1}. Rates of movement (determined by the distance moved over a given time), swimming speed and linearity are all indices frequently used to quantify and qualify how a species interacts with its surrounding environment (Sundström et al. 2001).

Scientists use swimming patterns to analyse the movement behaviour of shark species. Tortuous swimming patterns (repeated twists or turns) with slower rates of movement are inferred to be foraging or resting behaviours, whereas quicker more linear and directional movements are associated with commuting between habitat sites (Papastamatiou et al. 2009). Moreover, burst speed swimming may indicate hunting activity (Klimley et al. 2001b; Martin 2005). Common swimming patterns that have been described in white sharks throughout their range include inter-island cruising, stalking at depth, shallow water and offshore sweeps, bounce diving and down current circling (Carey et al. 1982; Strong et al. 1992; Goldman and Anderson 1999; Klimley et al. 2001a; Johnson et al. 2009). The fastest burst speed recorded for white sharks is 6–7 $m{\cdot}s^{-1}$ (Klimley et al. 2001b) around a seal colony with a maximum sustained rate of movement of 1.33 $m{\cdot}s^{-1}$ away from a seal colony (Bonfil et al 2005; Johnson et al. 2009). Development of accelerometers to measure tail beat frequency will further enhance our understanding of the swimming speeds of which white sharks are capable.

As predators hunting fast-moving prey in cool temperate waters, white sharks have evolved a suite of physiological adaptations (reviewed by Bernal et al. 2005). For example, their eyes are large and possess extra ocular muscles with an orbital vascular *rete* which increases the temperature of their eyes and brain allowing more efficient processing of visual information (Gruber and Cohen 1985; Demski and Northcutt 1996). Coupled with this, they can perform regional endothermy defending an elevated internal body temperature above ambient and keeping core and locomotor muscles warm. An individual white shark maintained an internal body temperature of 14.5°C above sea water in one study (Goldman 1997; 2002).

Individuals swimming and hunting patterns vary depending on the physical complexities of the site they are utilising. For example, around Seal Island, False Bay, the bathymetry of the surrounding sea displays a steep slope to depths of 25–30 m, and white sharks use this deep water to ambush seals; they have been observed to attack during dawn and dusk (Hammerschlag et al. 2006). Conversely, at Dyer Island, 80 km to the east, seal hunting patterns are a lot less structured than at Seal Island (pers. obs, Figure 1.3) but the depth of the bay surrounding the island is 7-15 meters (much shallower than at Seal Island) with thick patches of kelp forest. Regardless of regional differences, white sharks are capable of great endurance and impressive swimming speeds. Their ambush hunting behaviour occasionally results in a 'breach', particularly in South Africa, where the entire shark leaves the surface of the water (Klimley et al. 1996). This phenomenon which has been photographed and filmed extensively (Figures 1.3 and 1.4)

Historical records of white sharks in southern Africa

White sharks have been documented along the entire southern coastline of Africa from as far north as Angola on the west coast (Compagno et al. 1997) to regions of the western Indian Ocean north of Mozambique, off Madagascar, Mauritius and Kenya (Cliff et al. 2000). However, the epicentre of the distribution of the species in South Africa is the temperate waters of the Western Cape (Bass et al. 1975; Cliff et al. 1996b; Compagno 1991).

Reliable historical records confirming the presence of the species in South African waters are scarce prior to the 1850s. Written records in the form of letters were obtained describing large sharks in their hundreds ‘attacking and taking men’ from survivors of the British troopship *HMS Birkenhead*, a naval frigate which was wrecked by colliding with a reef offshore of Gansbaai in the Western Cape in 1852 (Colledge and Warlow 2006). Artisanal and then industrial whaling and sealing are well documented in South Africa from before Dutch settlers arrived in 1652 until the 1940s in the Western Cape and until the 1970s in KwaZulu-Natal (Best and Ross 1986; David and van Sittert 2008).

The fact that this exploitation of seals continued for decades suggests there was adequate prey available for white sharks to hunt in these areas. Conversely, Lewis’s (1948) angling guide, which referred specifically to fishing for sharks in the Western Cape, described how mako sharks may be present around the Hermanus area but commented that the real large ‘man eaters’ were more common off the whaling station/Durban pier. It is likely that the limitations of early fishing gear (no slider mechanisms to allow the fishing line to reach out behind the backline) prevented encounters between shore anglers and white sharks during the early 1900s. Photographs of dead whales brought in to the whaling station in Betty’s Bay clearly show large lunar bite marks, which are typical of large predatory shark species such as white sharks’ bite patterns, on the flanks and head of the whale carcasses (Figures 1.5 and 1.6).

The whaling station in Durban closed in 1975 and consequently catches of white sharks by anglers off the pier declined in size and number. The shark's presence is only described reliably and referred to as 'conspicuous in the Western Cape' after the 1970s (Wallett 1973; Bass et al. 1975). It was during this decade that certain game fish anglers seemingly turned their focus towards directly targeting and killing white sharks in belief that they were becoming aggressive towards their boats. In False Bay, Danie Schoeman and his brother captured and killed 18 sharks, and Theo Ferreira killed 30 (D Schoeman and T Ferreira pers. comms). Meanwhile 80 km to the east in Gansbaai white sharks were captured and killed for their oily livers, and jaws by various fishermen (W. Chivell pers. comm.). In 1987, South Africa's largest ever white shark was captured and killed accidentally in a trawler off Danger Point, Gansbaai. The shark was estimated to measure 5.67 m TL (Dudley 2012, Figures 1.7 and 1.8)

The shark cage diving industry in South Africa

Shark cage diving is a form of ecotourism whereby tourists enter a partially submerged dive cage which is attached to the leeward side of an anchored vessel to observe white sharks under and/or above water level. Unlike cage diving operations in Guadeloupe (Mexico) and the Neptune Islands (Australia), the South African shark cage diving industry does not require the use of SCUBA gear or passengers to be certified divers, because the cage is not submerged. Shark cage diving is ranked as one of the top priority attractions for international tourists when visiting the Western Cape of South Africa (Maharaj et al. 2003).

Legislation, permitting procedures and a code of conduct were developed to regulate and manage the South African shark cage diving industry by the then Department of Environmental Affairs and Tourism following the protection of white sharks in 1991. The Gansbaai region including Dyer Island is the most extensively utilised location in the world for cage diving and the only place where daily trips are conducted year round, weather permitting, In order to attract a white shark to the anchored cage diving vessel, a scent trail known as a chumslick is created from ground up bony fish products and a baitline is deployed. Chumming and baiting methods in South Africa are similar to those provided by Strong et al. (1992) except in the latter the government code of conduct states that intentional feeding of white sharks is prohibited (Maharaj et al. 2003).

Previous research on white sharks in South Africa.

White shark research in southern African waters has spanned more than 150 years, with 58 publications produced in the last two decades (Dudley 2012). Early field studies of white sharks in South Africa recognised that the regional centre of abundance for the species is the Western Cape waters (Wallett 1973; Bass et al. 1975).

Long term data has been obtained from large mesh gillnets put in place in the KwaZulu-Natal region for the purpose of bather protection (Cliff et al. 1989, 1996a; Cliff and Dudley 1992; Dudley and Simpfendorfer 2006; Dudley 2012). These catch data indicate a modal size class for both male and female white sharks in the KwaZulu-Natal region of 253–270 m TL (Total Length) and demonstrate an absence of mature female specimens in bather protection net catches (Dudley 2012). However, large mature females, including one pregnant specimen, have been recorded from the tropical western Indian Ocean, suggesting that these larger females may migrate in to warmer waters, possibly for breeding (Cliff et al. 2000; Zuffa et al. 2002). However, mature female white sharks measure >4.5m (Bruce and Bradford 2012) and gear selectivity may prevent these larger specimens from being sampled in the inshore KwaZulu-Natal region (Dudley 2012). Compagno (2001) suggested that intercontinental movement was likely with South African white sharks (based on tropical and offshore records) and that photographic identification of individuals and further advancements in tagging technologies would confirm this.

In the 1990s conventional tagging with spaghetti tags and larger plaque tags, enabled the first studies on white shark migration (Cliff et al. 1996b; Ferreira and Ferreira 1996). These early tagging studies showed movement of white sharks between Western Cape regions and longer distance movements to the KwaZulu-Natal waters on the east coast (Cliff et al. 1996b; Dudley 2012). Photographic identification studies in the 1990s indicated that white sharks may take up temporary residency in Western Cape locations and that some individuals show site fidelity to these regions (M. Scholl unpubl. data).

The development of satellite tags during the late 1990s allowed further investigation into migratory behaviour of white sharks; between 2002 and 2003 twenty six satellite tags (both real time and archival) were deployed in the Western Cape regions of Gansbaai, Struisbaai and Mossel Bay (Bonfil et al. 2005). This study supported earlier findings in other regions (Wallet 1973; Bass et al. 1975; Cliff et al. 1996b) that white sharks move between Western Cape locations and the KwaZulu-Natal region, and established the first recorded transoceanic migration of a subadult female white shark to Australia from Dyer Island, Gansbaai (Bonfil et al. 2005).

A number of ultrasonic acoustic tracking studies have recently been published or are in progress in the Western and Eastern Cape of South Africa (Johnson and Kock 2006; Johnson et al. 2009; M Dicken and M. Smale in progress; A.Kock; A.V. Towner and O. Jewell in progress). These studies involve the use of continuous acoustic tags which transmit ultrasonic signals, on a pre programmed frequency, which can be recorded via a hydrophone and receiver system on a vessel (Sundström et al. 2001). These tags have been used to actively track fine scale movements of white sharks within particular regions (Johnson and Kock 2006; Johnson et al. 2009), and provide temperature and depth data of the shark's immediate environment along with establishing swimming patterns (Johnson et al. 2009).

Conservation status, population estimates and threats.

Compared to many of their pelagic and demersal relatives, white sharks have received considerable international and domestic conservation attention (Bruce 2008). Their slow growth, late maturity and low levels of productivity (Cailliet et al. 1985; Wintner and Cliff 1999; Malcolm et al. 2001) are the reasons why they are particularly vulnerable to consumptive exploitation (Walker 1998; Watts 2001). We now know that they possess a little capacity for density-dependent compensation to rapid declines in population size (Bruce 2008). It is therefore reasonable to conclude that they are vulnerable to overfishing and all other forms of unnatural mortality (Francis 1996). In the early 21st century, fishing remains their biggest threat (Cliff et al. 1996b; Compagno 2001; Baum et al. 2003).

Sport and game fishermen directly targeted and exploited white sharks throughout their global range before protective measures were put in place. Their fins, teeth and jaws are sold at premium prices on the commercial market (Lai 1983; Chen 1996; Rose 1996). Trawl, long-line, gill-net, rod-and-reel fisheries have all taken white sharks as by-catch, and continue to do so (Cliff et al. 1996b;

Francis 1996; Uchida et al. 1996; Compagno 2001; Malcolm et al. 2001). Shore based catches continue today, as shown by an incident of a subadult white shark being caught in Mossel Bay in 2011 (Figure 1.9). The shark was returned to the ocean after having been fought for a number of hours.

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On 11 April 1991, fisheries legislation afforded white sharks protective status in South African territorial waters (Compagno 1991). This was precautionary in principle and based on the paucity of data available on the species at the time, along with its high notoriety and commercial value (Compagno 1991). These new regulations meant that targeting, killing, possessing or trading in white shark parts was illegal (unless exempted by written permit from the Department of Environmental Affairs). Shortly after this breakthrough in white shark conservation, parts of the USA issued protective legislation for white sharks between 1994 and 2000. In 2004, Australia and Madagascar jointly nominated the white shark for inclusion in Appendix II of the Convention of International Trade in Endangered Species of Fauna and Flora (CITES) which was subsequently accepted (Bruce 2008). By 2012, Australia, Namibia, Malta and Israel had protective legislation in place for white sharks. New Zealand prohibits targeting of them, but allows the sale of by-catch products. Mooney-Seus and Stone (1996) classified the species as *Severely Reduced* in New South Wales, *Data Deficient* in Queensland, and *Lower Risk / Conservation Dependent* in the Pacific Ocean coast of the USA. The white shark's status is rated at high risk of extinction and they are listed on CITES Appendix II and on the IUCN Red List as a vulnerable species A2cd+3cd ver 3.1, with unknown population trends (http://www.iucnredlist.org).

Genetic stock structure

Fine-scale genetic population structure was, until recently, unexpected in white sharks (Jorgensen et al. 2009, 2012). Pardini et al. (2001) used genetic evidence to hypothesise that mixing of gene pools probably occurs between sharks in South Africa and Australia and hypothesized that males move more extensively than females. Bonfil et al. (2005) confirmed this mixing of continental white shark stocks through satellite tagging. Their study revealed however that this mixing behaviour is not sex specific, because their tagged shark was a 3.4 m subadult female.

Even though connectivity of white shark stocks occurs, its extent is currently uncertain. Recent advances in molecular genetic analysis combined with improved sampling techniques have detected distinct genetic subdivisions within the global range of white sharks (Gubili et al. 2009, 2012; Jorgensen et al. 2009, 2012).

Differences in migratory behaviour appears to have evolved between white sharks in different regions (Francis et al. 2012) perhaps strengthening these divisions. Furthermore, mitochondrial DNA analyses have revealed marked population differentiation indicating the existence of fine-scale matrilineal structures which indicate clustering within these sub-groups (Pardini et al. 2001; Gubili et al. 2009, 2012; Jorgensen et al. 2009, 2012).

Reproduction and life history of white sharks.

White sharks are naturally rare and have low reproductive potential (Bruce 2008). They have slow growth rates (Cailliet et al. 1985; Wintner and Cliff 1999; Malcolm et al. 2001). Both sexes mature late, with females thought to mature at 12–17 years old, markedly later than males, which are believed to mature at 7–9 years (Cailliet et al. 1985; Winter and Cliff 1999; Malcolm et al. 2001).

Live birth of a white shark has never been observed and only one single observation of presumed mating behaviour has been described, from New Zealand waters, but there is no photographic evidence (Francis 1996). Cliff et al. (2000) reported on a single pregnant specimen caught in an artisanal fishery off the Kenyan coastline and a pregnant female record from Madagascar. This shark was estimated to measure 6.4 m and to be carrying at least seven embryos. The 14 records of pregnant white sharks obtained to date have mostly been poorly documented, often limited to second-hand observations (Francis 1996). Captures of pregnant females in the Pacific Ocean have been reported mainly off Japan (Uchida et al. 1996), Taiwan (Francis 1996), Australia (Bruce 1992) and New Zealand (Francis 1996). Mediterranean Sea records occurred off Egypt (Norman and Fraser 1937; Francis 1996) and off Tunisia (Fergusson 1996; Saidi et al. 2005). The largest litter size of near- term embryos was 14 off Queensland Australia (Paterson, 1986, JD. Stevens pers. comm.) (Table 1.1).

Parturition is believed to occur in spring and summer based on the capture of neonates and post-partum adults (Klimley 1985; Fergusson 1996; Francis 1996; Uchida et al. 1996). The presence of large amounts of yolk in the stomachs of some embryos suggests that white sharks are aplacental viviparous, with embryos exhibiting oophagy, or feeding on oocytes (Francis 1996; Uchida et al. 1996). Mollet and Cailliet (2002) estimated a three-year reproductive cycle, with an18-month gestation period followed by an 18-month resting period.

Growth ring deposits, in the white sharks vertebrae, have been successfully used to age them, as has been done with other species (Pratt and Casey 1983; Branstetter 1990; Mollet and Cailliet 2002). Assuming annual growth ring deposition, male white sharks in South Africa would mature at between 8–10 years (Cailliet et al. 1985; Wintner and Cliff 1999). Age at maturity for female white sharks in South Africa, would be 12–13 years (Wintner and Cliff 1999). Bruce and Bradford (2012) reviewed literature on white shark sizes with age and developed a series of categories based on accepted total length criteria from both field and laboratory studies (Table 1.2).

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Circulatory system and physiology

To facilitate their extreme diving behaviour, white sharks have a suite of complex biological and haematological characteristics ranging from their muscle design (Carey et al. 1982; Block and Carey 1985; Goldman 1997; Bernal et al. 2001, 2005) to their circulatory system structure (Emery 1985; McCosker 1987).

Lamnid sharks, tunas and billfishes have developed similar morphological and physiological adaptations that differ somewhat to most other fishes (Bernal et al. 2005). They possess more centrally located circulatory systems, distributed closer to core and locomotor muscles (Bernal et al. 2005). This allows them to perform regional endothermy via heat exchange (Goldman 1997; Bernal et al. 2005) keeping vital organs, particularly visceral and cranial regions warmer than ambient (Carey et al. 1982; Tricas and McCosker 1984; Casey and Pratt 1985; Goldman 1997). Furthermore, their blood composition may be similar to that of big eye tuna *Thunnus obesus* with an increased oxygen binding affinity at the gills and a decrease in affinity as the blood is warmed by the *rete mirable* (counter current heat exchangers) which may help to enhance oxygen delivery in low oxygen environments (Lowe et al. 2000; Nasby-Lucas et al. 2009).

Sexual segregation

Sexual segregation of white sharks, both spatially and temporally has been demonstrated at numerous localities (Klimley 1987; Bruce 1992; Goldman and Anderson 1999; Robbins 2007; Domeier and Nasby-Lucas 2012; Robbins and Booth 2012). This behaviour is a general characteristic of shark populations (Springer 1967; Klimley 1987) and in elasmobranches it may occur for a variety of reasons including; reproductive strategies associated with pre- or post-mating behaviours, differing seasonal habitat and resource requirements, refuge from mating aggressors, and prey availability (Sims et al. 2001). A recent tagging study showed that adult female white sharks only occupied the same activity space as males for 90–120 days over a two-year span in the north-east Pacific

Ocean (Domeier and Nasby-Lucas 2012). In Australia and South Africa, males are more commonly encountered during winter months in island waters (Klimley 1987; Strong et al. 1996; Malcolm 2001; Robbins 2007; Robbins and Booth 2012). It has tentatively been proposed that females may seek out warmer inshore waters in summer months to influence the developmental growth of their young or assist with their own higher growth rate demands (Robbins 2007; Domeier and Nasby-Lucas 2012; Robbins and Booth 2012).

Population estimates

Regional population estimates at aggregation sites suggest white shark numbers are small relative to other apex predators. Domeier and Nasby-Lucas (2007) identified 106 different individuals utilising photographic identification at Guadeloupe Island, in the Pacific. Chapple et al. (2011) used sequential Bayseian mark recapture alogarithm and predicted the central Californian population, to be 350 animals. However, Sosa-Nishizaki et al (2012) contested the findings of Chapple et al. (2011) and questioned the use of a closed population model for the region. Furthermore evidence of a possible increase in juvenile white shark sightings in the coastal regions of California and Mexico have been reported (Weng et al. 2007a,b; Domeier 2012, Sosa-Niishizaki 2012). The population in the region of Australia and New Zealand has been estimated to be 100–1,500 individuals from long-term tagging studies (Bruce 1992; Bruce et al. 2005a,b 2006) and a single South African population estimate has been made and this was 1,279 (CV 24%) individuals between Richards Bay in KwaZulu-Natal and Struisbaai in the Western Cape (Cliff et al. 1996b). Such estimates require larger data sets and extended studies to be reliable but highlight the fact that white sharks numbers are small throughout their range.

Oceanography of the Western Cape coast, South Africa.

The marine environment around southern Africa is one of the most diverse, complex, and variable anywhere in the world (Lutjeharms et al. 2000). Most of the complexity stems from the dynamic interactions of the Benguela Upwelling System, the Agulhas Current and the north-south migration of atmospheric high-pressure cells situated over the south-east Atlantic and south-west Indian Oceans (Roberts 2005).

The Benguela Upwelling System on southern Africa’s west coast forms the eastern boundary of the South Atlantic intercontinental gyre (Bakun 1993). It has an aerial extent of approximately 179,000 km^2, cover ing the shelf from the coast to 500 m depth (Hewitson and Cruickshank 1993). Within the Benguela Upwelling System, the general flow of water is northward, beginning off Cape Point at 34°S (Hardman-Mountford et al. 2003). It continues north towards the equator and parallel to the coastline where it meets with the Angolan front at 16°S (Moroshkin et al. 1970; Lutjeharms et al. 2000). Mean flow (0.25–0.50m s^{-1}) is strongest in the south of the current (Shannon 1985; Boyd et al. 1992; Shannon and Nelson et al. 1996; Hardman-Mountford et al. 2003) and migrates north with the south easterly trade winds. High-pressure belts move towards southern Africa, influencing the presence and intensity of south-easterly trade winds

(Peterson and Stramma 1991). These winds flow nearly parallel to the coast, equatorwards, causing offshore Ekman divergence of surface waters (Shannon 1985; Hardman-Mountford 2003). This forces cold, sub-thermocline, nutrient rich waters to the surface, a process known as 'upwelling' (Shannon and Nelson 1996).

The Cape Point cell at 34°S has been defined as the Benguela Upwelling System's southernmost boundary (Hart and Currie 1960; Andrews and Hutchings 1980) although upwelling can extend as far east as Cape Agulhas (35°S, 25°E) (Shannon 1985) which could be regarded as a more appropriate southern boundary for the system (Hardman-Mountford et al. 2003). The Benguela Upwelling System is one of the most productive eastern boundary systems of its kind (Boyd et al. 1992). Bottom water temperatures remain cold through the year, averaging 10–11°C on the shelf beyond the 100 m depth contour (Roberts 2005). Furthermore, dissolved oxygen levels are low and occasionally anoxic (Chapman and Shannon 1987; Boyd et al. 1992). The most intense upwelling cell is located in the north of the Benguela Upwelling System, adjacent to Lüderitz (Shannon 1985; Lutjeharms and Meeuwis 1987) and forms a biological and physical boundary between the northern and southern sections of the Benguela Upwelling System (Shannon 1985). In the Southern Benguela region, intense upwelling cells occur mainly during the summer, coinciding with the trade winds being furthest south, and pseudo windstress in the region being strongest (Parrish et al. 1983; Shannon 1985).

A strong shelf-edge front forms off the Cape Peninsula which is particularly strong in summer, being enhanced by the upwelling inshore and advection of warm Agulhas current water offshore (Shelton and Hutchings 1990). Associated with this strong front is a geostrophic equatorward jet known as the ‘Benguela jet current’ (Shelton and Hutchings 1982). It flows along the line of steepest bathymetric gradients around the Cape Peninsula to Cape Columbine (Shelton & Hutchings 1982).

The outer Agulhas bank and east coast regions are influenced by the warm faster flowing (2 m s^{-1}) Agulhas Current (Lutjeharms et al. 2000; Roberts 2005). The Agulhas Current is one of the most powerful western boundary currents in the world (Grundlingh and Lutjeharms 1979). It originates from the Mozambique Channel (Lutjeharms et al. 2000) and follows the continental shelf along the east coast of South Africa (Boyd and Shillington 1994). At the southern tip of the Agulhas Bank, the current undergoes a number of configurations, where meso-scale eddies pinch off and dissipate into the south Atlantic (Duncombe-Rae 1991). At this point the current retroflects back on itself where it converges back into the Indian Ocean (Gordon 1985; Quartly and Srokosz 1993). The dissipating Agulhas rings can measure 200–300 km average diameter (Lutjeharms and van Ballegooyen 1988; Hardman-Mountford et al. 2003) and carry pools of Indian Ocean water which can maintain a water temperature up to 5°C higher than the surrounding water (Gordon 1985). These features are an essential heat flux into the south Atlantic Ocean, and important component of the global circulation (McDonagh et al. 1999) possibly affecting global climate patterns (Gordon 1985). Furthermore, they affect the recruitment success of various important pelagic fish species (via advective loss of larvae) in the Western Cape/Agulhas Bank region (Duncombe-Rae et al. 1992; Hutchings et al. 1995).

The core water in the Agulhas Current is relatively nutrient poor in comparison to the Benguela Upwelling System, with more stable temperature variability (Hardman-Mountford et al. 2003). In contrast, dissolved oxygen remains relatively high with bottom dissolved oxygen (BDO) on the inner central bank highest of all parts of the Agulhas Bank greater then 6 ml l^{-1} (Roberts 2005). Primary productivity peaks when westerly winds cause more mixing and slight cooling of the water column in winter (Boyd and Shillington 1994). Furthermore, shear boundary processes such as break off filaments, eddies, meanders and anticyclone rings affect the dynamics of the Agulhas Current on the shelf edge, particularly during summer (Lutjeharms and van Balleygooyen 1988) (Figures 1.10 and 1.11).

Water properties of the inner shelf of the Western Agulhas bank.

The region between Cape Point and Cape Agulhas has characteristics of both the Agulhas and Benguela Upwelling System and has been regarded as a transitional zone (Bakun 1993; Lutjeharms et al. 2000; Hardman-Mountford et al. 2003). During winter months, May–September, low pressure belts occur more frequently in the southern African climate. The westerly wind belt expands and dominates the region, with large swells (Roberts 2005). The Agulhas Bank ecosystem off the Western Cape experiences a slight warming trend from the west to the east during winter. Bottom water temperatures on the inner shelf remain relatively stable at around 9–16°C (Roberts 2005). In summer months wind direction changes and easterly (upwelling favourable) winds intensify. Upwelling originates at the prominent capes and moves westwards (Schumann et al. 1995). Abrupt changes of temperature of more than 10°C have been recorded at coastal sites in the region (Schumann et al. 1982). Furthermore, Groschen and Schumann (1998) showed that there were marked differences in the response to wind forcing within the bays compared with sites along the open south coast.

Roberts (2005) reviewed the shelf oceanography along South Africa's south and west coast regions to assess favourable conditions for chokka squid *Loligo vulgaris reynaudii* spawning (Figures 1.7a and b). His study found that the Southern Cape Aghulas bank region was affected by low levels of dissolved oxygen in waters close to the shelf bottom (Low BDO). Eagle and Orren (1985) and Chapman and Largier (1989) showed that low BDO usually occurs on the inner central bank during late summer and autumn, when the thermocline is most pronounced. The minimum BDO for the region from Cape Point to Cape Aghulas is then 0.22 ml l^{-1} .(Roberts 2005).The mean range for the region is typically 3ml l^{-1-} BDO (Roberts 2005). Temperature and dissolved oxygen (DO) are the two potentially limiting factors most likely to influence vertical and horizontal distribution of pelagic fishes (Bernal et al. 2005).

ENSO and its effect on South African oceanography

El Nino/Southern Oscillation (ENSO) remains the most important coupled ocean–atmosphere phenomenon to cause global climate variability on seasonal to interannual time scales (Wolter and Timlin 2011). During these warm events, atmospheric pressure rises in the western Pacific Ocean and falls in the eastern Pacific Ocean weakening or even reversing the direction of south-easterly trade winds (Wilson et al. 2001). This causes suppression of the thermocline, with a pool of warm water surging eastwards along the equator, towards South America and reduction of the sea level in the western Pacific Ocean (Ramage 1987; Enfield 1987; Quinn and Neal 1992).

The Southern Oscillation Index (SOI) refers to the pressure difference between the South Pacific subtropical high-pressure region and the Indonesian equatorial low-pressure region. It is measured as a normalised sea level pressure difference between Tahiti and Darwin (Troup 1965; Allan 2000). SOI is negative during El Nino (warm episodes). Conversely, when SOI is positive, pressure over the Indian Ocean is greater than over the Pacific Ocean. South-easterly trade winds increase, re-establishing the thermocline with cold upwelled water surfacing in the eastern Pacific Ocean and warmer water remaining to the west. This cooler climatic episode often follows an El Nino and is known as a La Nina (Rasmusson and Carpenter 1982; Wolter and Timlin 1998).

The periodicity of ENSO events varies between 2 and 10 years (Rasmusson and Carpenter 1982; Quinn and Neal 1992), with an average period of three years (Philander 1990). These climatic episodes strongly impact marine ecosystems throughout the Pacific and Indian Oceans on various levels (Lenanton et al. 1991; Caputi et al. 1996, Bakun and Broad 2002) and routinely exerted powerful effects on the population dynamics of large number of fish stocks around the globe (Beamish 1995; Bakun and Broad 2002).

Multivariate ENSO Index (MEI).

The multivariate El Niño Southern Oscillation (ENSO) index (MEI) links six different meteorological parameters measured over the tropical Pacific Ocean (Wolter and Timlin 2011). MEI is a multivariate measure of the ENSO signal in the first principal component of six main observed variables over the tropical Pacific Ocean: sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and cloudiness of the sky (Wolter and Timlin 2011). As the MEI integrates more information than other indices, such as the SOI index based on Tahiti-Darwin pressure difference alone, it is thought to reflect the nature of the coupled ocean-atmosphere system better (Wolter and Timlin 1998). The highest values of MEI values represent the warm ENSO phase (El Niño) while the lowest values of MEI represent the cold ENSO phase (La Niña). Furthermore, the maxima and minima of MEI follow a 60 month cycle which can be reasonably be considered as an existing periodic forcing and a necessary condition of El Niño and La Niña (Mazarella et al. 2010).

The global ENSO cycle is an important component of climate variability along the South African south coast (Schumann et al. 1995; Roberts 1998). Shannon et al.(1986) highlighted a number of similarities between the 1963 and 1984 warm events in the Northern Benguela region and El Niño-Southern Oscillation (ENSO) events in the Pacific Ocean and suggested the term “Benguela Nino” to describe them (Hardman-Mountford et al. 2003). During these events, slacking of westerly winds in the equatorial belt causes an intrusion of warm water leading to downwelling in the Benguela region (Shannon et al. 1986; Gammelsrød et al.

1998). This results in stabilisation of the thermocline and replacement of the highly productive upwelled water with nutrient poor warm water; this drastically impacts the entire ecosystem. Such effects reported were suppression of phytoplankton production, displacement of fish stocks and a reduction in fish catches (Gammelsrød et al. 1998).

Kamstra (1985) and Taunton-Clark (1990) reported on an extended winter season near Cape Town, with higher interior pressures and an absence of anticyclones in the period of 1960–1985. They suggested a link between locally high SSTs and the Pacific Ocean warm (El Niño) event. Walker (1990) and Jury and Pathack (1993) demonstrated that SST anomalies in the Agulhas region to the east and southeast of Africa exert a control over summer rainfall of the adjacent interior. During the 1982/83 El Niño event, transition in wind directions at Port Elizabeth and Cape Town were recorded and corresponded to that event (Schumann et al. 1995). Furthermore, a decrease in coastal SSTs, due to intensified and extended upwelling, have been connected to positive ENSO events (La Niñas) in South Africa. A productive chokka season in 1998 was described by Roberts (1998), and was corresponded to the La Niña conditions extending the upwelling season and intensity thus, increasing productivity and local chokka catches (Roberts 2008).

Gansbaai (Gans Bay) and Dyer Island.

Gansbaai (Gans Bay) is a semi-enclosed embayment situated on the south coast of the Western Cape, South Africa. It is relatively exposed with the western and eastern boundaries being Danger Point (34°37.50S, 19°17.30E) and Quoin Point (34°47.28S, 19°39.15E), respectively.

Dyer Island lies 4km from the nearest shore within Gansbaai and was classified by BirdLife South Africa as one of 101 Important Bird Areas (IBAs) in South Africa (Barnes 1998). Five terrestrial and 12 seabird species breed on Dyer Island (Waller 2011). These include African penguins *Spheniscus demersus*, Cape *Phalacrocorax capensis* , white-breasted *Phalacrocrax lucidus* , bank *Phalacrocorax neglectus* and crowned *Phalacrocorax coronatus* cormorants, swift terns *Sterna bergii bergii*, kelp *Larus dominicanus* and Hartlaub's *Larus hartlaubii* gulls and African black oystercatchers *Haematopus moquini*. Geyser Island, lies approximately 150 m south west of Dyer Island, and has a breeding colony of Cape fur seals *Arctocephalus pusillus pusillus*, with c. 11,000 pups recorded in 2004 (Kirkman et al. 2007) and an estimated total population of c. 55,000 seals (CapeNature unpubl. data).

Samson Dyer, an American slave, first settled on Dyer Island in 1806 (Fourie 2002) and began the harvesting of Cape fur seals. Guano and penguin eggs were also harvested between the 17th and 19th century with penguin egg harvesting continuing on Dyer Island until 1968 (Fourie 2002). In 1979 the number of breeding pairs of African penguins on Dyer Island was estimated at 22,655 pairs, one of the largest colonies in the world (Shelton et al. 1984). However, by 2010, this had decreased to less than 2,000 pairs (Crawford et al. 2011). Dyer Island is one of the seabird breeding colonies in the southern Benguela Upwelling Ecosystem that is considered to be significantly impacted by predation by Cape fur seals (Makhado 2009; CapeNature unpubl. data). Furthermore GPS loggers placed on Dyer Island penguins have revealed these birds had greater foraging range, longer trip duration and travelled farther for pilchard *Sardinops ocellatus* and anchovy *Engraulis encrasicolus* than at other African penguin colonies (Waller 2011).

White sharks are known to fatally bite African penguins (Randall et al. 1988). However due to more substantial prey resources such as Cape fur seals in dense numbers, African penguins are not believed to form a significant part of the diet of white sharks around Dyer Island, with attack frequency reported to be minimal (Johnson et al. 2006).

The two islands are separated by a shallow channel, Shark Alley, which is c. 190 m in width at its widest point and 7 m deep and both islands are surrounded by dense forests of kelp (predominantly *Ecklonia maxima* and *Laminaria pallida*). The Uilkraalsmond River estuary enters the north eastern part of the bay and a 4.3 km stretch of sand and then gravel beach extends eastward from the mouth (Figure 1.9). Geelbek *Atractoscion aequidens*, silver kob *Argyrosomus inodorus*, galjoen *Dichistius capensis.annulatus* and white steenbras *Lithognathus lithognathus* are fish species seasonally abundant on inshore reefs close to the river mouth (Lubke and De Moor 1988, Whibley and Garratt 1989) as well as elasmobranches such as guitar shark *Rhinobatus annulatus*, smoothhound shark *Mustelus mustelus*, puffadder catshark *Haploblepharus edwardsii* and pyjama catshark *Poroderma africanum*. During winter months, yellowtail *Seriola lalandi* frequent the waters surrounding Dyer Island (Whibley and Garrat 1989).

Aims of study

The aim of this study was to investigate the occurrence of white sharks in the region of Gansbaai over a five-year study period. This I detailed in the following chapters:

Chapter 2 describes the size and numbers of sharks observed and, where possible these were separated according to gender.

Chapter 3 describes environmental parameters and investigates whether there was evidence that these parameters affected the number, size or gender composition of the sightings.

Chapter 4 integrates the findings of these chapters and proposes areas of research that may clarify aspects of the biology of this species in relation to the environmental conditions off South Africa.

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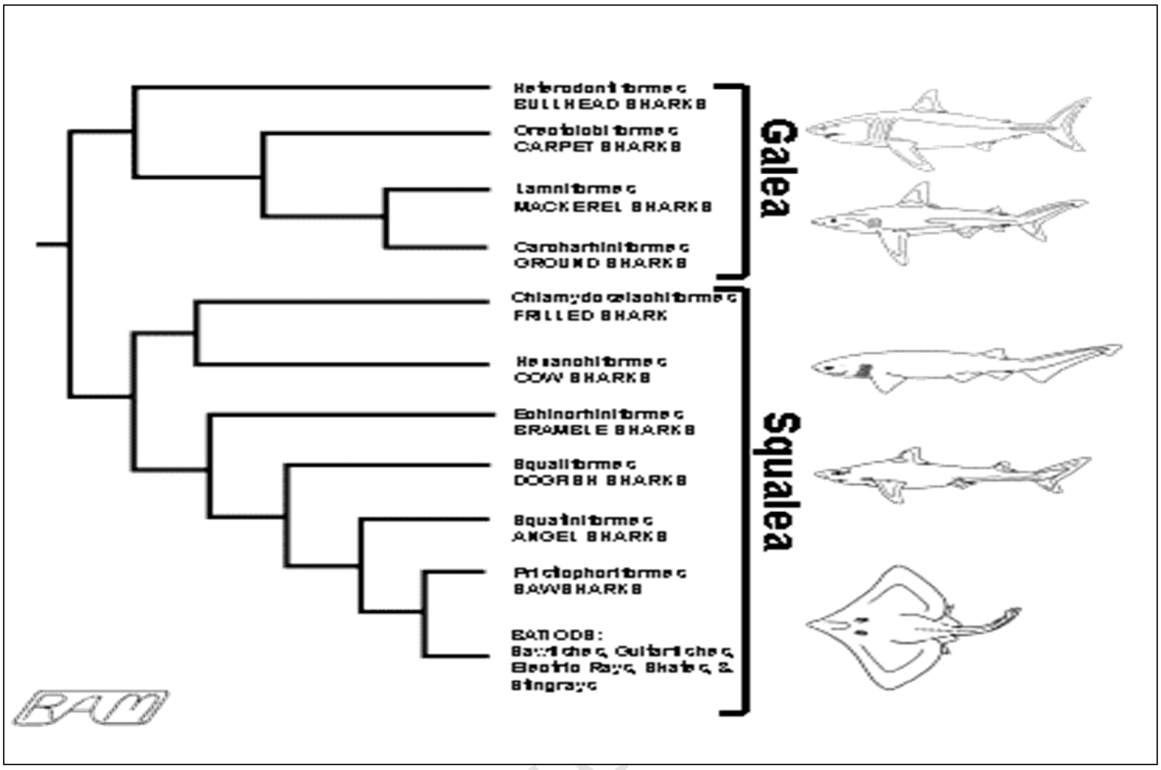

Figure 1.1: Galea and Squalea (Martin 2005.www.reefquest.org) Each bifurcating branch on a cladogram indicates an evolutionary split, or divergence, from a common ancestor.

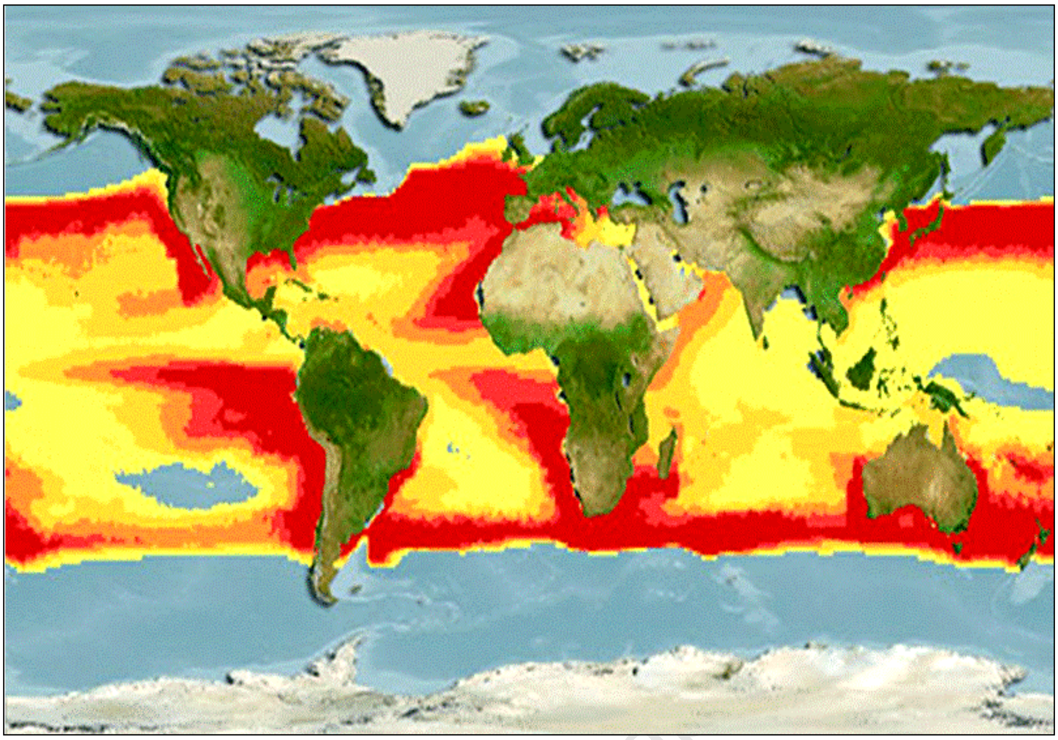

Figure 1.2: Aggregation sites and global distribution map for white sharks. Map sourced from OBIS Distribution map. Great white sharks, *Carcharodon carcharias.* www.marinebio.org

Figure 1.3: A white shark displaying hunting behaviour known as a 'breach' at Dyer Island, South Africa.

Figure 1.4; A breach in Shark Alley, Dyer Island (less than 5m deep) South Africa.

Figure 1.5: An industrial whaling station in Betty's Bay, Western Cape, South Africa, in operation from 1912–1930s.

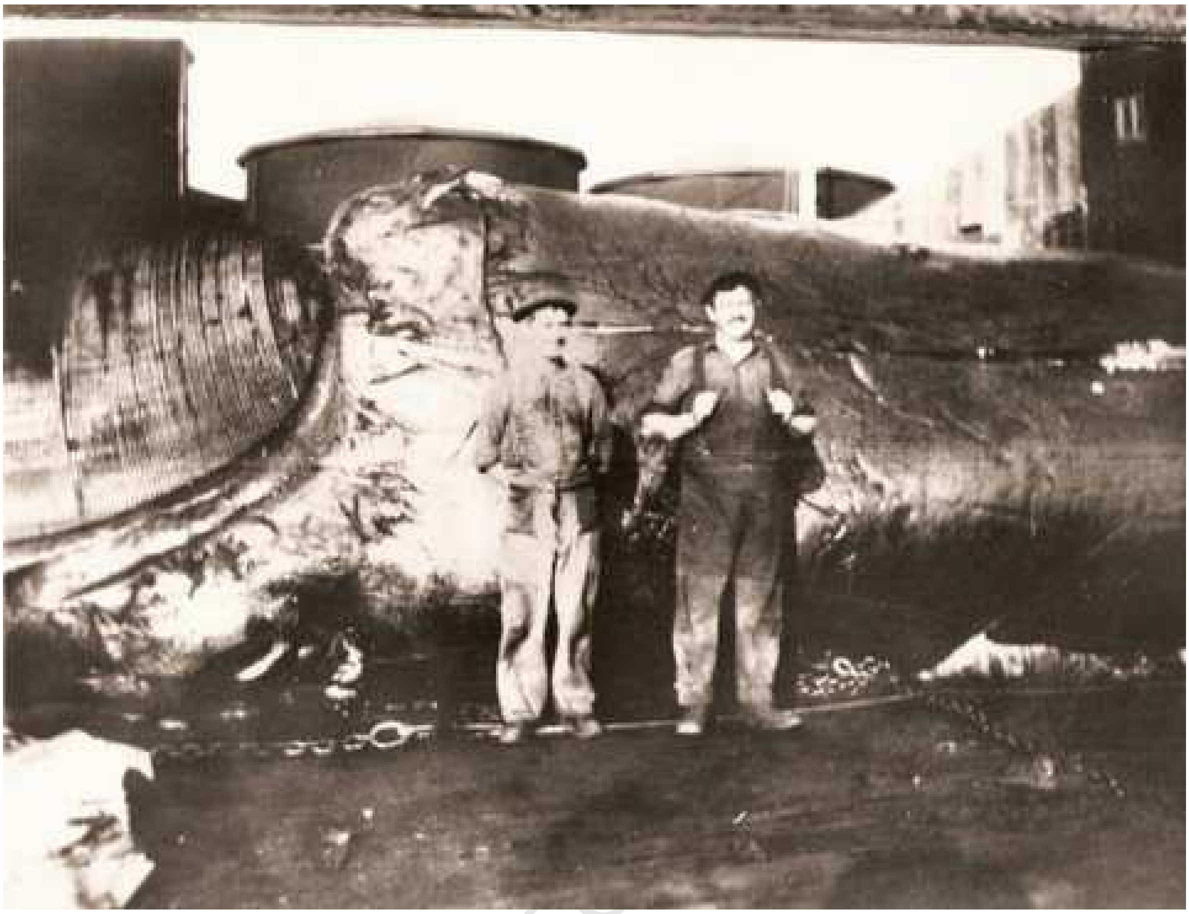

Figure 1 6: A whale carcass in Betty's Bay (pre 1930s). Large lunar bite marks are clearly visible (to the left of the workers) where large pieces of flesh have been removed from the carcass.

Figure 1.7: Record 5.9m (TL) white shark caught off Gansbaai in 1987. It was reported to weigh 1,24 Kilogramss excluding its stomach contents (Jan Fourie pers comm.). Photo credits: Johan Pieterse.

● VERVOLG OP BL. 2 ●

Haai laat vissers 3 uur spook

'n WITDOODHAAI van 5 m en sowat 1 250 kg het die bemanningslede van 'n visserskuit laat les opsê toe hy buite Gansbaai in hul lyne verstrengel geraak het.

Hulle was Vrydagoggend sowat 8 km van Danger Point af besig om vaalhaaie vir uitvoer te vang.

Die ses bemanningslede van die skuit Belinda K wou teen twaalfuur een van die lyne optrek, maar dit het vasgesteek. By nadere ondersoek het hulle vasgestel dat 'n haai met sy stert vassit in die lyn, met 'n breekkrag van 180 kg.

BENOUD

Mnr. Fanie Rautenbach van Gansbaai en eienaar van die skuit van 12 m, het gister vertel dat die bemanning geprobeer het om die haai op die skuit te trek. Die haai het egter geweldig gespook en die skuit aanhoudend met sy stert geslaan.

"Die manne was benoud. Hulle was bang dat hy die boot kon omslaan, maar gelukkig kon hy nie die skuit met sy kop bykom nie. Hy het te min krag in die stert gehad, anders was daar sekerlik probleme. Die skuit is gelukkig ook baie swaar."

Die bemanning kon eers ná 'n stryd van drie uur daarin slaag om die haai met die wen-as 'n ent uit die water te trek, 'n sterker tou om sy stert te bind en hom agter aan die skuit vas te maak.

SELDE

"By die kaai kon ons nie die haai met 'n bakkie uit die water trek nie omdat hy te swaar was en ons moes 'n hyskraan gebruik," het hy gesê.

Volgens hom word die witdoodhaaie nie dikwels in daardie omgewing aangetref nie en is dit baie selde dat mens hulle aan 'n hoek of in 'n net vang.

Die haai sal vandag na die museum in Kaapstad vervoer word, waar hy opgestop gaan word.

Foto: M.C. Botha

MNR. FANIE RAUTENBACH van Gansbaai hier op die rug van die groot witdoodhaai wat die bemanning van sy visserskuit Vrydag naby Danger Point gevang het. Hulle het drie uur gespook om die haai van 5 m lank en sowat 1 250 kg aan die skuit vas te bind sodat hulle hom na die Gansbaaise hawe kon sleep.

Figure 1.8: Record 5.9m (TL) white shark caught off Gansbaai in 1987. It was reported to weigh 1,245 Kilograms excluding its stomach contents (Jan Fourie pers comm.). Photo credits: Johan Pieterse.

Figure 1.9: A juvenile white shark fought for two hours by the angler and pulled onto the beach for a photograph in Mossel Bay, March 2012.

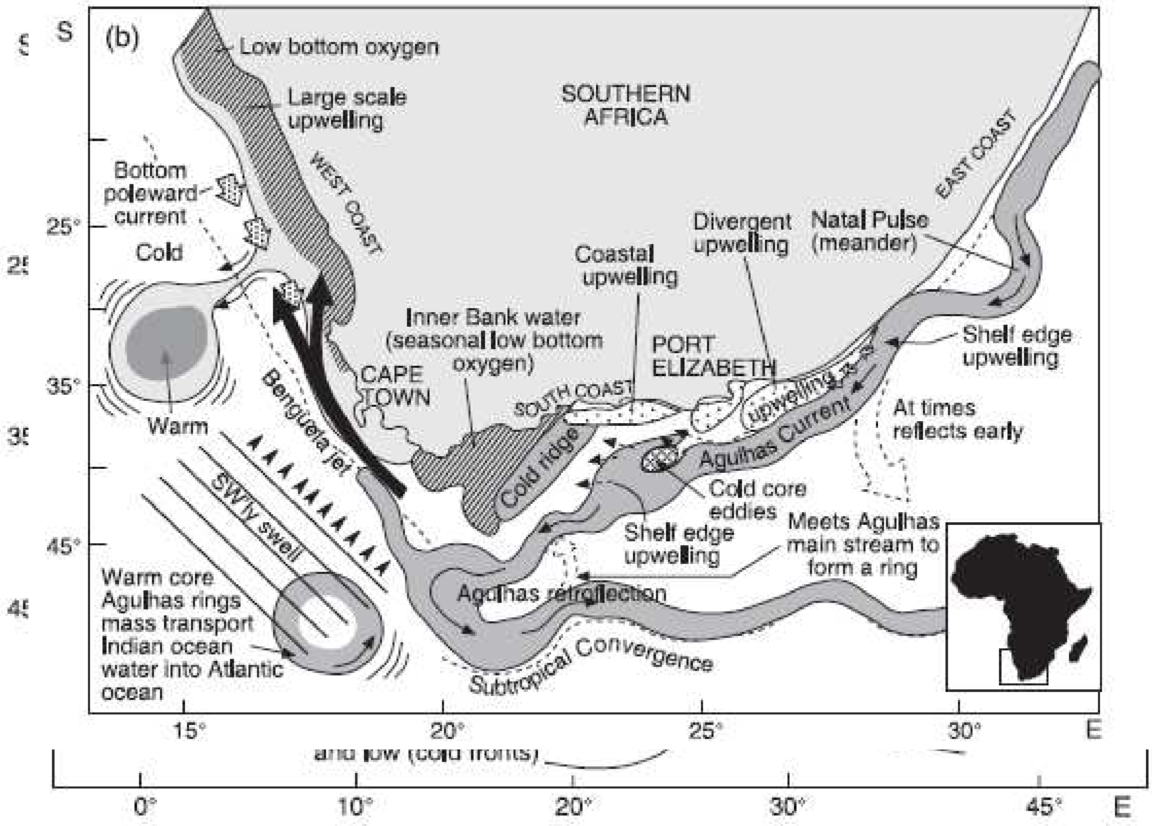

Figure 1.10: The complexity and variability of the marine environment around southern Africa is partly due to the latitude and associated weather. In summer, the oceanic high-pressure cells either side of southern Africa dominate the windfield, causing south-easterly winds on the west coast and north-easterly winds on the eastern Agulhas Bank and east coast. (Figure sourced from Roberts et al. 2005).

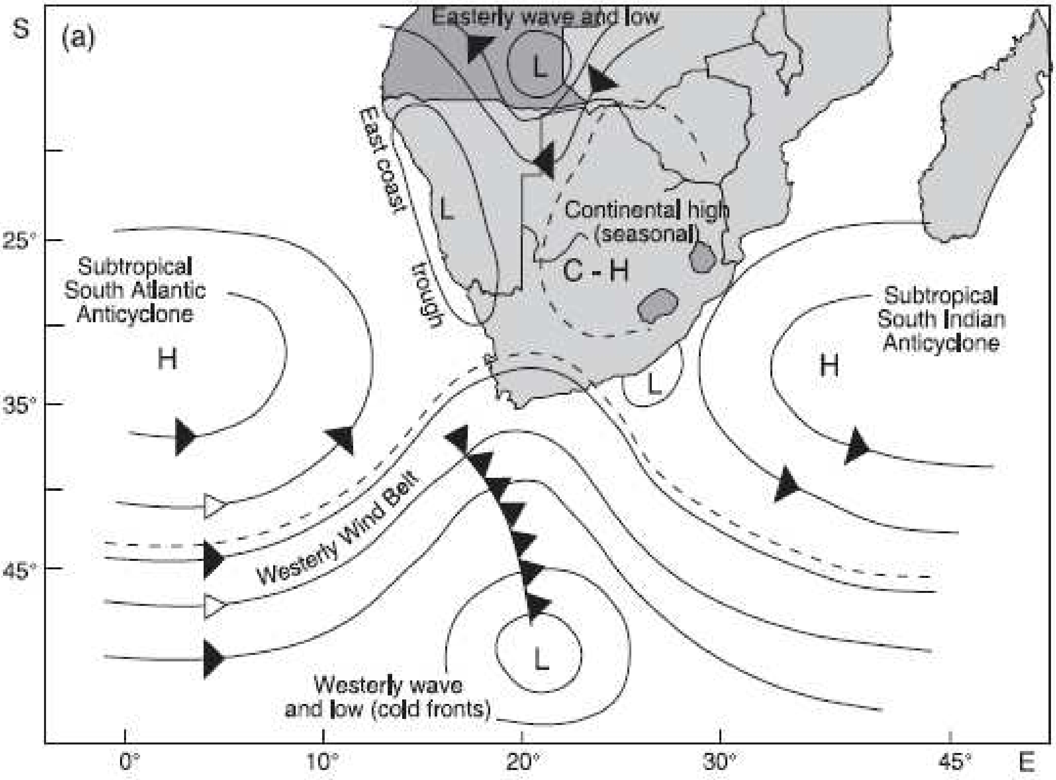

Figure 1.11: In winter, the westerly wind belt migrates north, moving cold fronts and strong westerly winds to southern Africa. The oceanography is dominated by the warm Agulhas and cold Benguela Upwelling System. These drive many of the physical processes and key features on the shelf .(Figures sourced from Roberts et al. 2005).

Figure 1.12: A white shark cage diving boat in Gansbaai with cage and baitline in view. (photo Marine Dynamics shark tours).

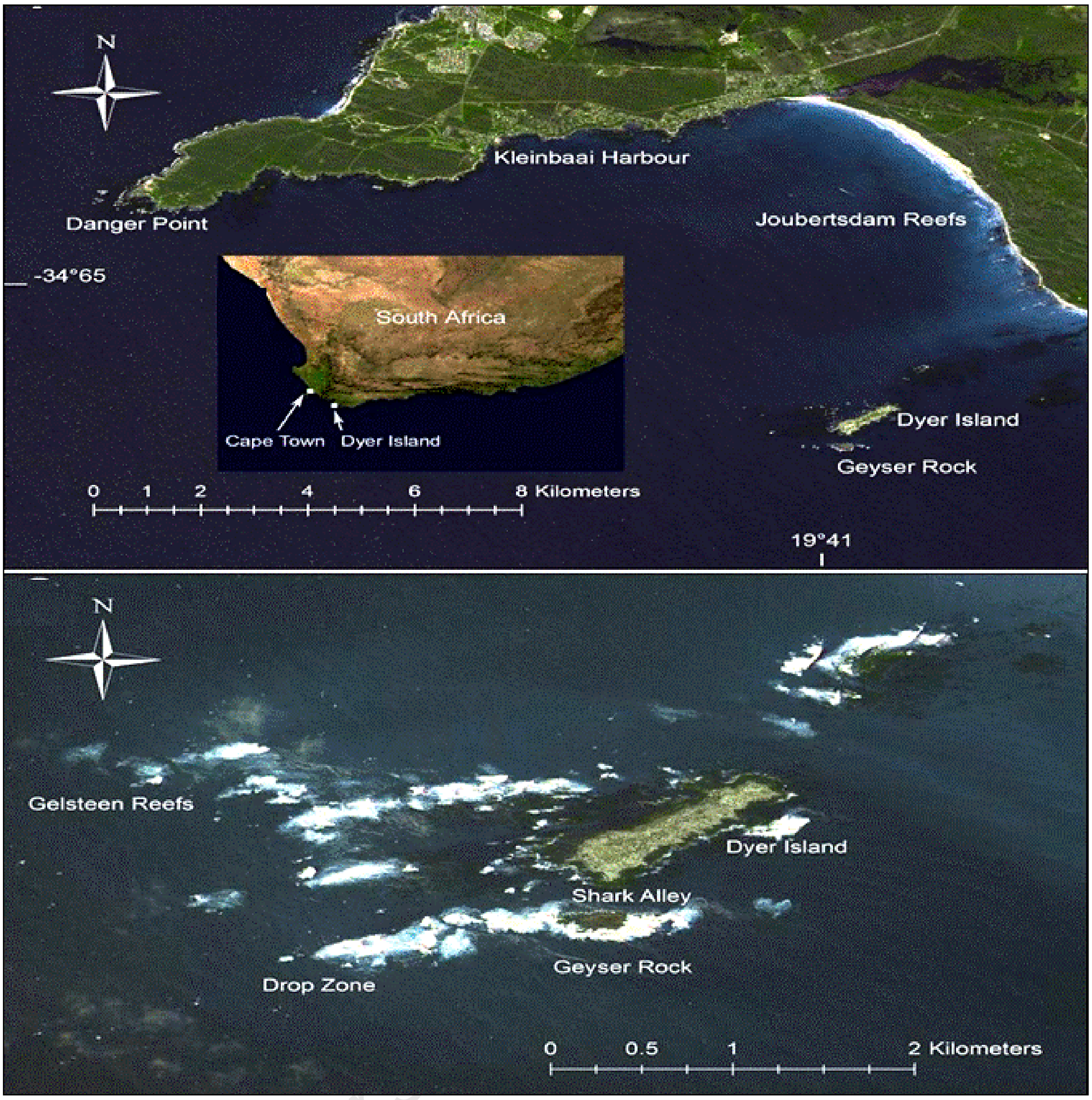

Figure **1.13**: Map of the Gansbaai (Gans Bay) region showing the inshore white shark habitat of Joubertsdam Reefs. Dyer Island is situated approximately 9km from the nearest harbour (Kleinbaai) and 4 km from the nearest shore. Illustration credits: Oliver Jewell.

Table 1 1: Pregnant female and embryonic white sharks

No.	*Date*	*Location*	*Female TL (m)*	*Embryo Observed (N)*	*Embryo TL (cm)*	**Reference**
1	Summer 1934	Alexandria, Egypt	4.3	9	61	Norman and Fraser (1937)
2					20-61.6	Bigelow & Schroeder (1948)
3	November 17, 1981 November 26, 1982 November 26, 1982	Queensland, Australia	3.20 4.00 4.20	4 11 14		Paterson (1986); J. D. Stevens (pers. comm.)
4	February 16, 1985 April 2, 1986	Kin, Okinawa, Japan Taiji, Wakayama, Japan	5.55 •4.70	0[1] 7	•100-110	Uchida et al. (1987); Ellis and McCosker (1991)
5	February-March 1988	Taiwan		3	•100	D. A. Ebert (pers. comm.)
6	October-November	South Australia	•4.20 •4.70 •5.20	11 13 6-7	•60 •5 •30	Bruce (1992)
7	November 13, 1991	North Cape, New Zealand	•5.36	7	143 145	This study
8	May 14, 1992 May 22, 1992	Uchinoura, Japan Toyo-cho, Kochi, Japan	4.80 5.15	5 10	130 135 151	Uchida et al. (Chapter 14)
9	September 1992	Cape Bon, Tunisia	•5.30	2		Fergusson (Chapter 30)
10	March 1994	South Australia		2[2]	127	J. D. Stevens (pers. comm.)
11	Summer 1996 1998	Malindi, Kenya Madagascar	6.0 Unk	•7 Unk	•1.0 Unk	Cliff et al. (2000)

TL, Total length; •, estimated length.

[1] Numerous ova were present in the uteri, but no embryos were visible.

[2] Two aborted embryos were taken from a litter of unknown size.

Source: Francis (1996)

Table 1.2: Recent life history stage definitions of white sharks.

Life-History Stage Definitions of white sharks

1. **Young-of-the-year (YOY)** sharks (• 1.75 m total length): Based on the size of full-term pups, the smallest free-swimming white sharks, and estimated growth rates from the literature (Cailliet et al. 1985; Francis 1996; Wintner and Cliff 1999; Malcolm et al. 2001), we define white sharks in their first year, young of the year, to be • 1.75 m TL.
2. **Juvenile White Sharks (JWS)** (> 1.75-3.0 m TL): Juvenile white sharks are those with sizes greater than YOY sharks but prior to the smallest sizes commonly observed visiting pinniped colonies (>3.0 m). At these sizes, sharks feed primarily on teleosts and other elasmobranchs (Malcolm et al. 2001).
3. **Subadult sharks** (>3.0-3.6 m TL for males and >3.0-4.8 m TL for females). Male and female white sharks mature to different sizes (Francis 1996; Pratt 1996). Subadult sharks are those between the size when first visiting pinniped colonies and the size on reaching maturity. Arrival at pinniped colonies defines a new predatory regime and ensuing predatory strategies in white sharks via the addition of marine mammal to their fish diet (Martin et al. 2005). The smallest size commonly observed at Australian pinniped colonies is 3.0 m (Bruce et al. 2006).
4. **Adult sharks** (>3.6 m TL for males and >4.8 m TL for females). Adult white sharks are those that have reached sexual maturity as defined by Pratt (1996) and Francis (1996). We use 4.8 m for maturity in females based on data for Australian sharks from Bruce (1992) and Malcolm et al. (2001).

Unless otherwise stated, all lengths refer to TL as defined by Mollet and Cailliet (1996). Other length measurements (e.g., fork length) have been converted to TL for comparison using equations derived by these authors.

Source: Bruce and Bradford (2012).

Chapter 2

Size and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai

Photo: Harry Stone

Chapter 2

Introduction.

White sharks *Carcharodon carcharias* undertake extensive oceanic migrations, yet they exhibit site fidelity to predictable coastal locations (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007a; Domeier and Nasby-Lucas 2008). Similar behaviour has been described in the Indian Ocean with extensive coastal migrations and site fidelity to Gansbaai (Bonfil et al. 2005). Furthermore, a return ocean basin crossing between South Africa and Australia has been recorded (Bonfil et al. 2005). Gansbaai (Gans Bay) is one of several seasonal aggregation sites along the South African coast, with others including False Bay, Struis Bay and Mossel Bay in the Western Cape and Algoa Bay in the Eastern Cape (Marks et al. 1997; Ferreira and Ferreira 1996; Kock and Johnson 2006) The Gansbaai white shark aggregation site became a focus for the ecotourism industry of shark cage diving during the 1990s (Maharaj et al. 2003).

The small coastal town of Kleinbaai, where tour boats launch to gain access to Gansbaai, is located approximately 80 km south east of Cape Point. Geyser Rock is a small offshore island 9 km southeast of Kleinbaai and hosts a resident population of Cape fur seals *Arctocephalus pusillus pusillus* of c. 55,000 individuals (Department of Environmental Affairs unpubl. data). Dyer Island lies north of Geyser Rock and is a provincial nature reserve which measures approximately 1.5 km long and 0.5 km wide (Ferreira and Ferreira 1996). It is inhabited by various breeding seabird species, including 950 breeding pairs of the "Endangered" African penguin *Spheniscus demersus* (CapeNature unpubl. data). The two islands are separated by a shallow channel, known locally as Shark Alley, which is c. 190 m in width at its widest point and 7 m deep. Both islands are surrounded by dense forests of kelp (predominantly *Ecklonia maxima* and *Laminaria pallida*). The Uilkraals River estuary enters the northeastern part of the bay and a 4.3 km stretch of sand and then a gravel beach extends eastward from the mouth (Figure 2.1).

Initial research in this area focused on predator-prey interactions between Cape fur seals and cormorants (Marks et al. 1997). A preliminary investigation of the sharks in the area revealed that white sharks aggregated around Dyer Island area throughout the year with the number of individuals present fluctuating over short time periods, often less than a month (Ferreira and Ferreira 1996; R. Johnson Oceans Research pers. comm.). Prior to the present study, it was concluded from using boat based sightings that 'medium sized' female white sharks measuring between 2–3.5 m are the most frequently observed size and sex class in Gansbaai (Ferreira and Ferreira 1996).. Typically male sharks of a similar size are seen off Dyer Island (R. Johnson, Oceans Research pers. comm.).

This chapter presents information collected on trends and seasonality in the numbers of white shark sightings made over a five-year period from 2007–2011 in Gansbaai from a shark cage diving boat. This type of study is important in order to better understand how many and at what times of year white sharks frequent South Africa's coastal areas, to maintain a balance between bather safety and protection of this endangered species. This chapter investigates trends in the size distribution and sex ratio of animals at this aggregation site. Size and sex segregation occurs in most elasmobranch species (Sims et al. 2001). Identifying patterns of sex segregation in white sharks is important to further the understanding of use of favoured areas by both sexes. Furthermore, sexual segregation enhances a species vulnerability to fisheries as segments of breeding stocks can be removed at once (Domeier and Nasby-Lucas 2012).

Materials and Methods

Shark cage diving operations take place consistently throughout the year at Gansbaai on all days when sea conditions are suitable (Chapter 1). This creates a platform from which non-invasive scientific observations of individual white sharks can be made in a consistent manner. During this study, observations were obtained from a 10.8 m long catamaran, with a 3.5 m long dive cage, from 2007 to September 2010. After this a 12 m catamaran with a 4.0 m long dive cage was used. Log sheets recording data on individual sharks and environmental parameters were completed during every outing.

Total length, from the snout tip to caudal fin tip of the shark, was estimated to 0.1 m as individuals swam past the dive cage, which was of known length (Figure 2.2). Digital video footage was recorded from on board the catamaran on every trip using a Panasonic HD video camera. In addition, when water visibility permitted, the camera would be placed in a custom-built housing and sharks were filmed underwater. Male sharks were distinguished from females only if the presence of claspers was clearly visible. Given the challenges of poor visibility and small shark size, if gender could not be confirmed, the shark was logged as being of unknown sex. Determining the sex of juvenile sharks is difficult as noted by Kabaskal et al. (2007)

Boat-based observations were made over a 59-month period. Data collection began on the 30 January 2007 and, for the purposes of this chapter, ended on the 31 December 2011; a total 1,606 trips were made, about 6,400 hours of observation. The Dyer Island

Conservation Trust intends to continue these shark observations into the future to develop a long-term data set.

Size distribution and sex ratios of sharks over time were estimated based on pooled size and sex data per day. Recounting of individuals on a single day was avoided where possible because individuals were distinguished by characteristic features of the dorsal fins and body patterning (Domeier and Nasby-Lucas 2007; Chapple et al. 2011). However on days where underwater visibility was poor (<2 m), recounting of individuals was possible and probably occurred to some extent. Furthermore, tracking of sharks using ultrasonic tracking methods shows that individual sharks may be in the same location as cage diving boats but not respond to the chum trail and consequently would not have been seen from the vessel (unpubl. data). Therefore the numbers of sharks recorded do not reflect absolute numbers.

I grouped the data into four seasons per year: December–February (Summer), March–May (Autumn), June–August (Winter) and September–November (Spring). These austral seasons related to observed patterns of shark behaviour (Chapter 1). This grouping generated 21 seasons: Season 1 consisted of January and February 2007, and then groups of three months per season, until Season 21 which consisted of the data for December 2011. I tabulated the lengths of all sharks, and male and female sharks by season. Environmental parameters that may influence shark behaviour are investigated in Chapter 3.

Correspondence analysis (Greenacre 1984) was used to display the patterns within the 21×4 matrices of counts of the four size classes over the 21 seasons. The size classes were 1= <2.0 m 2= 2–2.5 m, 3= 2.5–3.5 m, 4= >3.5 m. I investigated changes in size and sexual composition of sharks over time. Correspondence analysis and plots (Greenacre 1984) are used to facilitate visualisation of trends over time. All calculations were undertaken using Genstat Release 13.3 (VSN International 2010). Summarised mean lengths of great white sharks are displayed in Figure 2.6..

Results

The total number of shark sightings for which length estimates were available was 10263; many individuals would have been recorded several times during the five-year study period. The mean lengths for the males (n=1929) and females (n=3671) were 2.91 m and 2.89 m, respectively (Table 2.1). The overall mean length of all 10263 sharks was 2.78 m, with a range between 1.5 m and 5.0 m (Table 2.2).

In the 21 quarters into which the study period was divided, the sample size (i.e. the number of sharks for which length had been estimated) ranged from 119 sharks in Quarter 1, to 955 sharks in Quarter 11 (January 2007–December 2011) (Table 2.3). The second smallest sample was 212 in Quarter 10 (March–May 2009). Thus the sample sizes on which to base the following assessments are adequate.

A chi-squared test for no differences in proportions of sharks in each size class in each quarter was rejected (χ^2 = 3402, df=60, P<0.0001). During the study period there was a shift in size distribution away from the smallest size class (<2.0 m) towards the largest size class (>3.5 m) (Table 2.4). In Quarters 1 to 4 (January 2007–November 2007) of the study period, the percentage of sharks in the smallest size class exceeded 24.5% in each quarter; values as high as this high were never recorded subsequently and in the final 11 quarters (May 2009–December 2011) of the study period, this percentage exceeded 10% in only two quarters (Quarters 13 and 21, December 2009–February 2010 and December 2011) (Table 2.1). The minimum value was 0.5% (based on a sample of 820 sharks) near the end of the study period, in Quarter 18 (March–May 2011). The mean of the quarterly percentages of sharks in the smallest size class was 11.1% (Table 2.4).

The mean of the quarterly percentages of sharks in the largest size class was 15.1%. In Quarter 1 to Quarter 15 (January 2007–August 2010), the percentage of sharks in this largest size class was always below this mean value; in all except one of the subsequent six quarters it was above this mean, and reached a maximum value of 49.6% in Quarter 18 (March–May 2011) (Table 2.4).

This pattern was consistent for both females (Table 2.5) and for males (Table 2.6). The chi-squared tests for no differences in proportions were rejected (females – $\chi^2 = 1814$, df=60, P<0.0001; males – $\chi^2 = 887$, df=60, P<0.0001). For the females, the mean of the quarterly percentages in the smallest size class (<2.0m) was 37.5% (Table 2.5). For the first 10 quarters of the study period (January 2007–May 2009), the percentages of female sharks was above this value in all except Quarter 8, and was below this value for the final 11 quarters (January 2009–December 2011). The largest percentages in the <2.0 m class were in the first two quarters, when 7.7% and 35.8% of female sharks were in the smallest size category (Table 2.5). In the largest size class (>3.5m), the mean of the quarterly percentages was 20.4. This value was never reached prior to Quarter 15

(June–August 2010); during this earlier period the percentage of female sharks in the largest size class ranged from 0% to 17.7%.

For the final six quarters (September 2010–December 2011), the percentage of female sharks in the >3.5m size class was always above the mean of 20.4%, and ranged from 25.9% to 62.5% (Table 2.3). For females, there were interesting patterns for the two intermediate size classes (Table 2.5). For the second size class (2.0–2.75 m), percentages were generally increasing from Quarter 1 to Quarter 8, January 2007–November 2008 (smallest value of 29.2% in Quarter 1 and largest value of 47.6% in Quarter 6 January––March 2009), peaked in Quarters 9–12 December 2009–November 2010 (64. 1%, 58. 5%, 73. 1% and 59. 6%), and then decreased to values between 18.9% and 30.0% in Quarters 14–17 March 2010–February 2011and between 5.3% and 24.1% in the final four quarters (Quarters 18–21) March 2011–February 2012 (Table 2.5). The pattern for the third size class (2.75–3.5 m); the average of the quarterly percentages was 32. 6%. This value was exceeded in only three of the first 10 quarters (January 2007–May 2009), but exceeded in all except one of the final 11 quarters (June–August 2009), with a peak value of 64.5% in Quarter 14 (March–May 2010) (Table 2.5).

The pattern for males was similar to that for females (Table 2.6). There were generally decreasing percentages in the smallest size class (<2.0 m); the mean percentage for this size class was 6.0%; and was never exceeded in Quarters 11–21 June 2009–February 2012. In the 2.0–2.75 m size-class, there is an increase to maximum values of 70.9% (Quarter 11, March–May 2009) and 87.9% (Quarter 12, June–August 2009) followed by a decrease (between 8.5% and 22.3% in Quarters 17–21, January 2011–December 2011,the final five quarters) (Table 2.6). The third size class (2.75–3.5 m) had no distinct pattern, however, the most striking result of all for males was the discontinuity in the largest size class between Quarter 16 and Quarter 17 (September 2010–December 2011); in the first 16 quarters (January 2007–November 2010), the percentage of male sharks in this size class averaged 4.7% but after this, for the final five quarters (January 2011–December 2012) it averaged 38.9% (Table 2.6).

These patterns are also shown by the correspondence analyses (Figures 2.3–2.5). In the correspondence analysis for the count data that underlies Table 2.2, the first axis accounted for 73.7% of the inertia, and the second axis 18.2%, so that together they accounted for 91.9% of the inertia. In broad brush terms, this means that 91.9% of the information in the Table 2.2 is captured in Figure 2.3. Quarters 1–15 are to the left of the x-axis, and are associated with smaller size classes. Quarters 16 to 19 are successively farther to right, drawn in the direction of the largest size class. Subsequent Quarters drift back to left, a consequence of the smaller proportion of sharks in the largest size class during this period. The correspondence analysis for females (Figures 2.4) and males (Figure 2.5) explained 86.8% and 87.0% of the inertia associated with the data matrices of Table 2.5 (females) and Table 2.6 (males). The patterns of the points that represent the Quarters in these two figures confirm the results presented above.

Discussion

This is the first long-term data set on size frequency of white sharks, from a single site from South African waters. The changes in the relative abundance of the four size classes, by sex and between seasons, suggested that the white sharks are not resident for long periods, but that different size classes use the bay at different times, suggesting that there is movement into and out of the bay. This is supported by studies elsewhere of satellite tagged animals which has revealed favoured areas of the coast that are frequented by juvenile and subadult sharks, and that they move between these 'hotspots' (Klimley et al. 2002; Dewar et al. 2004; Weng et al. 2007b; Bruce and Bradford 2012). Two previous studies at Gansbaai have also illustrated movement from and return to this study site (Bonfil et al. 2005; Towner et al. 2012).

There was a statistically significant change of size distribution over the five year period for both male and female sharks. Most noticeably, 2007–2008 and 2009 saw a higher ratio of smaller sharks for both sexes. In contrast, the two larger size classes of sharks were more dominant in sighting data in 2010 and even more so in 2011.The trend of larger sizes being recorded later in the study could infer a change in the cohorts visiting the bay or individual growth of the same individuals exhibiting site fidelity. Although investigation of individual growth using fin and body patterns is beyond the scope of this thesis, individuals are re-sighted over multiple years (Towner et al. 2012), and growth of these individuals will be investigated in detail elsewhere.

The individual growth trend described in this study could reflect higher survival rate of white sharks brought about by a reduction in fishing pressure on the species in the past two decades. Legislation to protect white sharks from exploitation off the South African coast was introduced in 1991 (Compagno 1991; Chapter 1). Prior to this protection, known sources of mortality for white sharks in South African waters have included commercial fishing gears and fishing pressure for jaws fins and teeth by recreational and commercial fishermen (Compagno et al. 1997; Dudley 2012). In the Western Cape, 20 white sharks were killed between 1974–2006 in a False Bay inshore seine net fishery (Lamberth 2006) and 73 white sharks were the only reported specimens of ‘many’ rumoured to have been caught and killed by fishermen between Mossel Bay, Gansbaai and Langebaan Lagoon during the 1970s (Wallet 1978; Dudley 2012; D. Schoemann pers. comm.; C. Ferreira and T. Ferreira pers. comm.).

Mortalities off KwaZulu-Natal are considerably higher than in other regions along the South African coastline. In 1952, protective shark gill nets were introduced along the Durban coastline on the east coast of South Africa. With a rapid expansion of netted areas between 1966–72, a significant decline in white shark catch rate occurred, with 591 mortalities between 1974–1988 (Cliff et al. 1989) and with annual catches of 22–61 white sharks (Cliff et al. 1996a). However, between 1978 and 2003 this decline stabilised but was still estimated to be 36 per year with a decrease in length of females established (Dudley and Simpfendorfer 2006). Since 2007 the netted regions in KwaZulu-Natal have been significantly reduced, with some gill nets being replaced by more selective drumlines which target fewer sharks overall – although both (therefore mixed) fishing methods are still employed at some localities (Cliff and Dudley 2011).

A reduction in fishing mortality partially as a result of the protection of white sharks may explain the increased survival and progressive growth of cohorts of sharks showing fidelity to Gansbaai shown in this study. The increase in size shown here contrasts with the decline in size reported from the KwaZulu-Natal data set (Dudley and Simpfendorfer 2006), but may be a result of different movement patterns of parts of the population, but this deserves more investigation.

Long term monitoring of white sharks at the Neptune Islands in Australia (from cage diving logbook data) between 1999–2011 demonstrated that shark numbers vary with season, and between years (Bruce and Bradford 2011; Robbins and Booth 2012). Interannual variation (which is investigated in Chapter 3) makes it difficult to determine population level changes (Bruce and Bradford 2012). We now know that juvenile white sharks show strong site fidelity to particular beach areas (Weng et al. 2007b; Bruce and Bradford 2012) and hence it may be possible that white sharks returning to Gansbaai are increasing in length over the years.

An alternative explanation for the higher ratio of large sharks over the study period may be that smaller sharks move into nursery areas once large sharks have departed, to reduce competition for resources (Malcolm et al. 2001). Smaller sharks may have been more prevalent in 2007–09 because there were fewer large sharks in the area.

Furthermore, the period 2007–09 may have been more favourable for juvenile white sharks to return to Gansbaai because environmental conditions were favourable for their physiology. Seasonal variations in sea-surface temperature appear to play a role in the abundance and movements of white sharks (Robbins and Booth 2012). This will be addressed in Chapter 3 where a number of environmental factors will be investigated in relation to the presence and size of sharks in Gansbaai Between 2010–11 there was a large change in conditions due to a strong La Nina event (Wolter and Timlin 2011).

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Figures and Tables

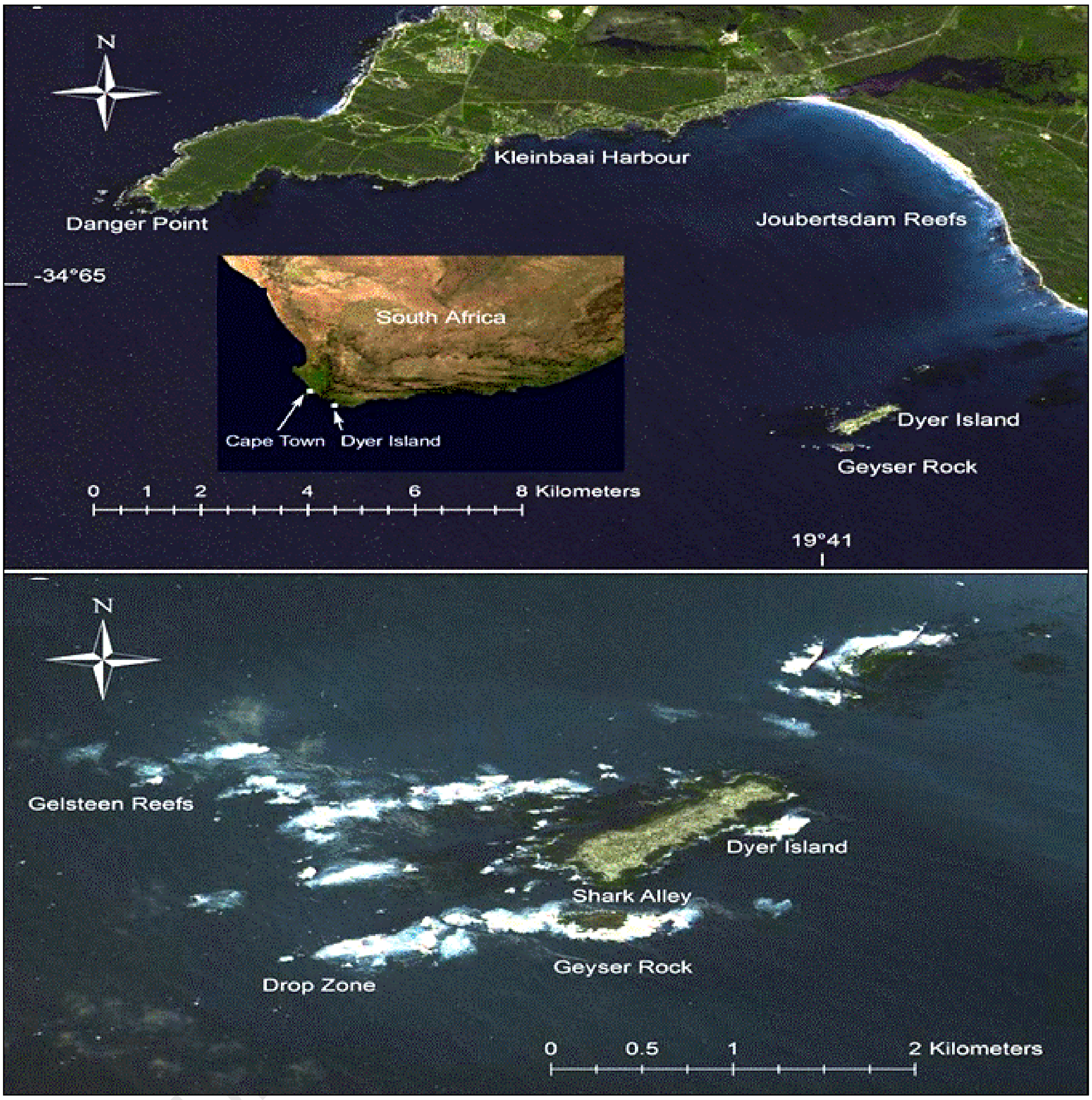

Figure 2.1: Map of the Gansbaai (Gans Bay) region showing the inshore white shark habitat of Joubertsdam Reefs. Dyer Island is situated approximately 9km from the nearest harbour (Kleinbaai) and 4km from the nearest shore.

Figure 2.2: Example of size estimation using a dive cage of known 3.5 and then 4m length. Total length (snout tip to upper caudal lobe tip) of white shark was estimated as it swam by the cage. (Photo Oliver Jewell, Marine Dynamics)

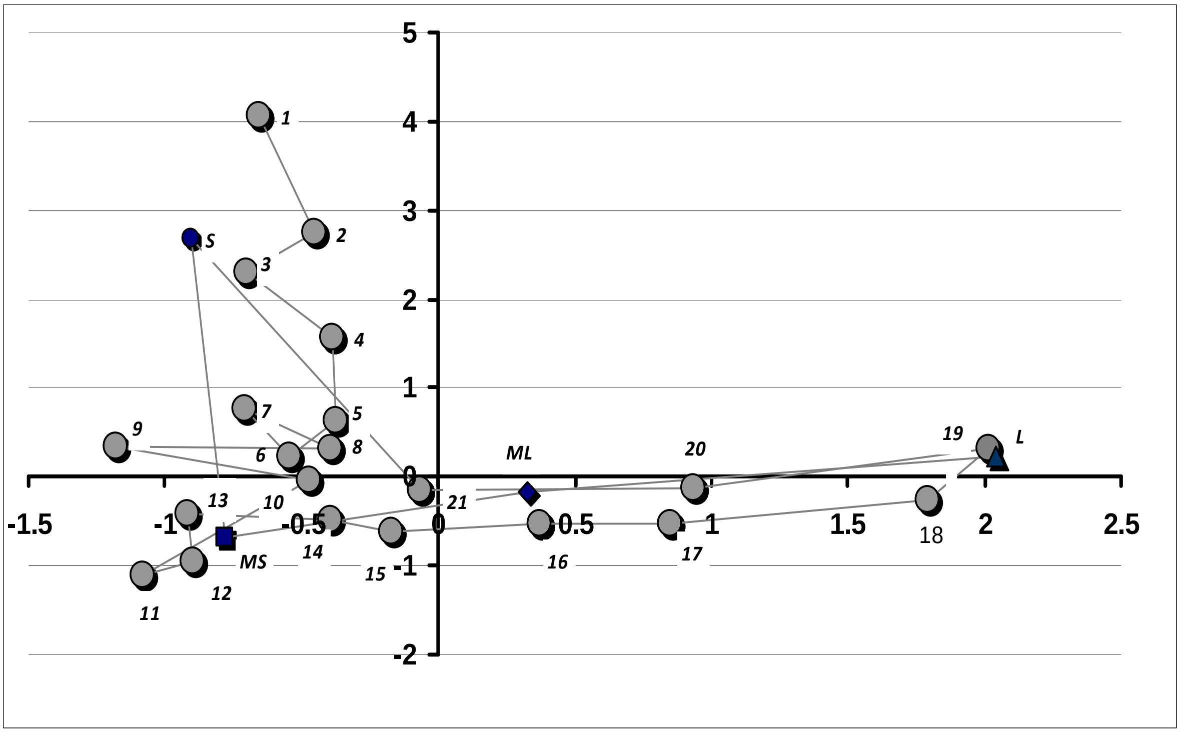

Figure 2.3: Correspondence analysis plot of all shark lengths for both sexes in Gansbaai 2007-2011. L= large (>3,5m TL) ML= Medium large (2.75-3.5m TL) MS= Medium/Small (2.0-2.75m TL) and S=small (<2.0m TL) The labels 1–21 represent quarterly periods of the year from January 2007–January 2012, defined in Table 2.4. The horizontal and vertical axes represent the first and second principal axes of the correspondence analysis and are dimensionless.

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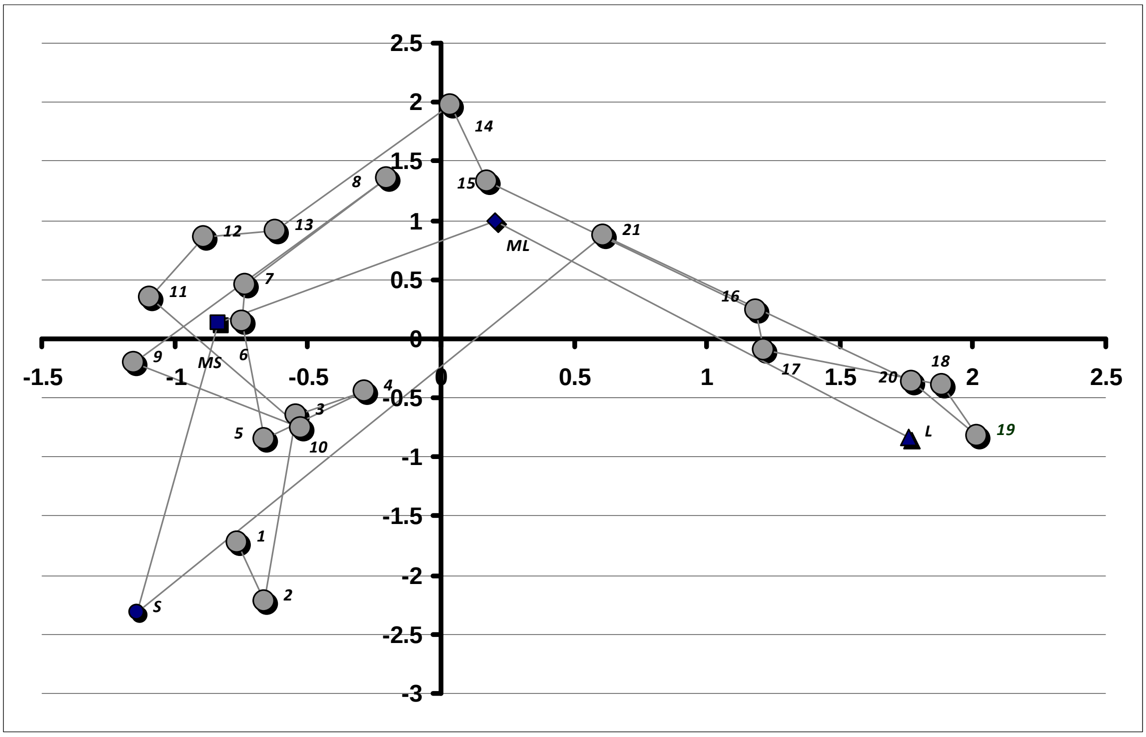

Figure 2.4: Correspondence analysis plot of all shark lengths for female white sharks in Gansbaai 2007-2011. L= large (>3,5m TL) ML= Medium large (2.75-3.5m TL) MS= Medium/Small (2.0-2.75m TL) and S=small (<2.0m TL). The labels 1–21 represent quarterly periods of the year from January 2007–January 2012, defined in Table 2.4. The horizontal and vertical axes represent the first and second principal axes of the correspondence analysis and are dimensionless.

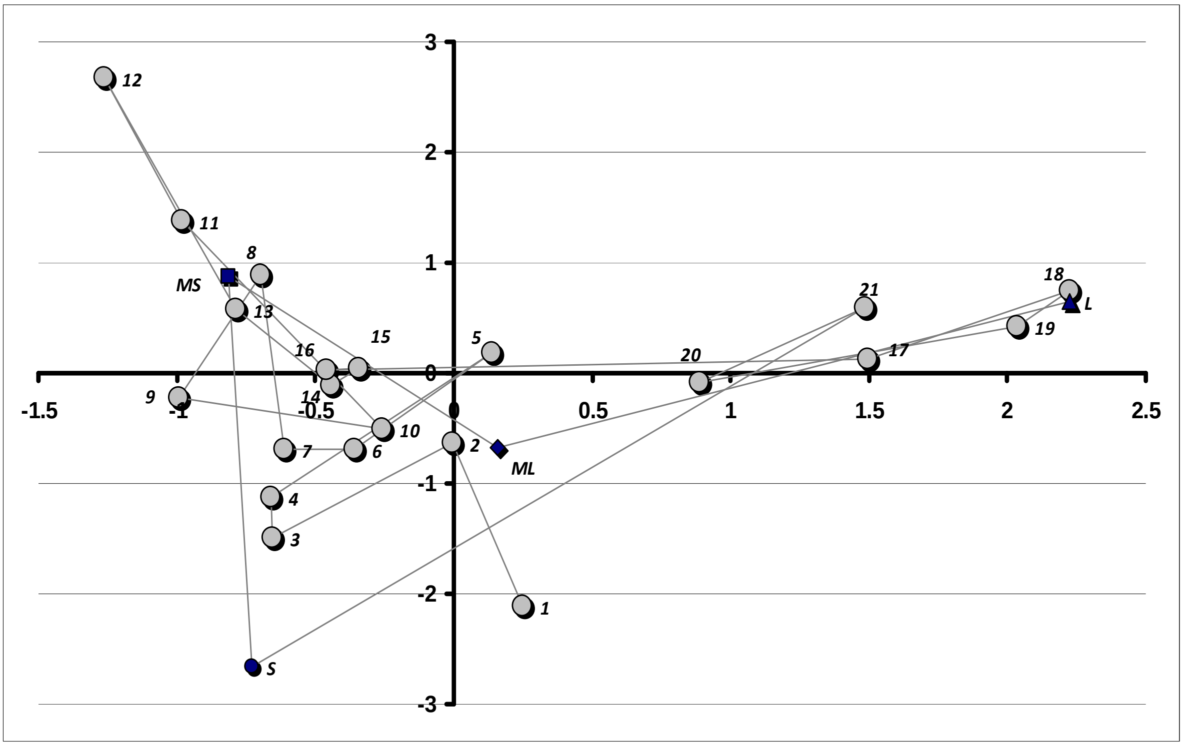

Figure 2.5: Correspondence analysis plot of all shark lengths for male white sharks in Gansbaai 2007-2011. L= large (>3,5m TL) ML= Medium large (2.75-3.5m TL) MS= Medium/Small (2.0-2.75m TL) and S=small (<2.0m TL). The labels 1–21 represent quarterly periods of the year from January 2007–January 2012, defined in Table 2.4. The horizontal and vertical axes represent the first and second principal axes of the correspondence analysis and are dimensionless.

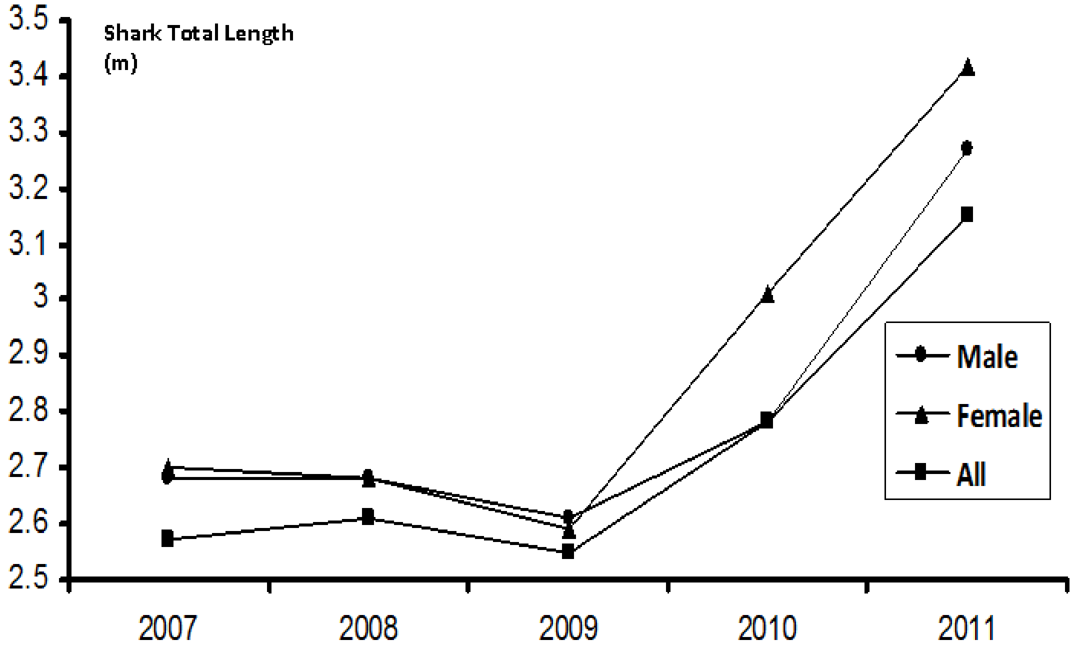

Figure 2.6: Annual mean lengths (m) of white sharks in Gansbaai, 2007–2011

Table 2.1: Overall summary statistics of the total lengths (m) of white sharks in Gansbaai, January 2007–December 2011.

	n	Mean	SD	Min	Lower quartile	Median	Upper quartile	Maximum
Males	1929	2.91	0.50	1.5	2.5	2.8	3.2	4.8
Females	3671	2.89	0.56	1.6	2.5	2.8	3.2	4.5
unsexed	4663	2.65	0.52	1.5	2.3	2.6	3	5
All	10263	2.78	0.55	1.5	2.5	2.7	3	5

Table 2.2: Annual summary statistics for lengths (m) of white sharks for males, females and all sharks in Gansbaai, 2007–2011.

	Male			**Female**			**All**		
Year	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**
2007	2.68	0.50	248	2.70	0.52	429	2.57	0.56	1258
2008	2.68	0.38	269	2.68	0.43	516	2.61	0.46	1332
2009	2.61	0.29	270	2.59	0.38	1225	2.55	0.37	2368
2010	2.78	0.35	446	3.01	0.49	625	2.78	0.48	2396
2011	3.27	0.47	696	3.42	0.49	876	3.15	0.55	2909
Overall	2.91	0.50	1929	2.89	0.56	3671	2.78	0.55	10263

Table 2.3: Quaterly summary statistics for lengths (m) of white sharks for males, females and all sharks in Gansbaai, 2007–2011.

	Male			***Female***			***All***		
Quarter	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**
1	2.9	0.37	23	2.59	0.57	22	2.44	0.61	119
2	2.75	0.6	83	2.62	0.64	78	2.57	0.64	305
3	2.57	0.43	98	2.7	0.53	60	2.53	0.54	290
4	2.62	0.42	36	2.75	0.49	234	2.61	0.53	481
5	2.89	0.34	39	2.66	0.5	160	2.66	0.53	271
6	2.72	0.37	87	2.64	0.43	104	2.62	0.46	289
7	2.6	0.39	114	2.61	0.37	98	2.55	0.41	324
8	2.64	0.35	30	2.79	0.37	164	2.65	0.45	383
9	2.56	0.34	27	2.45	0.35	102	2.45	0.37	301
10	2.76	0.34	34	2.72	0.65	130	2.66	0.58	212
11	2.62	0.28	175	2.54	0.34	542	2.53	0.34	955
12	2.54	0.18	33	2.62	0.33	425	2.58	0.33	802
13	2.68	0.29	57	2.72	0.36	149	2.57	0.38	567
14	2.76	0.34	135	2.95	0.36	124	2.72	0.4	605
15	2.78	0.36	152	2.96	0.46	230	2.78	0.45	732
16	2.77	0.36	79	3.24	0.48	102	2.91	0.53	472
17	3.2	0.42	138	3.23	0.55	106	3.02	0.49	573
18	3.4	0.42	223	3.48	0.46	282	3.29	0.49	820
19	3.36	0.52	141	3.49	0.49	331	3.32	0.58	724
20	3.08	0.48	193	3.39	0.47	170	3.04	0.55	807
21	3.17	0.44	32	3.07	0.47	58	2.74	0.51	231

Table 2.4: Percentages in each of four size classes of white sharks (all sharks) sighted in Gansbaai 2007–2011. Size class 1 = <2.0 m, Size class 2 = 2–2.75 m, Size class 3 = 2.75–3.5 m, Size class 4 = >3.5 m

	Quarter	***<2.0m***	***2.0-2.75m***	***2.75-3.5m***	***>3.5m***	**Count**
2007	1	43.7	19.3	31.1	5.9	119
	2	33.8	33.1	19.7	13.4	305
	3	31.4	36.6	25.2	6.9	290
	4	24.5	36.2	28.5	10.8	481
2008	5	17.7	44.3	26.6	11.4	271
	6	15.2	44.3	35.6	4.8	289
	7	19.8	41	38	1.2	324
	8	14.9	37.9	42.6	4.7	383
2009	9	19.9	62.1	16.6	1.3	301
	10	13.7	54.2	19.8	12.3	212
	11	8.9	71.4	17.4	2.3	955
	12	8.6	61.5	29.1	0.9	802
2010	13	12.7	59.8	25.2	2.3	567
	14	8.9	42.3	45.5	3.3	605
	15	7	42.2	42.6	8.2	732
	16	5.3	37.1	38.1	19.5	472
2011	17	2.8	28.4	42.9	25.8	573
	18	0.5	15.2	41.5	42.8	820
	19	3.9	11.9	34.7	49.6	724
	20	5.5	24.9	41.6	28	807
	21	10.4	42.4	33.3	13.9	231
	Count	11.1	40.5	33.3	15.1	10263

Table 2.5: Percentages in each of four size classes of female white sharks sighted in Gansbaai 2007–2011. Size class 1 = <2.0 m, Size class 2 = 2–2.75 m, Size class 3 = 2.75–3.5 m, Size class 4 = >3.5 m

	Quarter	*<2.0m*	*2.0-2.75m*	*2.75-3.5m*	*>3.5m*	**Count**
2007	1	31.8	31.8	27.3	9.1	22
	2	33.3	32.1	20.5	14.1	78
	3	18.3	41.7	28.3	11.7	60
	4	15	38.9	30.3	15.8	234
2008	5	17.5	50	20	12.5	160
	6	13.5	48.1	33.7	4.8	104
	7	16.3	36.7	46.9	0	98
	8	6.7	30.5	56.7	6.1	164
2009	9	13.7	64.7	19.6	2	102
	10	11.5	58.5	12.3	17.7	130
	11	6.1	73.2	17.5	3.1	542
	12	6.1	59.8	32.9	1.2	425
2010	13	4	55.7	34.2	6	149
	14	1.6	26.6	64.5	7.3	124
	15	2.2	30	53	14.8	230
	16	0	19.6	39.2	41.2	102
2011	17	1.9	18.9	35.8	43.4	106
	18	0.7	5.3	37.2	56.7	282
	19	0.9	6.9	29.6	62.5	331
	20	0	10	34.7	55.3	170
	21	1.7	24.1	48.3	25.9	58
	Count	7	39.5	32.9	20.6	3671

Table 6: Percentages in each of four size classes of male white sharks sighted in Gansbaai 2007–2011. Size class 1 = <2.0 m, Size class 2 = 2–2.75 m, Size class 3 = 2.75–3.5 m, Size class 4 = >3.5 m

	Quarter	*<2.0m*	*2.0-2.75m*	*2.75-3.5m*	*>3.5m*	**Count**
2007	1	8.7	13	69.6	8.7	23
	2	16.9	39.8	25.3	18.1	83
	3	22.4	43.9	28.6	5.1	98
	4	16.7	44.4	36.1	2.8	36
2008	5	0	35.9	51.3	12.8	39
	6	8	39.1	48.3	4.6	87
	7	13.2	46.5	36.8	3.5	114
	8	3.3	60	33.3	3.3	30
2009	9	14.8	59.3	25.9	0	27
	10	5.9	38.2	50	5.9	34
	11	4	70.9	24	1.1	175
	12	0	87.9	12.1	0	33
2010	13	3.5	57.9	38.6	0	57
	14	3.7	44.4	48.9	3	135
	15	3.9	44.7	45.4	5.9	152
	16	2.5	45.6	49.4	2.5	79
2011	17	2.2	14.5	43.5	39.9	138
	18	0	8.5	35.9	55.6	223
	19	2.1	9.2	36.9	51.8	141
	20	2.6	22.3	47.7	27.5	193
	21	0	18.8	40.6	40.6	32
	Count	5.5	36	39.1	19.4	1929

Chapter 3

What factors influence the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa?

Photo: Dickie Chivell

Chapter 3

Introduction

White sharks *Carcharodon carcharias* are large apex predators that occur circumglobally in cool temperate marine systems (Compagno 2001). Until the 1990s they were thought to be a primarily coastal species (Compagno 1984a). Aggregations occur at predictable coastal locations in the USA, Mexico, South Africa, New Zealand and Australia (Carey et al. 1982; Casey and Pratt 1985; Compagno 1987; Skomal et al. 2012). The predictability of white sharks at known locations and their apparent site fidelity suggest that they select these locations at specific times of the year (Jorgensen et al. 2012).

We now know, through advances in tagging technologies, that these predators may embark on extensive pelagic migrations, crossing deep tropical ocean basins before returning and exhibiting fidelity to these temperate coastal aggregation sites (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007a; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2009; Block et al. 2011; Bruce and Bradford 2012; Jorgensen et al. 2012). Furthermore, while in the tropics/open ocean, they are capable of diving to depths often exceeding 500 m and as deep as 1 200 m (Bonfil et al. 2005; Weng et al. 2007b; Nasby-Lucas et al. 2009; Bruce and Bradford 2012; Domeier and Nasby-Lucas 2012; Duffy et al. 2012; Francis et al. 2012). Prey availability, breeding and mating are associated with such migratory behaviour in the species (Klimley et al. 1996; Bonfil et al. 2005; Domeier and Nasby-Lucas 2008; Duffy et al. 2012; Francis et al. 2012; Jorgensen et al. 2012). Furthermore, environmental cues such as changes in water temperature and upwelling may influence the time spent in the pelagic and coastal phases of these migrations (Pyle et al. 1996; Bruce et al. 2006; Jorgensen et al. 2009; Nasby-Lucas et al. 2009; Block et al. 2011; Bruce and Bradford 2012; Duffy et al. 2012; Francis et al. 2012; Jorgensen et al. 2012).

During deep dives in oceanic waters, mature white sharks experience cold and hypoxic conditions; tracking evidence has indicated they can tolerate extremes of 4°C and less than 1 mgl^{-1} of oxygen (Nasby-Lucas et al. 2009; Bruce and Bradford 2012; Francis et al. 2012; Domeier and Nasby-Lucas 2012). Whilst most fish species return to the surface soon after enduring dives below the thermocline (Bernal et al. 2005) satellite tagging studies have shown that larger white sharks (>3.5m TL) are capable of spending longer time periods (greater than 12 hours) than other fish species in these environments (Nasby-Lucas et al. 2009; Duffy et al. 2012; Francis et al. 2012). Juvenile white sharks have been tracked into water temperatures of 6.8°C in Australia (Bruce and Bradford 2012) and into waters of 2.5°C in New Zealand (Francis et al. 2012) but dives are limited to 10–15 minutes (Bruce and Bradford 2012). The fact that white sharks possess one of the fastest routine metabolic rates of an endotherm (Bernal et al. 2005; Ezcurra et al. 2012) and that they return to the surface after long deep dives (Bonfil et al. 2005; Francis et al. 2012) suggest that they possibly return to warmer surface waters to regulate and recover their optimal physiological condition. One female white shark off

South Africa made regular dives to depths of 400–900 m but spent 60% of her time in the top 15 m (Bonfil et al. 2005). This extreme deep diving behaviour is possible because white sharks have a suite of complex biological and haematological characteristics ranging from their muscle design (Carey et al. 1982; Block and Carey 1985; Goldman 1997; Bernal et al. 2003, 2005; Chapter 1) to their cardio vascular design (Emery 1985; Bernal et al. 2005) and blood composition (Emery 1985; Nasby-Lucas et al. 2009).

Animals have to make movement decisions that optimize the acquisition of food and mates, the evasion of predators and the selection of appropriate environmental conditions (Papastamatiou and Lowe 2012). On returning to temperate coastal areas, white sharks dive less frequently and to shallower depths, because they are confined to the shallow depths of the continental shelf (Francis et al. 2012). White sharks on the coastal shelf in Australia, California and New Zealand spend most of their time between the surface and 50 m where water temperatures remain more stable (Francis et al. 2012). Furthermore, different size classes of white sharks may seek out different physical environments when visiting coastal regions (Robbins 2007; Robbins and Booth 2012). These may be determined by prey availability or suitable environmental conditions, or both. Adult and juvenile female white sharks (Bruce and Bradford 2012; Chapter 1) are more frequently documented inshore in summer months throughout their range (Dewar et al. 2004; Dicken 2008; Bruce and Bradford 2012) than male sharks (Strong et al. 1992; Robbins 2007; Robbins and Booth 2012).

El Nino/Southern Oscillation (ENSO) is the most important coupled ocean-atmosphere phenomenon to cause global climate variability on seasonal to interannual time scales (Wolter and Timlin 2011). During warm events, atmospheric pressure rises in the western Pacific Ocean and falls in the eastern Pacific Ocean, weakening or even reversing the direction of south east trade winds (Wilson et al. 2001; Chapter 1).This causes suppression of the thermocline (pushing it deeper) with a pool of warm water surging eastwards along the equator, towards South America and reduction of the sea level in the western Pacific Ocean (Enfield and Allan 1980; Ramage 1987; Quinn and Neal 1992). It is an important component of climate variability along the South African south coast (Schumann et al. 1995; Roberts 1998). The periodicity of ENSO events varies between two and 10 years (Rasmusson and Carpenter 1982; Quinn and Neal 1992) with an average return period of three years (Philander and Pacanowski 1986). In South Africa, the phenomenon has been studied in detail particularly in relation to commercially important fish species such as anchovy, sardine and squid (Boyd and Shillington 1994; Roberts 2005). There is a higher capture rate of juvenile male white sharks in the anti-shark nets off the KwaZulu-Natal coast during a positive Southern Oscillation Index SOI or La Nina cool season (Cliff et al. 1996b).

Gansbaai, in the Western Cape, South Africa, is visited seasonally by various size classes and both sexes of white sharks (Ferreira and Ferreira 1996; R. Johnson pers. comm.). In summer, intensified south easterly trade winds favour upwelling (Jury 1985) causing cold water of Benguela origin to enter the bay (Chapter 1). In winter, the westerly wind belt moves north and becomes the dominant prevailing wind, reducing upwelling of cold water and increasing the leakage of warmer water of Agulhas Bank origin into the bay (Lutjeharms et al. 2000). The variability of water temperature with season, along with changing environmental parameters such as swell height, wind speed and turbidity between seasons, makes Gansbaai an ideal study site to monitor the influence of environmental parameters on white shark numbers.

This chapter aims to investigate the seasonal occurrence of white sharks visiting Gansbaai over a five-year period through sightings data. I aim to investigate the environmental parameters that may influence the number of white sharks and the gender composition of the animals in the bay. Additionally, I aim to investigate how inter-annual variability in sightings may be linked to a strong positive ENSO (Negative MEI) event which occurred during sampling (Chapter 1).

Materials and Methods

Gansbaai is a semi-enclosed embayment situated on the south coast of the Western Cape, South Africa. It is relatively exposed with the western and eastern boundaries being Danger Point (34°37.50S, 19°17.30E) and Quoin Point (34°47.28S, 19°39.15E), respectively. White sharks were observed most commonly in this study area at two distinct localities: around the periphery of Dyer Island (34°40.669S, 19°23.863E) located 8 km offshore of the nearest harbour town (Kleinbaai), and at Joubertsdam (34°38.366S, 19°25.158E), a reef system running parallel to a sandy beach where sharks occurred in areas as shallow as 2 m deep, immediately behind the surf zone (Figure 1.1).

During this study, data were collected from a 10.8 m catamaran purpose-built for cage diving with white sharks between January 2007 and September 2010; from October 2010 until the end of the study in December 2011 a 12 m catamaran was used. Data was recorded on log sheets for individual sharks and environmental parameters were completed on every outing. All observations were made from a platform 1 m above sea level (Figure 1.12).

Chumming was initiated on arrival after anchoring at a site at which sharks were expected to be found. Chumming was undertaken by pouring a mixture of sardine oils and mashed teleost based chum onto the water to create a scent trail on the surface which would orientate and attract the sharks towards the boat (Strong et al. 1992; Chapter 1). The anchoring position and water depth were recorded using the boat's navigational equipment, a Furuno GPS (model GP32). Sea surface temperature (SST, measured to the nearest 0.1°C) was recorded during 2007–2009 using a probe located 2 m below sea surface in the tunnel of the hull. A conductivity temperature depth meter (CTD) and a Yellow Springs Instruments (YSI) probe were used to measure these parameters during 2010–2011. These instruments were calibrated with the previously used boat sensors to maintain consistency.

Wind and current directions were determined from the direction of the chum line, a clearly visible slick on the surface, and the orientation and angle of the baitline. Underwater visibility (m) was estimated by marked reference points on a dive cage and a secchi disc. Swell height (m), sea condition (classified as: swell, windchop or calm) and percentage cloud cover (nearest 10%) were recorded on anchoring. Wind speed (knots) and direction (16 compass points) were obtained from a local weather buoy (located offshore of Franskraal, 34°38.329S, 19°25.440E).

The sex of each shark was determined, if possible, by surface observations and underwater video records of the pelvic fin area. Chapter 1 describes the criteria used to sex sharks.

Generalized linear models using the Poisson distribution were fitted to counts of great white sharks per trip. The variables discussed above were used as explanatory variables in these models. Model selection was undertaken largely by use of the Akaike Information Criterion. Models were fitted for the total number of sharks per trip, for the number of sharks classified as male and for the number of sharks classified as female.

Results

A total of 1647 trips were made over the five year study period, 923 to offshore sites and 724 to inshore sites (Table 3.1, Figure 3.2). Trips were made to offshore sites mainly from March to August (the winter months in the southern hemisphere) but offshore trips were made in all months except December. Inshore trips took place mainly during summer, from October to February, with September being the month of transition, with 77 offshore trips and 65 inshore trips; no inshore trips were made in April, May and June (Table 3.1, Figure 3.2).

The mean number of sharks per trip varied from 4.0 sharks in January to 8.4 sharks in May; from April to October, the mean number of sharks per trip exceeded 6.0 (Table 3.2). The mean maxima for males and females were both in May and July (2.5 and 3.7 sharks/trip respectively) however, the mean minima for males were in October and in February for females (0.9 and1.7 sharks/trip respectively) (Table 3.2). The overall annual mean sea surface temperature was 14.9°C, and the monthly means did not show any strong annual pattern of seasonality (Table 3.2).

Three generalized linear models were fitted: for the total number of sharks per trip (Table 3.3), for the number of sharks classified as male (Table 3.4), and the number of sharks classified as female (Table 3.5). Preliminary model-building for the three models demonstrated that four of the explanatory variables were important: seasonality (monthly factors), sea surface temperature, the long term trend and Multivariate ENSO Index (MEI, described in Chapter 1).

For all sharks (Table 3.3), the model including these four explanatory variables explained 23.8% of the deviance; it had an AIC value of 2354. Each explanatory variable was omitted from the model in turn: with seasonality removed, the remaining explanatory variables accounted for 15.1% of the deviance, with an AIC of 2596. With sea surface temperature omitted, 23.4% of the deviance was explained, and AIC was 2362; with the long term trend term omitted, 16.3% of the deviance was explained, with AIC=2578. With MEI omitted, 21.4% of the deviance was explained, and AIC=2424. From this, seasonality and trend appear to be the two key explanatory variables; however, the model with only these two explanatory variables explained 20.8% of the deviance, with AIC=2439.

It is also clear that after the seasonality and trend have been included in the model, the value of MEI as an explanatory variable is larger than that of sea surface temperature. In the final analysis, each of the four explanatory variables plays an important role in the model. In a conventional modelling approach, all were formally statistically significant (Table 3.3). The coefficient of the trend variable was positive, indicating an increasing trend in the total numbers of sharks per trip over the five-year study period. The coefficient of the sea surface temperature variable was positive, indicating that, over and above the effects of the monthly seasonality factors and MEI, there was a tendency for the number of sharks per trip to be larger when the sea was warmer. Likewise, the coefficient of the MEI was positive, indicating a positive relationship between shark numbers per trip and MEI.

For male sharks (Table 3.4), the model including these four explanatory variables explained 12.1% of the deviance, and had an AIC value of 1418. Each explanatory variable was omitted from the model in turn: with seasonality removed, the remaining explanatory variables accounted for 0.8% of the deviance, with AIC=1574. With sea surface temperature omitted, 10.8% of the deviance was explained, and AIC=1437; with the long term trend term omitted, 11.7% of the deviance was explained, with AIC=1422. With MEI omitted, 11.2% of the deviance was explained, and AIC=1430.

Seasonality appears to be the key explanatory variable; however, the model with only this single explanatory variables explained 9.5% of the deviance, with AIC=1453. Although the best model for males in relation to explanatory variables accounted for less of the deviance than for the total number of sharks, each of the four explanatory variables plays an important role in the model. The four variables were all formally statistically significant (Table 3.4). The coefficient of the trend variable was positive, indicating an increasing trend in the numbers of male sharks per trip over the five-year study period. The coefficient of the sea surface temperature variable was positive. In contrast, the coefficient of the MEI was negative, indicating a negative relationship between shark numbers per trip and MEI.

For female sharks (Table 3.5), the model including these four explanatory variables explained 12.9% of the deviance, and had an AIC value of 1869. Each explanatory variable was omitted from the model in turn: with seasonality removed, the remaining explanatory variables accounted for 7.5% of the deviance, with AIC=1961. With sea surface temperature omitted, 12.6% of the deviance was explained, and AIC=1872; with the long term trend term omitted, 12.9% of the deviance was explained, with AIC=1867 and with MEI omitted, 6.2% of the deviance was explained, with AIC=2007.

The model for females in relation to explanatory variables which had the smallest AIC excluded long term trend, and this variable is not significant in Table 3.5. The coefficients of the model which excludes trend as an explanatory variable (Table 3.6) is very similar to the model which includes it (Table 3.5). The remaining three explanatory variables were all formally statistically significant (Table 3.6). In contrast to the model for males (Table 3.4), the regression coefficient for MEI was negative and that for MEI was positive (Tables 3.5 and 3.6).

Discussion

The average number of white shark sightings was higher in winter months (March until mid September), at Dyer Island and at Geyser Rock than in summer months (Table 3.2). During summer months, sightings were generally female biased when sighting effort shifted to the inshore region of the bay (Tables 3.1 and 3.2), with the exception of the summer of 2010–2011 when sea surface temperature was abnormally cold due to the La Nina event in place (Figure 3.3). Gansbaai is similar to other aggregations sites on that mixing of both sexes occurs over several months at seal colonies located in coastal sites and offshore islands (Ferreira and Ferreira 1996; Bruce et al. 2006; Bruce 2008; Domeier and Nasby-Lucas 2012; Duffy et al. 2012; Francis et al. 2012; Robbins and Booth 2012). Explanations for the co-occurrence of both sexes at the same location are for foraging for the same prey resources; and in the case of mature animals, possibly for mating purposes (Domeier and Nasby-Lucas 2012; Jorgensen et al. 2012). Reproduction is unlikely to be the cause of both sexes co-occurring at this study site however, because most female white sharks visiting Gansbaai were too small to be sexually mature (Chapter 2; Dudley 2012), and they did not exhibit fresh bites and scarring typical of mating behaviour (Domeier and Nasby-Lucas 2007).

Predation by white sharks on Cape fur seals has been observed at Dyer Island, especially in winter months May-September (Ferreira and Ferreira 1996; Johnson et al. 2008; A Towner unpubl. data). Cape fur seals pup annually and synchronously in November (Shaughnessy and Best 1982). Yearlings suckle until about five to six months of age, when they start limited foraging in shallow bays in the vicinity of their natal colony (David and Rand 1986). By the age of about seven months (in July–August), the pups may stay away from the colony for short periods of about three days (Rand 1967). Even though the peak in shark sightings for both sexes coincides with a time that may be ideal for hunting inexperienced seals, if this was the only incentive for white sharks to visit Dyer Island one would expect the seasonality trend to be the most significant variable when modelling environmental variables on shark abundance. Furthermore, inter annual variability of sightings (Figure 2a and 2b) suggests that other factors may be influencing shark numbers visiting Gansbaai.

Robbins and Booth (2012) suggested that temperature may be an indirect controlling factor on white shark distribution and that white sharks are influenced by one or more other variables that are closely associated with SST. The long term and monthly trend showed a significant relationship with shark sightings of both male and females. However, the results here suggests that sea surface temperature has a greater effect on numbers than seasonal and monthly trend. The statistically significantly positive SST trend indicated that there were more sharks in warmer water temperatures. During summer the water column is stratified with solar warming of the surface layers. If south easterly winds blow intensively this causes cold water upwelling (Shannon 1985; Lutjeharms and Meeuwis 1987; Shillington 1998). If these winds persist over a number of days the thermocline breaks down and surface water temperatures can drop to as low as 9°C, therefore water temperature conditions are highly variable. During autumn and winter months in South Africa, the westerly wind belt migrates north, cyclonic low pressure systems pass south of the African continent and are accompanied by northwesterly winds which push surface waters onshore, and upwelling is minimal (Lutjeharms et al. 2000; Hardman-Mountford et al. 2003). The thermocline (which remains prominent throughout summer months) breaks down with increased Agulhas leakage and mixing of the water column occurs. Thus, water properties are more stable, particularly within the Agulhas Bank region and Gansbaai (Lutjeharms et al. 2000; Hardman-Mountford et al. 2003; Roberts 2005). These more stable winter conditions would presumably be less physiologically stressful to white sharks possibly making the region more favourable for white sharks over a wide size range.

There were more female white sharks sighted in positive MEI years although the relationship with SST was not significant. (Tables 3.5 and 3.6). This supports a previous study in which it was proposed that pregnant female sharks may seek out warmer waters to enhance the development of their foetuses (Economakis and Lobel 1998). This has been described as the 'thermal niche hypothesis.' It has also been supported in the northeastern Pacific Ocean where satellite tagged mature females remained offshore in warmer water temperatures for prolonged time periods whereas males migrated back to cooler coastal regions in California annually (Domeier and Nasby-Lucas 2012; Jorgensen et al. 2012). One 4.8 m female shark was observed to move inshore from a remote offshore region but made a rapid return offshore before reaching the continental shelf at a time that the tag reported water temperatures at a minimum of 13.6°C (Jorgensen et al. 2012).

The authors suggested that she may have been pregnant (from evidence of mating bites during tagging and large size of the female) and that the cold water may not have been favourable for parturition. To date, most documented pregnant female white sharks have been recorded during warm water events, positive MEI/El Nino cycles, particularly in the 1990s (Norman and Fraser 1937; Klimley 1985; Fergusson 1996; Francis 1996; Uchida et al. 1996; Cliff et al. 2000; Saidi et al. 2005) (Figure 3.1). Studies on the reproductive biology of female white sharks in South Africa have been limited by a lack of mature females (Dudley 2012). However, the majority of female white sharks encountered in Gansbaai are believed to be sexually immature

(Chapter 2; Dudley 2012). Therefore other factors may be leading to the abundance of females peaking in Gansbaai during positive MEI years

One explanation could be that female white sharks prefer coastal aggregation sites in warmer conditions to augment their own growth rate. In order to reach sexual maturity, a female white shark must attain a larger size than male sharks, approximately 4.5 m total length (Wintner and Cliff 1999). Investing less energy into thermoregulation by seeking out warmer more stable areas could provide more scope for growth, even though they can tolerate extremely low temperatures while in pelagic phases of their migrations (Bonfil et al. 2005; Nasby-Lucas et al. 2009; Francis et al. 2012).

The results of this study showed that the most significant factor affecting numbers of both sexes was the Multivariate Enso Index (MEI). It has become clear that climatic conditions exert powerful effects on fish stocks; with most variability occurring not annually but rather at decadal scales (Bakun and Broad 2002). It may be possible that Multivariate ENSO (MEI) phenomenon is playing a part in structuring the sexual composition of white sharks showing fidelity to the Gansbaai region and, presumably, other parts of their range. In this study, more females were seen in Gansbaai overall in warmer water/positive MEI years. Conversely, the opposite trend was observed for males. Therefore, in cool water years (2010–2011) sightings of males sharks were significantly higher than in previous years. The same trend has been observed in the Neptune Islands where male sharks favour cool water conditions, and were more common than in warm water years (Robbins 2007, Robbins and Booth 2012). One explanation the authors propose for the greater abundance of males in cooler water years is that the absence of larger females may reduce competition for prey resources. Competitive exclusion by larger conspecifics may occur at white shark aggregations where larger more experienced sharks occupy prime hunting areas excluding smaller less experienced sharks (Klimley et al. 2001a). Sexual segregation has been also been observed in white sharks at other locations (Domeier and Nasby-Lucas 2012; Robbins and Booth 2012). Another explanation is that females may time their visits to areas when fewer males are around, or seek out inshore areas to avoid mating harassment (Sims et al. 2001). MEI linked trends with white shark population composition may not have been demonstrated in other aggregation areas due to their shorter sampling periods (Domeier and Nasby-Lucas 2012). For example, in South Australia, Bruce (1992) and Malcolm et al. (2001) reported on a sex ratio bias towardsfemale white sharks in the Dangerous Reef areas. This study was then contradicted by Robbins and Booth (2012) who reported on a sex ratio bias towards males in 2003–2007 with a larger and more consistent data set in the same region. In Gansbaai, earlier studies report female bias population composition of white sharks in Gansbaai with an overall paucity of males, particularly in summer months (Ferreira and Ferreira 1996; Johnson 2003). One similarity between these earlier studies is the timing in the early and late 1990s when El Nino conditions had impacts on various pelagic fish stocks worldwide, from anchovy and sardine to salmon and tuna (Bakun and Broad 2002; Wolter and Timlin 2011). During 2003 and again in 2010, La Nina (cold water conditions) were in place, the latter being one of the most intense events in 50 years (Wolter and Timlin 2011; Figure 1.1)

Two previous studies have investigated the possible effects of El Nino Southern Oscillation (a less complex index than MEI) on white sharks and their distribution. Martin (2005) found no correlation between the number of white shark reports of strandings, photographs or fishing records in the northern latitude regions of the Pacific Ocean. He concluded that if anything, there was a slight positive, but not significant, correlation with La Nina (cooler SST) years. Similarly, Cliff et al. (1996b) investigated trends in catch per unit effort in the shark nets in KwaZulu-Natal and found a slight increase in inshore catches during La Nina years. Decreased turbidity inshore (due to higher summer rainfall) and cooler upwelled water were proposed as conditions that may possibly favour juvenile sharks in this subtropical part of the South African coast.

Even though white sharks are able to tolerate large changes in temperature while diving (Bonfil et al 2005; Nasby-Lucas et al. 2009; Bruce and Bradford 2012; Domeier and Nasby Lucas 2012; Francis et al. 2012; Jorgensen et al. 2012; Nasby-Lucas and Domeier 2012) the relationship between the white shark's spatial and temporal distribution and water temperature is complex. Different size and age classes of white sharks are likely to have different tolerances towards their physical environment, as well as different prey requirements (Papastamatiou and Lowe 2012), and this will probably influence their movements. Similar to other marine predators, different sizes and sexes of white sharks prefer particular coastal regions during specific environmental conditions (Bakun and Broad 2002). Even though juvenile and subadult white sharks do not face many threats from other marine predators, utilising the coastal regions at a time when larger sharks are less abundant could be favourable for their hunting as well as reducing risk from predation. These periods of favourable environmental conditions (often termed cyclical loopholes or optimum environmental windows) are correlated with Southern Oscillation phenomena and have been discussed in detail by Bakun and Broad (2002) who compared a wide variety of marine fishes and vertebrates with similar peaks and declines correlated with MEI. Furthermore, subadult white sharks are predominantly piscivorous (Hussey et al. 2012) and negative MEI conditions (cooler La Nina induced) are associated with increased productivity (largely linked to the increased upwelling of nutrient rich waters) which could have increased the availability of fish prey species resulting in more subadult white sharks being attracted to the area.

It is clear from this study that MEI affected male and female white sharks numbers in Gansbaai in opposite ways, and these trends were highly significant. Management of South African white sharks in the Western Cape has been largely based on short term studies with seasonal sampling (Ferreira and Ferreira 1996; Martin et al. 2005; Hammerschlag et al. 2006; Kock and Johnson 2006; Laroche et al. 2007). This study highlights the importance of long term data collection to white shark research. Furthermore this study suggests that environmental features such as MEI form important cues of white shark population abundance and composition at particular locations.

Recent speculations of an increasing white shark population in the Western Cape were rejected by Kock and Johnson (2006) who suggested that patterns of white shark habitat use may be shifting (Dudley 2012). Kock and Johnson (2006) suggested that white shark inshore habitat use may be influenced by a seasonal migration of fish species inshore. The results in this study clearly indicate that environmental influences may play a more important role in local white shark abundance than previously thought, and should be addressed when drafting management plans for swimmer safety and white shark management. It may be possible to create a predictive model of risk of shark/human interaction once these variables are better understood. This would be of considerable benefit to reduce the risk of attack by sharks on humans in the Western Cape, particularly if this could be incorporated into the Shark Spotter programme in False Bay (Kock et al. 2012).

The relationships between the various environmental factors measured are probably only a fraction of those which potentially influence this shark species. There is a range of environmental conditions within which this shark can survive. Within this range would be optimal conditions – such as high prey availability and benign physical conditions. However, these need not always coincide and white sharks have evolved the ability to avoid unsuitable environments. By examining these physical environmental factors, we are better able to understand some aspects of their habitat, but we still need to factor in other aspects such as the availability of suitable prey. Nevertheless, this study has shown that environmental variables may be assessed to better understand the dynamic relationship between this apex predator and its habitat.

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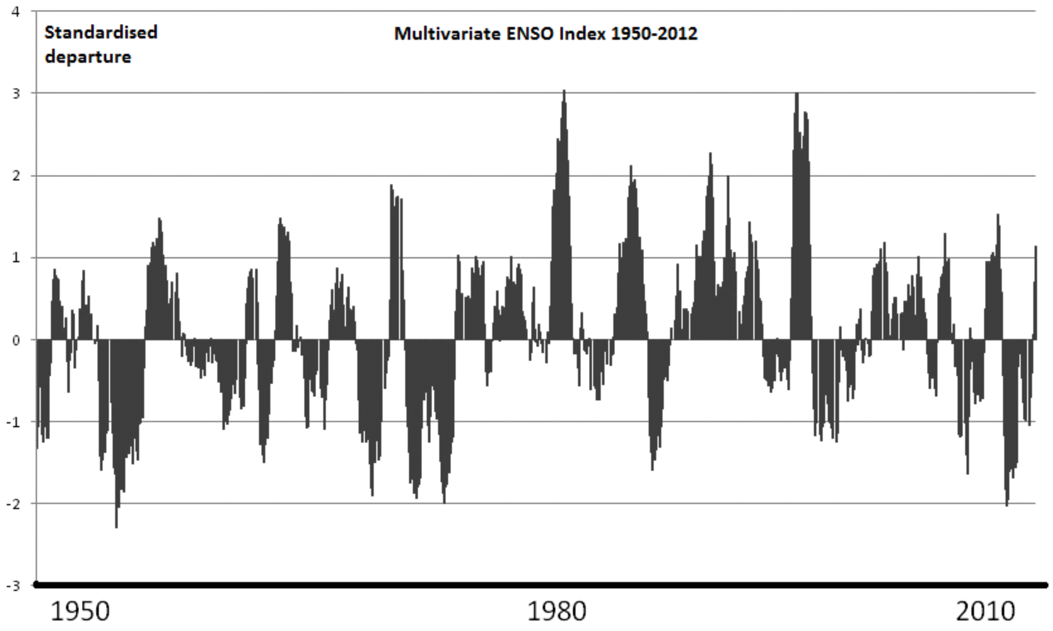

Figure 3.1: Multivariate ENSO index (MEI) data 1950–2010 (Wolter and Timlin 2011 and NOAA). Data sourced from www.noaa.com

Table 3.1; Summary of the total number of shark cage-diving trips per month, inshore and offshore, between January 2007 and December 2011 in Gansbaai South Africa.

Month	*Offshore*	*Inshore*	**Total**
January	29	104	133
February	42	107	149
March	124	35	159
April	124	0	124
May	95	0	95
June	113	0	113
July	123	28	151
August	116	23	139
September	77	65	142
October	50	119	169
November	30	134	164
December	0	109	109
Totals	923	724	1647

Table 3.2: Mean total numbers of white sharks seen per month in total, and the mean numbers of female and male sharks and the mean monthly sea surface temperatures in Gansbaai, 2007 to 2011. The sum of the numbers for males and females for each month does not add to the total number seen, because the gender of some sharks could not be determined (see text).

	Mean Total sharks	S.D	Mean Female	S.D	Mean Male	S.D	Mean SST°C	**S.D**
January	3.977	2.17	2.204	1.64	1.293	1.46	14.2	2.06
February	4.557	3.20	1.746	1.77	1.339	1.35	15.43	2.68
March	5.289	3.48	1.977	1.63	1.915	1.46	13.72	1.86
April	6.919	4.00	2.762	1.64	1.845	1.45	13.45	1.93
May	8.411	4.32	3.766	2.50	2.598	1.79	14.94	1.43
June	7.69	4.51	3.452	2.5	2.337	1.95	15.16	1.10
July	7.172	3.84	3.521	2.76	1.607	1.47	14.52	0.62
August	7.094	3.66	3.207	2.51	1.613	1.46	14.65	1.05
September	6.486	3.22	2.879	2.43	1.224	1.32	15.3	1.36
October	6.041	3.21	2.729	2.05	0.991	1.17	15.67	1.89
November	5.902	3.16	3.178	2.41	1.719	2.18	16.19	2.70
December	5.495	2.81	2.646	1.62	1.192	0.75	14.64	2.20

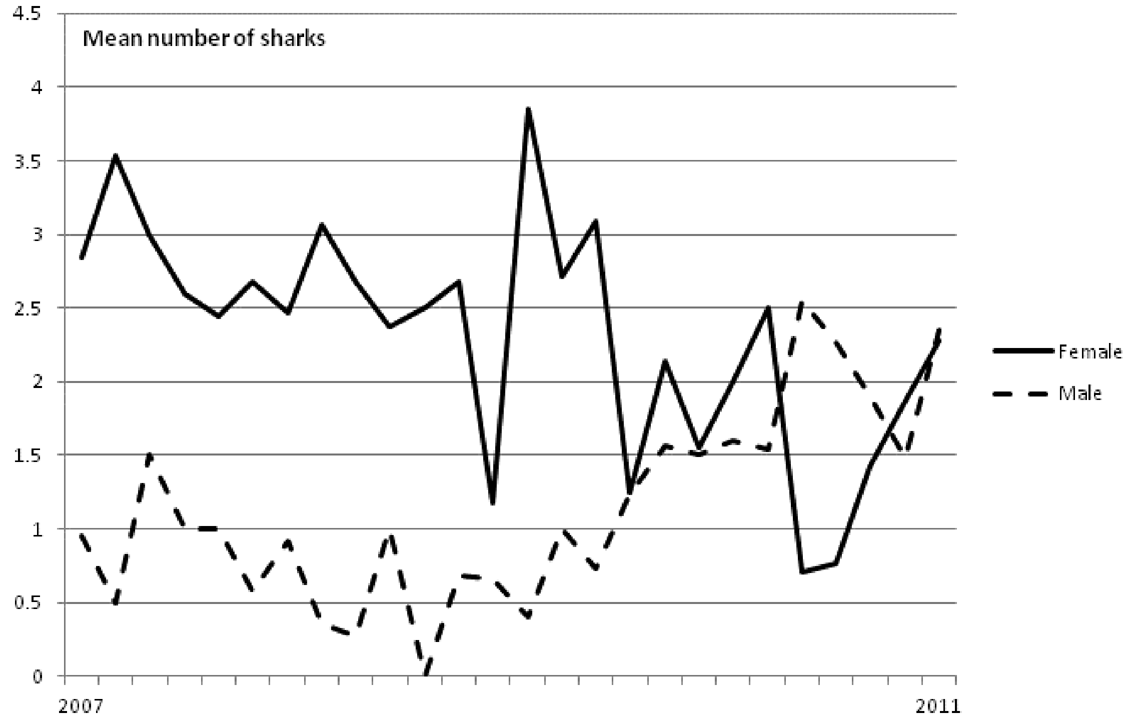

Figure 3.2: Interannual variability in male and female shark sightings at the inshore site, Gansbaai 2007-2011

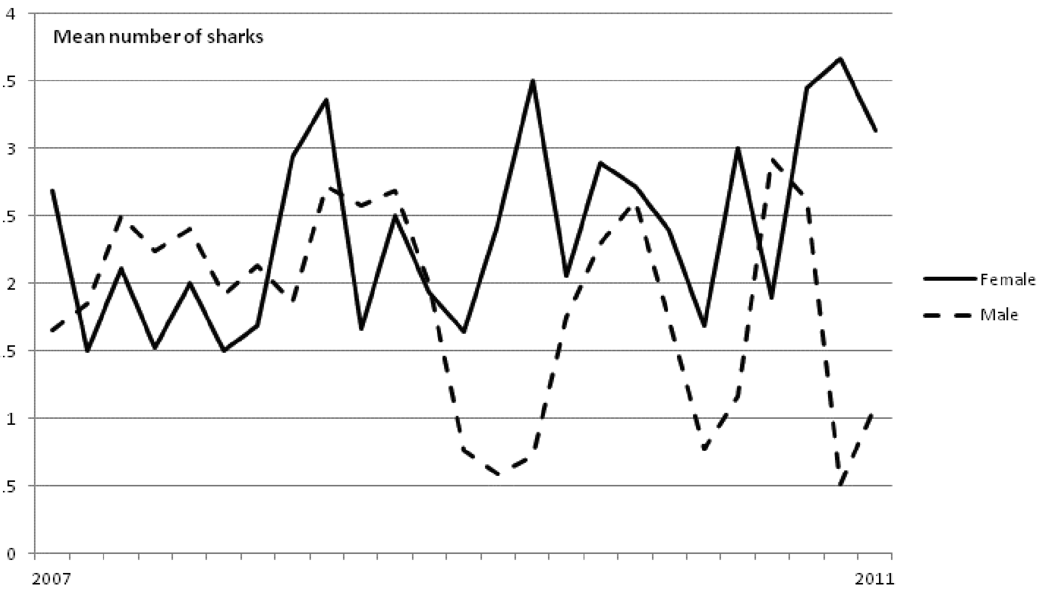

Figure 3.3: Interannual variability in male and female shark sightings at Dyer Island, 2007–2011

Table 3.3: Results of generalized linear model relating total number of great white sharks observed per trip at Gansbaai to the explanatory variables month (with January as the base month), trend (per month), seasonal sea surface temperature (SST) and multivariate ENSO index (MEI).

Parameter	*Regression Estimate*	*Standard Error*	*t(*)*	**P-value**
January	0.7685	0.0963	7.98	<.001
February	-0.0468	0.0667	-0.7	0.483
March	0.1781	0.0617	2.89	0.004
April	0.3986	0.0618	6.45	<.001
May	0.5729	0.0605	9.47	<.001
June	0.521	0.0587	8.88	<.001
July	0.4653	0.0564	8.25	<.001
August	0.4612	0.0573	8.06	<.001
September	0.3879	0.0584	6.64	<.001
October	0.2896	0.0581	4.98	<.001
November	0.2641	0.0592	4.46	<.001
December	0.1941	0.0647	3	0.003
SST°C	0.01886	0.00597	3.16	0.002
Trend	0.12568	0.00841	14.94	<.001
MEI	0.0977	0.0115	8.53	<.001

Table 3.4: Results of generalized linear model relating total number of male great white sharks observed per trip at Gansbaai to the explanatory variables month (with January as the base month), trend (per month), seasonal sea surface temperature (SST) and multivariate ENSO index (MEI).

Parameter	*Regression estimate*	*Standard Error*	*t(*)*	**P.Value**
January	-1.004	0.233	-4.32	<.001
February	-0.073	0.157	-0.46	0.642
March	0.476	0.133	3.58	<.001
April	0.463	0.144	3.23	0.001
May	0.842	0.133	6.33	<.001
June	0.708	0.131	5.42	<.001
July	0.367	0.13	2.82	0.005
August	0.324	0.133	2.44	0.015
September	-0.081	0.147	-0.55	0.58
October	-0.351	0.152	-2.31	0.021
November	0.067	0.169	0.4	0.69
December	-0.067	0.238	-0.28	0.777
SST°C	0.0653	0.0144	4.52	<.001
Trend	0.0452	0.0181	2.49	0.013
MEI	-0.1083	0.0297	-3.64	<.001

Table 3.5. Results of generalized linear model relating total number of female great white sharks observed per trip at Gansbaai to the explanatory variables month (with January as the base month), seasonal sea surface temperature (SST) and multivariate ENSO index (MEI).

Parameter	*Regression Estimate*	*Standard Error*	*t(*)*	**P.Value**
January	1.257	0.158	7.96	<.001
February	-0.229	0.105	-2.18	0.029
March	-0.2179	0.0998	-2.18	0.029
April	0.0363	0.0984	0.37	0.712
May	0.3589	0.0947	3.79	<.001
June	0.3038	0.0896	3.39	<.001
July	0.3149	0.0844	3.73	<.001
August	0.2593	0.0878	2.95	0.003
September	0.2863	0.0897	3.19	0.001
October	0.2085	0.0894	2.33	0.02
November	0.3684	0.0934	3.95	<.001
December	0.068	0.119	0.57	0.568
SST°C	-0.0238	0.0102	-2.33	0.02
Trend	0.0053	0.0137	0.39	0.699
MEI	0.2243	0.0188	11.91	<.001

Table 3.6. Results of generalized linear model relating total number of female great white sharks observed per trip at Gansbaai to the explanatory variables month (with January as the base month), seasonal sea surface temperature (SST) and multivariate ENSO index (MEI).

Parameter	*Regression Estimate*	*Standard Error*	*t(*)*	**P.Value**
January	1.263	0.157	8.02	<.001
February	-0.234	0.104	-2.25	0.025
March	-0.2207	0.0996	-2.22	0.027
April	0.0365	0.0984	0.37	0.711
May	0.359	0.0947	3.79	<.001
June	0.3039	0.0896	3.39	<.001
July	0.3159	0.0844	3.74	<.001
August	0.2608	0.0877	2.97	0.003
September	0.2873	0.0897	3.2	0.001
October	0.2091	0.0894	2.34	0.019
November	0.3686	0.0933	3.95	<.001
December	0.069	0.119	0.58	0.562
SST°C	-0.02293	0.00997	-2.3	0.021
MEI	0.2244	0.0189	11.9	<.001

Chapter 4

Final Discussion and Synthesis

Photo: Harry Stone

Chapter 4

Knowledge of white shark ecology and distribution in South African waters has improved significantly in recent decades (Dudley 2012). In the 1970s white sharks off South Africa were known to be most abundant in Western Cape waters, although they were known to move into coastal waters of KwaZulu-Natal (Wallet 1973; Bass et al. 1975). Subsequent work has supported this information with evidence that white sharks show site fidelity to aggregation sites in the Western Cape (Cliff et al. 1996a; Ferreira and Ferreira 1996; Kock and Johnson 2006). Tagging studies provided direct evidence that individuals migrate along the entire southern coastline of Africa as far as Mozambique (Bonfil et al. 2005), and records from Western Indian Ocean islands (Cliff et al. 2000; Zuffa et al. 2002) and Australia (Bonfil et al. 2005) indicated that they move more widely and are able to cross the Indian Ocean basin. Furthermore, some individuals were shown to be capable of moving large distances (>11,000 km) and returning to the Western Cape in less than a year (Bonfil et al. 2005).

Despite these advances, our knowledge regarding important life history stages such as breeding, gestation and pupping habitats of this predator in South Africa remains limited (Dudley 2012). Coastal white shark aggregations have been identified in South Africa, particularly near islands where fur seals occur (Cliff et al. 1996a; Ferreira and Ferreira 1996; Kock and Johnson 2006; Dicken 2008). However breeding and mating aggregation sites have not yet been identified, although mature males are known to occur in South African waters, mature females are rarely encountered by researchers (Dudley 2012). Intriguingly, there are records of large and pregnant females in the western Indian Ocean (Cliff et al. 2000; Zuffa et al. 2002) so it is possible that mating sites are located beyond South African waters.

Cliff et al. (1996a) estimated the size of the white shark population off South Africa (between Richards Bay in KwaZulu-Natal and Struisbaai in the Western Cape) to be 1279 (CV 24%), based on a spaghetti tag and recapture study. More recent research in the Western Cape regions has used dorsal fin photo identification techniques to estimate abundance of white sharks in regions. To date, 128 individuals were counted in False Bay between 2004–2005 (A. Kock unpubl. data), 198 individuals in Mossel Bay between 2001–2005 (R. Johnson unpubl. data) and 1500 in Gansbaai (M. Scholl unpubl. data). No error estimates were provided because no population modelling has yet been published using these data. Dudley and Simpfendorfer (2006) found that there was a decline in the size of females caught by the KwaZulu-Natal Sharks Board bather protection nets between 1978 and 2003, suggesting some change in this segment of the population, although they concluded that the KwaZulu-Natal net catches were likely to have had only a small impact on the population. It is worth noting that their catch is made up largely of immature individuals of both sexes and that mature females have not been caught there, possibly because of gear selectivity, or habitat selection differences (Dudley and Simpfendorfer 2006; Dudley 2012).

Seasonal and size related trends in population dynamics have been identified in some regions. For example, evidence suggests that Algoa Bay in Port Elizabeth may be a nursery ground for the species, due to a high percentage of neonates observed in the region (Ferreira and Ferreira 1996; Dudley 2012; M. Dicken and M. Smale pers. comm.). Juveniles, subadults and adults are more common in Western Cape waters than elsewhere along the coastline, but it is reasonable to conclude that white shark distribution still warrants further investigation in order to fully understand the extent of their range, and the importance of offshore areas of the Atlantic and Western Indian Oceans in their life history patterns, particularly with regard to maturation, and reproduction (Cliff et al. 2000).

A significant result from this study was the apparent increase in size and numbers of white sharks recorded from a white shark cage diving vessel in the Gansbaai region (Chapter 2), which may be a consequence of conservation measures introduced in South Africa and elsewhere. White sharks exhibit slow growth and late maturity compared to other shark species (Wintner and Cliff 1999; Mollet and Cailliet 2002). This finding of an increase in size and numbers of sharks recorded over five year study off Gansbaai may infer reduced mortality in the population following the introduction of protective legislation for white sharks in 1991, and a stabilisation in catch rate by KwaZulu-Natal shark nets which occurred between 1978–2003 (Dudley and Simpfendorfer 2006; Dudley 2012). This appears to be the first quantitative support of the suggestion from anecdotal evidence by Compagno (2001) of increased survival of white sharks to larger sizes following their protection.

Prior to the promulgation of protective legislation, larger (subadult and adult) white sharks were targeted by fishermen in the Western Cape regions for trophy fishing and this activity appears to have been reduced or ceased.

An alternative interpretation for the trends of apparently increasing size and numbers is that individuals may be staying longer in the Gansbaai region, because cage diving operations expanded to become a year-round activity since 1991 (Maharaj et al. 2003). Extended stays by white sharks have been reported by Bruce and Bradford (2011) at the Neptune Islands, Australia. This study was conducted using passive acoustic tracking of 20 sharks during one season (2010–2011) and comparing results obtained to an earlier study (2001–2003) when there were fewer boats in the area and chumming effort was less. Operators in the Neptune Islands use teaser baits and they allow the sharks to consume food. In Gansbaai, feeding of individual sharks is avoided in compliance with legislation. Each South African white shark cage diving operator has a bait handler who is trained by experienced personnel on board to minimise consumption of baits by sharks. Increases in the population size of sharks may naturally extend shark residency times if animals were competing for access to the same resource such as seals/sealions (Bruce and Bradford 2011). Average residency times of white sharks in Gansbaai are reported to be less than two months from preliminary photo identification and manual tracking studies (Kock and Johnson 2006; unpubl. data). Furthermore, Laroche et al. (2007) found no associated conditioning in white sharks at Seal Island in False Bay and they concluded that the effects of chumming were probably minimal. This topic warrants further investigation because of the perceived threat of this operation on other marine users such as bathers and surfers. Ultrasonic acoustic tagging studies incorporating both active and passive tracking, would be a useful approach to monitor fine scale movements of white sharks to investigate their behaviour in relation to the presence of cage diving vessels. This approach could allow specific testing of the behaviour and residency in bays if cage diving boat activities are simultaneously monitored.

The study of environmental effects on white sharks in a bay (Chapter 3) is the most comprehensive of its type to date. The strength of this work lies in the quality and quantity of data collected over five years, which is longer than at other locations worldwide. The fortuitous occurrence of a significant MEI event during the sampling phase and a robust statistical analysis allowed a deeper understanding of the impacts of the environment on white shark occurrence in the bay.

The hypothesis tested in this study was that female white sharks prefer warmer water temperatures, and these results supported this hypothesis and agree with previous work in South Australia by Robbins and Booth (2012), where female white sharks were more abundant in warmer water temperatures and more sharks of both sexes were sighted in stable winter months. One question, which has remained unclear to date, has been whether white sharks can acclimatize to rapidly changing thermal environments such as those found in coastal regions when upwelling events occur. Large female white sharks are more commonly documented in tropical open ocean environments where they can dive below the thermocline if surface conditions are above optimum (Fergusson 1996; Francis 1996; Uchida et al. 1996; Cliff et al. 2000; Zuffa et al. 2002; Saidi et al. 2005). To escape unsuitable conditions in the dynamic coastal environment a shark would have to migrate more extensively alongshore, presumably requiring more energy. The results in this study suggest that white sharks may time their visits to coastal regions in relation to water temperature regimes. One way to appropriately investigate this further would be to undertake a satellite tagging study combining both Pop Up Archival (PAT) and Smart Position Only Tags (SPOT) tags to monitor temperature and depth data in the environments white sharks inhabit through austral seasons, over a series of months and years.

The results in Chapter 3 indicate that both sexes of white sharks overlap in habitat use in winter months when coastal upwelling has subsided and/or is at its weakest on the inshore of the Agulhas Bank (Lutjeharms et al.. 2000). The second hypothesis of Chapter 3 was to determine whether males and females differ in their thermal preferences, which has been suggested by other studies (Robbins 2007; Domeier et al. 2012; Jorgensen et al. 2012; Robbins and Booth 2012). Variation in the proportion of females and males was partially explained when sightings data was modelled using MEI indices. It may be that their ability to maintain body temperatures above ambient contributes towards masking this effect .This is the first study of its kind to successfully document such a clear sex specific link with environmental factors in white sharks, and also in relation to interannual climate variability. Sightings of male sharks in Gansbaai were significantly higher in 'negative MEI years' whereas females were less common in negative MEI years, they tended to show preference for warmer positive MEI years. Gender specific thermal preferences may have an as yet unappreciated role in determining sexual segregation in sharks (Sims 2005). Sex related preferences for different water temperatures have been described in other shark species including grey reef sharks *Carcharhinus amblyrhynchos* (Economakis and Lobel 1998), other members of the Carcharhinidae (Bass et al. 1973), pelagic and common thresher *Alopias pelagicus* (Compagno 1984a) and *Alopias vulpinus* (Moreno et al. 1989).

The results from Chapter 3 of this study suggest that water temperature could be a key factor related to sex segregation in South African white sharks. This could be a result of sex specific physiological requirements, for example females may favour warmer waters for their higher growth rate demand (Sims et al. 2006) or (when pregnant) to provide optimal conditions for foetal development (Robbins and Booth 2012). Another example of a species which shows sex specific sensitivity to water temperature is the dogfish *Scyliorhinus canicula*; males show less tolerance to warmer waters than females,displaying sensitivity to warm water temperatures (Sims et al. 2006). This could apply to smaller male white sharks. Arriving in a region separately from the other sex may reduce competition for resources, particularly between juvenile and mature sharks (Bruce and Bradford 2011) or reduce mating harassment (Sims et al. 2006). Further studies into white shark thermo-physiology and size need to be carried out to explore the relationship between different size classes and water temperature. One good approach would be the use of acoustic tags with muscle temperature probes. These are currently being tested in Mossel Bay (E. Gennari pers. comm.). The importance of such work lies within the fact that sexual segregation enhances a species vulnerability to stock depletion as large segments of breeding stock may be captured at a time if encountered by commercial fisheries, and stock vulnerability would be heightened if they were adult female.

A long term and integrated approach to understanding the distribution patterns of different size and sex classes of white sharks would be a productive investigation. Such a study should provide information on large scale movements of individuals of different sizes and sex over a temporal period long enough to see if these movements change between seasons. Weather station and remote sensing satellite data (MODIS, Sea−WiFS) should be included to test the affects of sea temperature and other parameters on shark movements. This approach would allow hypotheses of distribution patterns and habitat choice of males and females (Domeier 2012) to be tested rigorously in a different population of white sharks.

A potential use for this information is the development of a bather protection alert system that incorporates environmental data and predicted shark abundance since these parameters appear to influence white sharks occurring in specific areas. This could be incorporated into shark spotting programmes, such as the one in False Bay (Kock et al. 2012). Linking environmental parameters with modelled risk assessments and direct observations could augment the existing shark spotting programme and potentially reduce interactions of bathers and surfers (with consequent negative impacts on tourism).

Another important finding in this study (Chapter 3) is that the abundance of white sharks inshore may not be as tightly linked to the summer season as previously suggested in South Africa (Kock and Johnson 2006). The current study showed that white sharks may occur inshore throughout the year depending on local conditions and, possibly, availability of prey although this aspect was not investigated here. An explanation suggested for their use of inshore environments has been that they may rest in calm warmer water pockets in summer (Robbins 2007; Bruce and Bradford 2012; Robbins and Booth 2012; Chapter 3). An alternative explanation may be that they are following potential prey items such as elasmobranchs and teleosts, which are known prey of subadults (Cliff et al. 1989; Hussey et al. 2012). A possible approach to investigate the relative abundance of prey in different areas may be the use of underwater cameras and bait stations in each austral season (Brooks et al. 2011). Shark behaviour could be monitored and tested against “prey hot spots” and other parts of the bay to investigate whether they favour the “prey hot spots.”

Future studies on white sharks in South Africa need to be conducted on four scales of time and space:

- active tracking by boats following sharks to investigate microhabitat use. This could resolve whether different habitats are preferred for hunting during different seasons

- passive tracking (movements monitored by listening stations deployed around the bay) to understand how their use of different habitats changes on a longer time scale and along the coast. A strength of passive tracking is that it allows monitoring of tagged sharks during extreme weather events (such as high swells and winds) when conditions are not favourable for active tracking using boats.

- Baited remote underwater video surveys (BRUVS) are a novel, non-invasive method of generating relative abundance indices for a number of marine species, including sharks (Brooks et al. 2011). Prey distribution studies using this tool may provide another component to better understand white shark distribution around putative 'white shark hotspots'.

- Use of real time satellite tags to investigate movements on a regional (and potentially global) scale.

To conclude this study, it is likely that improved knowledge of the interrelationship between white sharks and the environment, combined with an understanding of how they respond to prey changes should help us better predict their spatial and temporal distribution patterns. This in turn will help to inform management decisions with regards to white shark protection, and contribute to the effectiveness of bather safety programs such as shark spotters and mitigate potential risk of human/shark interactions. Understanding the responses of marine species to environmental parameters will contribute to our ability to predict the effects of climate change on various species (Lehodey et al. 2006) and how they will respond to anthropogenic alteration of inshore environments such as coastal development. A multi-faceted collaborative research initiative incorporating the above studies should be expanded in South Africa to better understand and preserve what may be one of the few remaining apparently healthy populations of white sharks in the world.

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